MAP: RAVEN BIOLOGY 12TH EDITION



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This text was compiled on 05/01/2026

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1.1: The Science of Life

Biology is the science that studies life. What exactly is life? This may sound like a silly question with an obvious answer, but it is not easy to define life. For example, a branch of biology called virology studies viruses, which exhibit some of the characteristics of living entities but lack others. It turns out that although viruses can attack living organisms, cause diseases, and even reproduce, they do not meet the criteria that biologists use to define life.

From its earliest beginnings, biology has wrestled with four questions: What are the shared properties that make something “alive”? How do those various living things function? When faced with the remarkable diversity of life, how do we organize the different kinds of organisms so that we can better understand them? And, finally—what biologists ultimately seek to understand—how did this diversity arise and how is it continuing? As new organisms are discovered every day, biologists continue to seek answers to these and other questions.

Properties of Life

All groups of living organisms share several key characteristics or functions: order, sensitivity or response to stimuli, reproduction, adaptation, growth and development, regulation, homeostasis, and energy processing. When viewed together, these eight characteristics serve to define life.

Order

Organisms are highly organized structures that consist of one or more cells. Even very simple, single-celled organisms are remarkably complex. Inside each cell, atoms make up molecules. These in turn make up cell components or organelles. Multicellular organisms, which may consist of millions of individual cells, have an advantage over single-celled organisms in that their cells can be specialized to perform specific functions, and even sacrificed in certain situations for the good of the organism as a whole. How these specialized cells come together to form organs such as the heart, lung, or skin in organisms like the toad shown in Figure **1.1.1** will be discussed later.



Figure 1.1.1: A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems. (credit: "Ivengo(RUS)"/Wikimedia Commons)

Sensitivity or Response to Stimuli

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light or respond to touch (Figure **1.1.2**). Even tiny bacteria can move toward or away from chemicals (a process called chemotaxis) or light (phototaxis). Movement toward a stimulus is considered a positive response, while movement away from a stimulus is considered a negative response.



Figure 1.1.2: The leaves of this sensitive plant (Mimosa pudica) will instantly droop and fold when touched. After a few minutes, the plant returns to its normal state. (credit: Alex Lomas)

CONCEPT IN ACTION

Watch this video to see how the sensitive plant responds to a touch stimulus.

Reproduction

Single-celled organisms reproduce by first duplicating their DNA, which is the genetic material, and then dividing it equally as the cell prepares to divide to form two new cells. Many multicellular organisms (those made up of more than one cell) produce specialized reproductive cells that will form new individuals. When reproduction occurs, DNA containing genes is passed along to an organism's offspring. These genes are the reason that the offspring will belong to the same species and will have characteristics similar to the parent, such as fur color and blood type.

Adaptation

All living organisms exhibit a "fit" to their environment. Biologists refer to this fit as adaptation and it is a consequence of evolution by natural selection, which operates in every lineage of reproducing organisms. Examples of adaptations are diverse and unique, from heat-resistant Archaea that live in boiling hot springs to the tongue length of a nectar-feeding moth that matches the size of the flower from which it feeds. All adaptations enhance the reproductive potential of the individual exhibiting them, including their ability to survive to reproduce. Adaptations are not constant. As an environment changes, natural selection causes the characteristics of the individuals in a population to track those changes.

Growth and Development

Organisms grow and develop according to specific instructions coded for by their genes. These genes provide instructions that will direct cellular growth and development, ensuring that a species' young (Figure **1.1.3**) will grow up to exhibit many of the same characteristics as its parents.



Figure 1.1.3: Although no two look alike, these kittens have inherited genes from both parents and share many of the same characteristics. (credit: Pieter & Renée Lanser)

Regulation

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, such as the transport of nutrients, response to stimuli, and coping with environmental stresses. For example, organ systems such as the digestive or circulatory systems perform specific functions like carrying oxygen throughout the body, removing wastes, delivering nutrients to every cell, and cooling the body.

Homeostasis

To function properly, cells require appropriate conditions such as proper temperature, pH, and concentrations of diverse chemicals. These conditions may, however, change from one moment to the next. Organisms are able to maintain internal conditions within a narrow range almost constantly, despite environmental changes, through a process called homeostasis or “steady state”—the ability of an organism to maintain constant internal conditions. For example, many organisms regulate their body temperature in a process known as thermoregulation. Organisms that live in cold climates, such as the polar bear (Figure **1.1.4**), have body structures that help them withstand low temperatures and conserve body heat. In hot climates, organisms have methods (such as perspiration in humans or panting in dogs) that help them to shed excess body heat.



Figure 1.1.4: Polar bears and other mammals living in ice-covered regions maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin. (credit: "longhorndave"/Flickr)

Energy Processing

All organisms (such as the California condor shown in Figure **1.1.5**) use a source of energy for their metabolic activities. Some organisms capture energy from the Sun and convert it into chemical energy in food; others use chemical energy from molecules they take in.



Figure 1.1.5: A lot of energy is required for a California condor to fly. Chemical energy derived from food is used to power flight. California condors are an endangered species; scientists have strived to place a wing tag on each bird to help them identify and locate each individual bird. (credit: Pacific Southwest Region U.S. Fish and Wildlife)

Levels of Organization of Living Things

Living things are highly organized and structured, following a hierarchy on a scale from small to large. The atom is the smallest and most fundamental unit of matter. It consists of a nucleus surrounded by electrons. Atoms form molecules. A molecule is a chemical structure consisting of at least two atoms held together by a chemical bond. Many molecules that are biologically important are macromolecules, large molecules that are typically formed by combining smaller units called monomers. An example of a macromolecule is deoxyribonucleic acid (DNA) (Figure 1.1.6), which contains the instructions for the functioning of the organism that contains it.

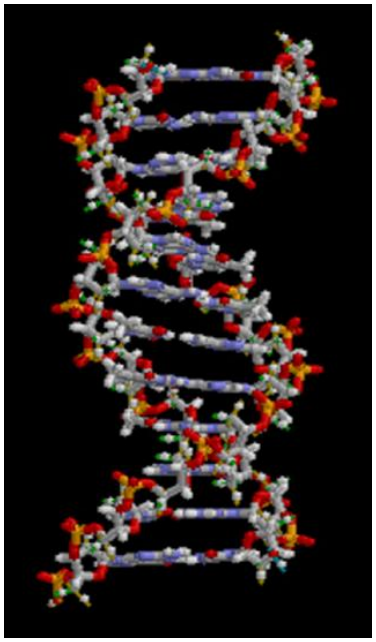


Figure 1.1.6: A molecule, like this large DNA molecule, is composed of atoms. (credit: "Brian0918"/Wikimedia Commons)

CONCEPT IN ACTION



To see an animation of this DNA molecule, click here.

Some cells contain aggregates of macromolecules surrounded by membranes; these are called organelles. Organelles are small structures that exist within cells and perform specialized functions. All living things are made of cells; the cellitself is the smallest fundamental unit of structure and function in living organisms. (This requirement is why viruses are not considered living: they are not made of cells. To make new viruses, they have to invade and hijack a living cell; only then can they obtain the materials they need to reproduce.) Some organisms consist of a single cell and others are multicellular. Cells are classified as prokaryotic or eukaryotic. Prokaryotes are single-celled organisms that lack organelles surrounded by a membrane and do not have nuclei surrounded by nuclear membranes; in contrast, the cells of eukaryotes do have membrane-bound organelles and nuclei.

In most multicellular organisms, cells combine to make tissues, which are groups of similar cells carrying out the same function. Organs are collections of tissues grouped together based on a common function. Organs are present not only in animals but also in plants. An organ system is a higher level of organization that consists of functionally related organs. For example vertebrate animals have many organ systems, such as the circulatory system that transports blood throughout the body and to and from the lungs; it includes organs such as the heart and blood vessels. Organisms are individual living entities. For example, each tree in a forest is an organism. Single-celled prokaryotes and single-celled eukaryotes are also considered organisms and are typically referred to as microorganisms.

ART CONNECTION

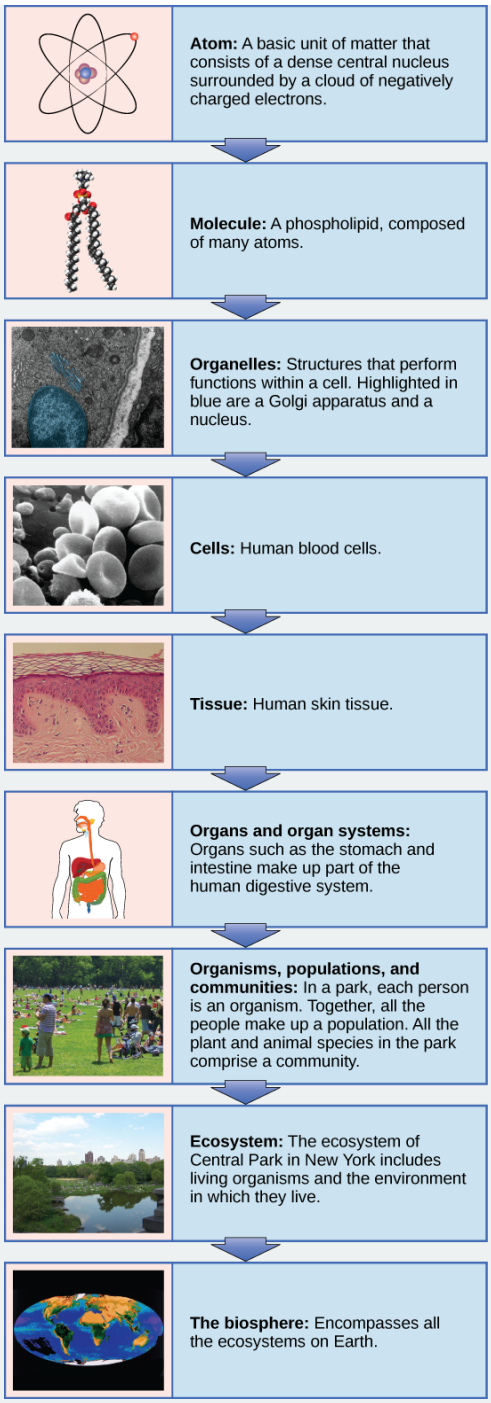


Figure 1.1.7: From an atom to the entire Earth, biology examines all aspects of life. (credit "molecule": modification of work by Jane Whitney; credit "organelles": modification of work by Louisa Howard; credit "cells": modification of work by Bruce Wetzel, Harry Schaefer, National Cancer Institute; credit "tissue": modification of work by "Kilbad"/Wikimedia Commons; credit "organs": modification of work by Mariana Ruiz Villareal, Joaquim Alves Gaspar; credit "organisms": modification of work by Peter Dutton; credit "ecosystem": modification of work by "gigi4791"/Flickr; credit "biosphere": modification of work by NASA)

Which of the following statements is false?

A. Tissues exist within organs which exist within organ systems.
B. Communities exist within populations which exist within ecosystems.
C. Organelles exist within cells which exist within tissues.
D. Communities exist within ecosystems which exist in the biosphere.

Answer

B

All the individuals of a species living within a specific area are collectively called a population. For example, a forest may include many white pine trees. All of these pine trees represent the population of white pine trees in this forest. Different populations may live in the same specific area. For example, the forest with the pine trees includes populations of flowering plants and also insects and microbial populations. A community is the set of populations inhabiting a particular area. For instance, all of the trees, flowers, insects, and other populations in a forest form the forest's community. The forest itself is an ecosystem. An ecosystem consists of all the living things in a particular area together with the abiotic, or non-living, parts of that environment such as nitrogen in the soil or rainwater. At the highest level of organization (Figure **1.1.7**), the biosphere is the collection of all ecosystems, and it represents the zones of life on Earth. It includes land, water, and portions of the atmosphere.

The Diversity of Life

The science of biology is very broad in scope because there is a tremendous diversity of life on Earth. The source of this diversity is evolution, the process of gradual change during which new species arise from older species. Evolutionary biologists study the evolution of living things in everything from the microscopic world to ecosystems.

In the 18th century, a scientist named Carl Linnaeus first proposed organizing the known species of organisms into a hierarchical taxonomy. In this system, species that are most similar to each other are put together within a grouping known as a genus. Furthermore, similar genera (the plural of genus) are put together within a family. This grouping continues until all organisms are collected together into groups at the highest level. The current taxonomic system now has eight levels in its hierarchy, from lowest to highest, they are: species, genus, family, order, class, phylum, kingdom, domain. Thus species are grouped within genera, genera are grouped within families, families are grouped within orders, and so on (Figure **1.1.8**).

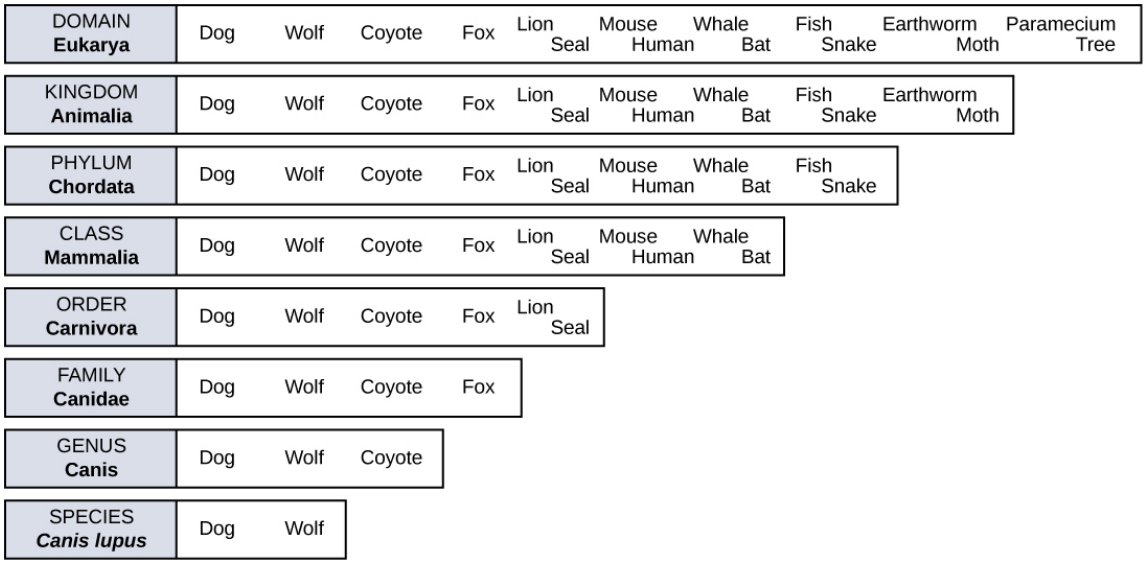


Figure 1.1.8: This diagram shows the levels of taxonomic hierarchy for a dog, from the broadest category—domain—to the most specific—species.

The highest level, domain, is a relatively new addition to the system since the 1990s. Scientists now recognize three domains of life, the Eukarya, the Archaea, and the Bacteria. The domain Eukarya contains organisms that have cells with nuclei. It includes the kingdoms of fungi, plants, animals, and several kingdoms of protists. The Archaea, are single-celled organisms without nuclei and include many extremophiles that live in harsh environments like hot springs. The Bacteria are another quite different group of single-celled organisms without nuclei (Figure **1.1.9**). Both the Archaea and the Bacteria are prokaryotes, an informal name for cells without nuclei. The recognition in the 1990s that certain "bacteria," now known as the Archaea, were as different genetically and biochemically from other bacterial cells as they were from eukaryotes, motivated the recommendation to divide life into three domains. This dramatic change in our knowledge of the tree of life demonstrates that classifications are not permanent and will change when new information becomes available.

In addition to the hierarchical taxonomic system, Linnaeus was the first to name organisms using two unique names, now called the binomial naming system. Before Linnaeus, the use of common names to refer to organisms caused confusion because there were regional differences in these common names. Binomial names consist of the genus name (which is capitalized) and the species name (all lower-case). Both names are set in italics when they are printed. Every species is given a unique binomial which is recognized the world over, so that a scientist in any location can know which organism is being referred to. For example, the North American blue jay is known uniquely as *Cyanocitta cristata*. Our own species is *Homo sapiens*.



(a) (b) (c) (d)

Figure 1.1.9: These images represent different domains. The scanning electron micrograph shows (a) bacterial cells belong to the domain Bacteria, while the (b) extremophiles, seen all together as colored mats in this hot spring, belong to domain Archaea. Both the (c) sunflower and (d) lion are part of domain Eukarya. (credit a: modification of work by Rocky Mountain Laboratories, NIAID, NIH; credit b: modification of work by Steve Jurvetson; credit c: modification of work by Michael Arrighi; credit d: modification of work by Frank Vassen)

EVOLUTION IN ACTION: Carl Woese and the Phylogenetic Tree

The evolutionary relationships of various life forms on Earth can be summarized in a phylogenetic tree. A phylogenetic tree is a diagram showing the evolutionary relationships among biological species based on similarities and differences in genetic or physical traits or both. A phylogenetic tree is composed of branch points, or nodes, and branches. The internal nodes represent ancestors and are points in evolution when, based on scientific evidence, an ancestor is thought to have diverged to form two new species. The length of each branch can be considered as estimates of relative time.

In the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists, and bacteria. The pioneering work of American microbiologist Carl Woese in the early 1970s has shown, however, that life on Earth has evolved along three lineages, now called domains—Bacteria, Archaea, and Eukarya. Woese proposed the domain as a new taxonomic level and Archaea as a new domain, to reflect the new phylogenetic tree (Figure **1.1.10**). Many organisms belonging to the Archaea domain live under extreme conditions and are called extremophiles. To construct his tree, Woese used genetic relationships rather than similarities based on morphology (shape). Various genes were used in phylogenetic studies. Woese's tree was constructed from comparative sequencing of the genes that are universally distributed, found in some slightly altered form in every organism, conserved (meaning that these genes have remained only slightly changed throughout evolution), and of an appropriate length.

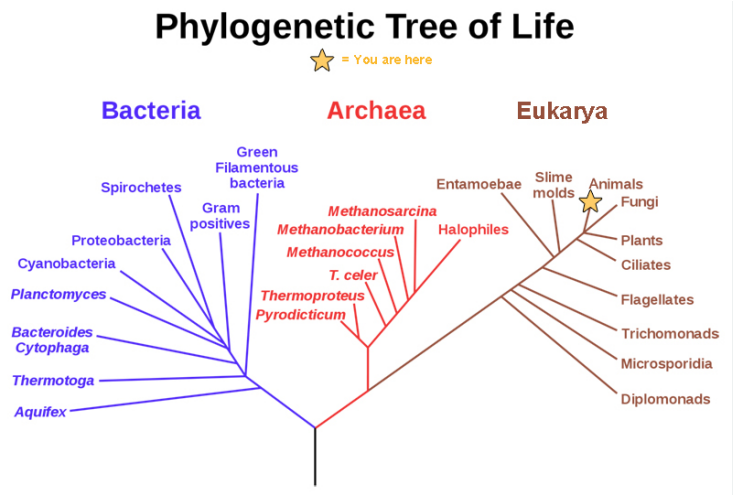


Figure 1.1.10: This phylogenetic tree was constructed by microbiologist Carl Woese using genetic relationships. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are organisms without a nucleus or other organelles surrounded by a membrane and, therefore, are prokaryotes. (credit: modification of work by Eric Gaba)

Branches of Biological Study

The scope of biology is broad and therefore contains many branches and sub disciplines. Biologists may pursue one of those sub disciplines and work in a more focused field. For instance, molecular biology studies biological processes at the molecular level, including interactions among molecules such as DNA, RNA, and proteins, as well as the way they are regulated. Microbiology is the study of the structure and function of microorganisms. It is quite a broad branch itself, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

Another field of biological study, neurobiology, studies the biology of the nervous system, and although it is considered a branch of biology, it is also recognized as an interdisciplinary field of study known as neuroscience. Because of its interdisciplinary nature, this sub discipline studies different functions of the nervous system using molecular, cellular, developmental, medical, and computational approaches.



Figure 1.1.11: Researchers work on excavating dinosaur fossils at a site in Castellón, Spain. (credit: Mario Modesto)

Paleontology, another branch of biology, uses fossils to study life's history (Figure 1.1.11). Zoology and botany are the study of animals and plants, respectively. Biologists can also specialize as biotechnologists, ecologists, or physiologists, to name just a few areas. Biotechnologists apply the knowledge of biology to create useful products. Ecologists study the interactions of organisms in their environments. Physiologists study the workings of cells, tissues and organs. This is just a small sample of the many fields that biologists can pursue. From our own bodies to the world we live in, discoveries in biology can affect us in very direct and important ways. We depend on these discoveries for our health, our food sources, and the benefits provided by our ecosystem. Because of this, knowledge of biology can benefit us in making decisions in our day-to-day lives.

The development of technology in the twentieth century that continues today, particularly the technology to describe and manipulate the genetic material, DNA, has transformed biology. This transformation will allow biologists to continue to understand the history of life in greater detail, how the human body works, our human origins, and how humans can survive as a species on this planet despite the stresses caused by our increasing numbers. Biologists continue to decipher huge mysteries about life suggesting that we have only begun to understand life on the planet, its history, and our relationship to it. For this and other reasons, the knowledge of biology gained through this textbook and other printed and electronic media should be a benefit in whichever field you enter.

CAREERS IN ACTION: Forensic Scientist

Forensic science is the application of science to answer questions related to the law. Biologists as well as chemists and biochemists can be forensic scientists. Forensic scientists provide scientific evidence for use in courts, and their job involves examining trace material associated with crimes. Interest in forensic science has increased in the last few years, possibly because of popular television shows that feature forensic scientists on the job. Also, the development of molecular techniques and the establishment of DNA databases have updated the types of work that forensic scientists can do. Their job activities are primarily related to crimes against people such as murder, rape, and assault. Their work involves analyzing samples such as hair, blood, and other body fluids and also processing DNA (Figure **1.1.12**) found in many different environments and materials. Forensic scientists also analyze other biological evidence left at crime scenes, such as insect parts or pollen grains. Students who want to pursue careers in forensic science will most likely be required to take chemistry and biology courses as well as some intensive math courses.



Figure 1.1.12: This forensic scientist works in a DNA extraction room at the U.S. Army Criminal Investigation Laboratory. (credit: U.S. Army CID Command Public Affairs)

Summary

Biology is the science of life. All living organisms share several key properties such as order, sensitivity or response to stimuli, reproduction, adaptation, growth and development, regulation, homeostasis, and energy processing. Living things are highly organized following a hierarchy that includes atoms, molecules, organelles, cells, tissues, organs, and organ systems. Organisms, in turn, are grouped as populations, communities, ecosystems, and the biosphere. Evolution is the source of the tremendous biological diversity on Earth today. A diagram called a phylogenetic tree can be used to show evolutionary relationships among organisms. Biology is very broad and includes many branches and sub disciplines. Examples include molecular biology, microbiology, neurobiology, zoology, and botany, among others.

Glossary

atom

a basic unit of matter that cannot be broken down by normal chemical reactions

biology

the study of living organisms and their interactions with one another and their environments

biosphere
a collection of all ecosystems on Earth

cell
the smallest fundamental unit of structure and function in living things

community
a set of populations inhabiting a particular area

ecosystem
all living things in a particular area together with the abiotic, nonliving parts of that environment

eukaryote
an organism with cells that have nuclei and membrane-bound organelles

evolution
the process of gradual change in a population that can also lead to new species arising from older species

homeostasis
the ability of an organism to maintain constant internal conditions

macromolecule
a large molecule typically formed by the joining of smaller molecules

molecule
a chemical structure consisting of at least two atoms held together by a chemical bond

organ
a structure formed of tissues operating together to perform a common function

organ system
the higher level of organization that consists of functionally related organs

organelle
a membrane-bound compartment or sac within a cell

organism
an individual living entity

phylogenetic tree
a diagram showing the evolutionary relationships among biological species based on similarities and differences in genetic or physical traits or both

population
all individuals within a species living within a specific area

prokaryote
a unicellular organism that lacks a nucleus or any other membrane-bound organelle

tissue
a group of similar cells carrying out the same function

Contributors and Attributions

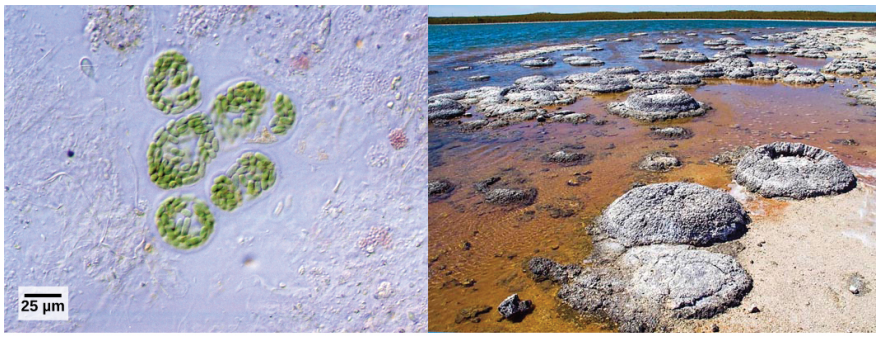
- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

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1.2: The Nature of Science

Like geology, physics, and chemistry, biology is a science that gathers knowledge about the natural world. Specifically, biology is the study of life. The discoveries of biology are made by a community of researchers who work individually and together using agreed-on methods. In this sense, biology, like all sciences is a social enterprise like politics or the arts.



(a) (b)

Figure 1.2.1: Formerly called blue-green algae, the (a) cyanobacteria seen through a light microscope are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; scale-bar data from Matt Russell; credit b: modification of work by Ruth Ellison)

The methods of science include careful observation, record keeping, logical and mathematical reasoning, experimentation, and submitting conclusions to the scrutiny of others. Science also requires considerable imagination and creativity; a well-designed experiment is commonly described as elegant, or beautiful. Like politics, science has considerable practical implications and some science is dedicated to practical applications, such as the prevention of disease (Figure **1.2.2**). Other science proceeds largely motivated by curiosity. Whatever its goal, there is no doubt that science, including biology, has transformed human existence and will continue to do so.

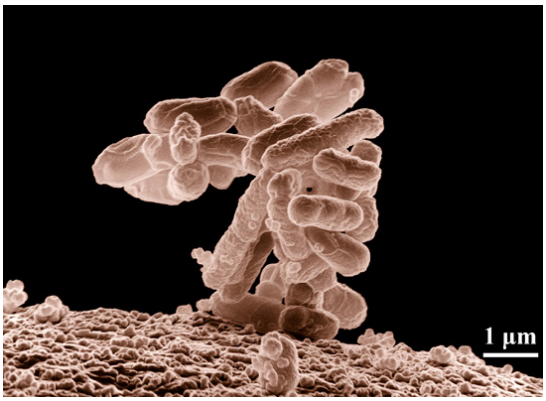


Figure 1.2.2: Biologists may choose to study *Escherichia coli* (*E. coli*), a bacterium that is a normal resident of our digestive tracts but which is also sometimes responsible for disease outbreaks. In this micrograph, the bacterium is visualized using a scanning electron microscope and digital colorization. (credit: Eric Erbe; digital colorization by Christopher Pooley, USDA-ARS)

The Nature of Science

Biology is a science, but what exactly is science? What does the study of biology share with other scientific disciplines? Science (from the Latin *scientia*, meaning "knowledge") can be defined as knowledge about the natural world.

Science is a very specific way of learning, or knowing, about the world. The history of the past 500 years demonstrates that science is a very powerful way of knowing about the world; it is largely responsible for the technological revolutions that have taken place during this time. There are however, areas of knowledge and human experience that the methods of science cannot be applied to. These include such things as answering purely moral questions, aesthetic questions, or what can be generally categorized as spiritual questions. Science has cannot investigate these areas because they are outside the realm of material phenomena, the phenomena of matter and energy, and cannot be observed and measured.

The scientific method is a method of research with defined steps that include experiments and careful observation. The steps of the scientific method will be examined in detail later, but one of the most important aspects of this method is the testing of hypotheses. A hypothesis is a suggested explanation for an event, which can be tested. Hypotheses, or tentative explanations, are generally produced within the context of a scientific theory. A scientific theory is a generally accepted, thoroughly tested and confirmed explanation for a set of observations or phenomena. Scientific theory is the foundation of scientific knowledge. In addition, in many scientific disciplines (less so in biology) there are scientific laws, often expressed in mathematical formulas, which describe how elements of nature will behave under certain specific conditions. There is not an evolution of hypotheses through theories to laws as if they represented some increase in certainty about the world. Hypotheses are the day-to-day material that scientists work with and they are developed within the context of theories. Laws are concise descriptions of parts of the world that are amenable to formulaic or mathematical description.

Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A planetarium? Gems and minerals? Or maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics (Figure **1.2.3**). However, those fields of science related to the physical world and its phenomena and processes are considered natural sciences. Thus, a museum of natural sciences might contain any of the items listed above.

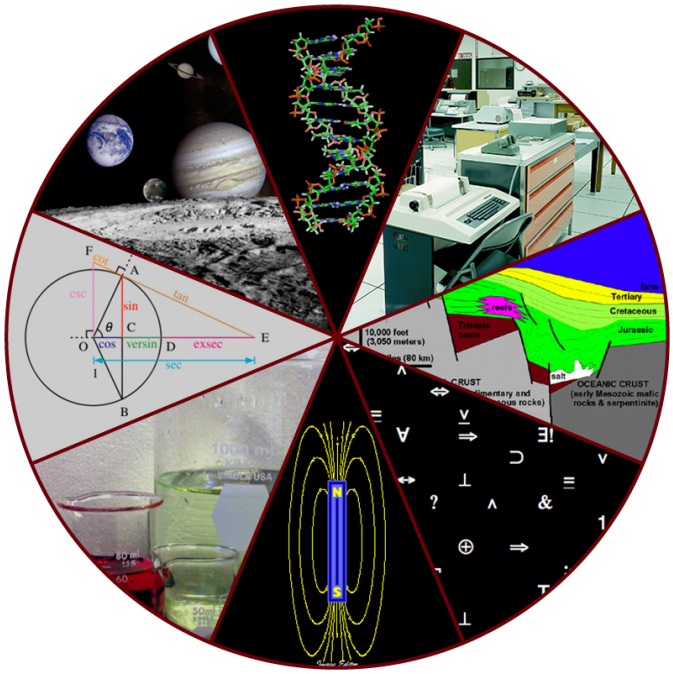


Figure 1.2.3: Some fields of science include astronomy, biology, computer science, geology, logic, physics, chemistry, and mathematics. (credit: "Image Editor"/Flickr)

There is no complete agreement when it comes to defining what the natural sciences include. For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into life sciences, which study living things and include biology, and physical sciences, which study nonliving matter and include astronomy, physics, and chemistry. Some disciplines such as biophysics and biochemistry build on two sciences and are interdisciplinary.

Scientific Inquiry

One thing is common to all forms of science: an ultimate goal “to know.” Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. Two methods of logical thinking are used: inductive reasoning and deductive reasoning.

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data

can be qualitative (descriptive) or quantitative (consisting of numbers), and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies often work this way. Many brains are observed while people are doing a task. The part of the brain that lights up, indicating activity, is then demonstrated to be the part controlling the response to that task.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reasoning, the pattern of thinking moves in the opposite direction as compared to inductive reasoning. Deductive reasoning is a form of logical thinking that uses a general principle or law to forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. For example, a prediction would be that if the climate is becoming warmer in a region, the distribution of plants and animals should change. Comparisons have been made between distributions in the past and the present, and the many changes that have been found are consistent with a warming climate. Finding the change in distribution is evidence that the climate change conclusion is a valid one.

Both types of logical thinking are related to the two main pathways of scientific study: descriptive science and hypothesis-based science. Descriptive (or discovery) science aims to observe, explore, and discover, while hypothesis-based science begins with a specific question or problem and a potential answer or solution that can be tested. The boundary between these two forms of study is often blurred, because most scientific endeavors combine both approaches. Observations lead to questions, questions lead to forming a hypothesis as a possible answer to those questions, and then the hypothesis is tested. Thus, descriptive science and hypothesis-based science are in continuous dialogue.

Hypothesis Testing

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific method was used even in ancient times, but it was first documented by England's Sir Francis Bacon (1561–1626) (Figure **1.2.4**), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost anything as a logical problem-solving method.



Figure 1.2.4: Sir Francis Bacon is credited with being the first to document the scientific method.

The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let's think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a

student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: “Why is the classroom so warm?”

Recall that a hypothesis is a suggested explanation that can be tested. To solve a problem, several hypotheses may be proposed. For example, one hypothesis might be, “The classroom is warm because no one turned on the air conditioning.” But there could be other responses to the question, and therefore other hypotheses may be proposed. A second hypothesis might be, “The classroom is warm because there is a power failure, and so the air conditioning doesn’t work.”

Once a hypothesis has been selected, a prediction may be made. A prediction is similar to a hypothesis but it typically has the format “If . . . then . . . .” For example, the prediction for the first hypothesis might be, “*If* the student turns on the air conditioning, *then* the classroom will no longer be too warm.”

A hypothesis must be testable to ensure that it is valid. For example, a hypothesis that depends on what a bear thinks is not testable, because it can never be known what a bear thinks. It should also be falsifiable, meaning that it can be disproven by experimental results. An example of an unfalsifiable hypothesis is “Botticelli’s *Birth of Venus* is beautiful.” There is no experiment that might show this statement to be false. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. This is important. A hypothesis can be disproven, or eliminated, but it can never be proven. Science does not deal in proofs like mathematics. If an experiment fails to disprove a hypothesis, then we find support for that explanation, but this is not to say that down the road a better explanation will not be found, or a more carefully designed experiment will be found to falsify the hypothesis.

Each experiment will have one or more variables and one or more controls. A variable is any part of the experiment that can vary or change during the experiment. A control is a part of the experiment that does not change. Look for the variables and controls in the example that follows. As a simple example, an experiment might be conducted to test the hypothesis that phosphate limits the growth of algae in freshwater ponds. A series of artificial ponds are filled with water and half of them are treated by adding phosphate each week, while the other half are treated by adding a salt that is known not to be used by algae. The variable here is the phosphate (or lack of phosphate), the experimental or treatment cases are the ponds with added phosphate and the control ponds are those with something inert added, such as the salt. Just adding something is also a control against the possibility that adding extra matter to the pond has an effect. If the treated ponds show lesser growth of algae, then we have found support for our hypothesis. If they do not, then we reject our hypothesis. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid (Figure **1.2.5**). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

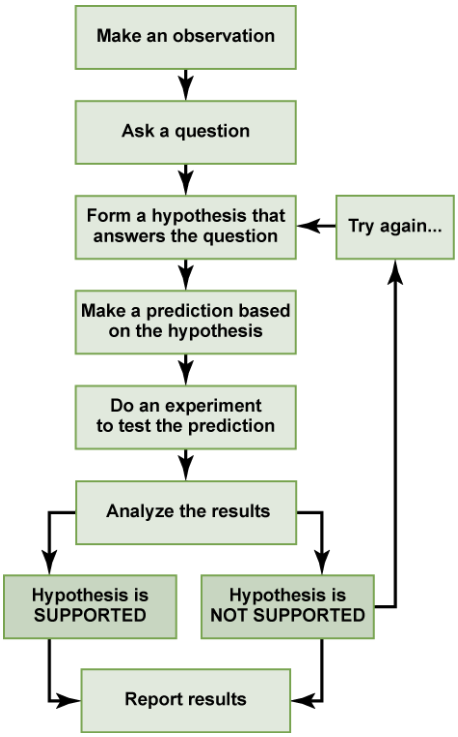


Figure 1.2.5: The scientific method is a series of defined steps that include experiments and careful observation. If a hypothesis is not supported by data, a new hypothesis can be proposed.

Example 1.2.1

In the example below, the scientific method is used to solve an everyday problem. Which part in the example below is the hypothesis? Which is the prediction? Based on the results of the experiment, is the hypothesis supported? If it is not supported, propose some alternative hypotheses.

1. My toaster doesn't toast my bread.
2. Why doesn't my toaster work?
3. There is something wrong with the electrical outlet.
4. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
5. I plug my coffeemaker into the outlet.
6. My coffeemaker works.

Solution

The hypothesis is #3 (there is something wrong with the electrical outlet), and the prediction is #4 (if something is wrong with the outlet, then the coffeemaker also won't work when plugged into the outlet). The original hypothesis is not supported, as the coffee maker works when plugged into the outlet. Alternative hypotheses may include (1) the toaster might be broken or (2) the toaster wasn't turned on.

In practice, the scientific method is not as rigid and structured as it might at first appear. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests.

Basic and Applied Science

The scientific community has been debating for the last few decades about the value of different types of science. Is it valuable to pursue science for the sake of simply gaining knowledge, or does scientific knowledge only have worth if we can apply it to solving a specific problem or bettering our lives? This question focuses on the differences between two types of science: basic science and applied science.

Basic science or “pure” science seeks to expand knowledge regardless of the short-term application of that knowledge. It is not focused on developing a product or a service of immediate public or commercial value. The immediate goal of basic science is knowledge for knowledge’s sake, though this does not mean that in the end it may not result in an application.

In contrast, applied science or “technology,” aims to use science to solve real-world problems, making it possible, for example, to improve a crop yield, find a cure for a particular disease, or save animals threatened by a natural disaster. In applied science, the problem is usually defined for the researcher.

Some individuals may perceive applied science as “useful” and basic science as “useless.” A question these people might pose to a scientist advocating knowledge acquisition would be, “What for?” A careful look at the history of science, however, reveals that basic knowledge has resulted in many remarkable applications of great value. Many scientists think that a basic understanding of science is necessary before an application is developed; therefore, applied science relies on the results generated through basic science. Other scientists think that it is time to move on from basic science and instead to find solutions to actual problems. Both approaches are valid. It is true that there are problems that demand immediate attention; however, few solutions would be found without the help of the knowledge generated through basic science.

One example of how basic and applied science can work together to solve practical problems occurred after the discovery of DNA structure led to an understanding of the molecular mechanisms governing DNA replication. Strands of DNA, unique in every human, are found in our cells, where they provide the instructions necessary for life. During DNA replication, new copies of DNA are made, shortly before a cell divides to form new cells. Understanding the mechanisms of DNA replication enabled scientists to develop laboratory techniques that are now used to identify genetic diseases, pinpoint individuals who were at a crime scene, and determine paternity. Without basic science, it is unlikely that applied science would exist.

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits and the exact location of each gene. (The gene is the basic unit of heredity; an individual’s complete collection of genes is his or her genome.) Other organisms have also been studied as part of this project to gain a better understanding of human chromosomes. The Human Genome Project (Figure 1.2.6) relied on basic research carried out with non-human organisms and, later, with the human genome. An important end goal eventually became using the data for applied research seeking cures for genetically related diseases.

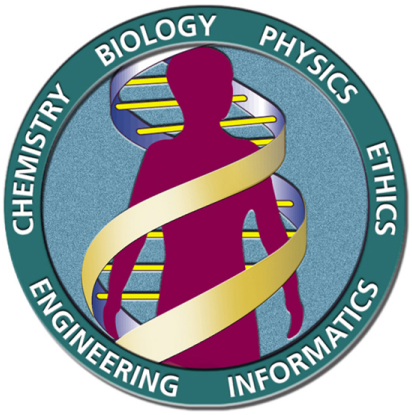


Figure 1.2.6: The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project was completed in 2003. (credit: the U.S. Department of Energy Genome Programs)

While research efforts in both basic science and applied science are usually carefully planned, it is important to note that some discoveries are made by serendipity, that is, by means of a fortunate accident or a lucky surprise. Penicillin was discovered when biologist Alexander Fleming accidentally left a petri dish of *Staphylococcus* bacteria open. An unwanted mold grew, killing the bacteria. The mold turned out to be *Penicillium*, and a new antibiotic was discovered. Even in the highly organized world of science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

Reporting Scientific Work

Whether scientific research is basic science or applied science, scientists must share their findings for other researchers to expand and build upon their discoveries. Communication and collaboration within and between sub disciplines of science are key to the

advancement of knowledge in science. For this reason, an important aspect of a scientist's work is disseminating results and communicating with peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the limited few who are present. Instead, most scientists present their results in peer-reviewed articles that are published in scientific journals. Peer-reviewed articles are scientific papers that are reviewed, usually anonymously by a scientist's colleagues, or peers. These colleagues are qualified individuals, often experts in the same research area, who judge whether or not the scientist's work is suitable for publication. The process of peer review helps to ensure that the research described in a scientific paper or grant proposal is original, significant, logical, and thorough. Grant proposals, which are requests for research funding, are also subject to peer review. Scientists publish their work so other scientists can reproduce their experiments under similar or different conditions to expand on the findings. The experimental results must be consistent with the findings of other scientists.

There are many journals and the popular press that do not use a peer-review system. A large number of online open-access journals, journals with articles available without cost, are now available many of which use rigorous peer-review systems, but some of which do not. Results of any studies published in these forums without peer review are not reliable and should not form the basis for other scientific work. In one exception, journals may allow a researcher to cite a personal communication from another researcher about unpublished results with the cited author's permission.

Summary

Biology is the science that studies living organisms and their interactions with one another and their environments. Science attempts to describe and understand the nature of the universe in whole or in part. Science has many fields; those fields related to the physical world and its phenomena are considered natural sciences.

A hypothesis is a tentative explanation for an observation. A scientific theory is a well-tested and consistently verified explanation for a set of observations or phenomena. A scientific law is a description, often in the form of a mathematical formula, of the behavior of an aspect of nature under certain circumstances. Two types of logical reasoning are used in science. Inductive reasoning uses results to produce general scientific principles. Deductive reasoning is a form of logical thinking that predicts results by applying general principles. The common thread throughout scientific research is the use of the scientific method. Scientists present their results in peer-reviewed scientific papers published in scientific journals.

Science can be basic or applied. The main goal of basic science is to expand knowledge without any expectation of short-term practical application of that knowledge. The primary goal of applied research, however, is to solve practical problems.

Glossary

applied science
a form of science that solves real-world problems

basic science
science that seeks to expand knowledge regardless of the short-term application of that knowledge

control
a part of an experiment that does not change during the experiment

deductive reasoning
a form of logical thinking that uses a general statement to forecast specific results

descriptive science
a form of science that aims to observe, explore, and find things out

falsifiable
able to be disproven by experimental results

hypothesis
a suggested explanation for an event, which can be tested

hypothesis-based science
a form of science that begins with a specific explanation that is then tested

inductive reasoning
a form of logical thinking that uses related observations to arrive at a general conclusion

life science
a field of science, such as biology, that studies living things

natural science
a field of science that studies the physical world, its phenomena, and processes

peer-reviewed article
a scientific report that is reviewed by a scientist's colleagues before publication

physical science
a field of science, such as astronomy, physics, and chemistry, that studies nonliving matter

science
knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method

scientific law
a description, often in the form of a mathematical formula, for the behavior of some aspect of nature under certain specific conditions

scientific method
a method of research with defined steps that include experiments and careful observation

scientific theory
a thoroughly tested and confirmed explanation for observations or phenomena

variable
a part of an experiment that can vary or change

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SECTION OVERVIEW

1.3: An Example of Scientific Inquiry- Darwin and Evolution

1.3.1: Evolution of Life

1.3.2: Scientific Theories

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1.3.1: Evolution of Life

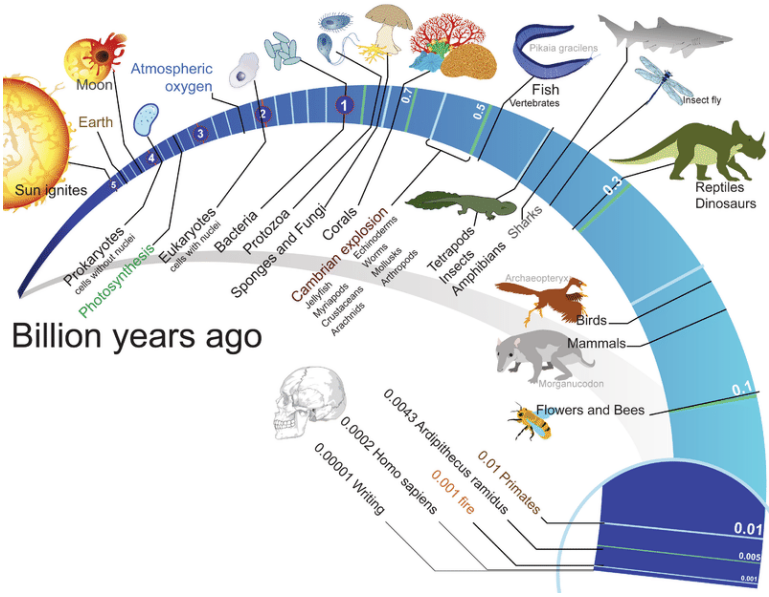


Are dinosaurs evidence of past life forms?

Evolution can be described as *a change in species over time*. Dinosaur fossils are significant evidence of evolution and of past life on Earth.

Evolution of Life

The diversity of life on Earth today is the result of evolution. Life began on Earth at least 3.5 to 4 billion years ago, and it has been evolving ever since. At first, all living things on Earth were simple, single-celled organisms. Much later, the first multicellular organisms evolved, and after that, Earth's biodiversity greatly increased. **Figure** below shows a timeline of the history of life on Earth. You can also find an interactive timeline of the history of life at the link below.http://www.johnkyrk.com/evolution.html



This timeline shows the history of life on Earth. In the entire span of the time, humans are a relatively new addition.

Today, the most accepted theory of life on Earth is evolution, and there is a vast amount of evidence supporting this theory. However, this wasn't always the case.

An introduction to evolution and natural selection can be viewed at http://www.youtube.com/watch?v=GcjgWov7mTM.



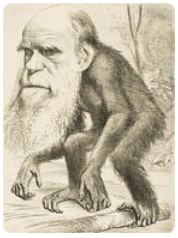
> *As you view Introduction to Evolution and Natural Selection,focus on these concepts:*
>
> 1. *the relationship between evolution and natural selection,*
> 2. *the relationship between natural selection and variation,*
> 3. *the evolution of the peppered moth.*

Darwin and the Theory of Evolution

The idea of evolution has been around for centuries. In fact, it goes all the way back to the ancient Greek philosopher Aristotle. However, evolution is most often associated with Charles Darwin. Darwin published a book on evolution in 1859 titled *On the Origin of Species*. In the book, Darwin stated the theory of evolution by natural selection. He also presented a great deal of evidence that evolution occurs.

Evolution is a change in the characteristics of living things over time. As described by Darwin, evolution occurs by a process called **natural selection**. In natural selection, some members of a species, being better adapted or suited to their environment, produce more offspring than others, so they pass "advantageous traits" to their offspring. Over many generations, this can lead to major changes in the characteristics of the species. Evolution explains how living things are changing today and how modern living things have descended from ancient life forms that no longer exist on Earth. As living things evolve, they generally become better suited for their environment. This is because they evolve adaptations. An **adaptation** is a trait that helps an organism survive and reproduce in a given environment.

Despite all the evidence Darwin presented, his theory was not well-received at first. Many people found it hard to accept the idea that humans had evolved from an ape-like ancestor, and they saw evolution as a challenge to their religious beliefs. Look at the cartoon in **Figure** below. Drawn in 1871, it depicts Darwin himself as an ape. The cartoon reflects how many people felt about Darwin and his theory during his own time. Darwin had actually expected this type of reaction to his theory and had waited a long time before publishing his book for this reason. It was only when another scientist, named Alfred Russel Wallace, developed essentially the same theory of evolution that Darwin put his book into print.



Charles Darwin's name is linked with the theory of evolution. This cartoon from the 1870s makes fun of both Darwin and his theory.

Although Darwin presented a great deal of evidence for evolution in his book, he was unable to explain how evolution occurs. That's because he knew nothing about genes. As a result, he didn't know how characteristics are passed from parents to offspring,

let alone how they could change over time.

Evolutionary Theory After Darwin

Since Darwin's time, scientists have gathered even more evidence to support the theory of evolution. Some of the evidence comes from fossils, and some comes from studies that show how similar living things are to one another. By the 1930s, scientists had also learned about genes. As a result, they could finally explain how characteristics of organisms could pass from one generation to the next and change over time.

Using modern technology, scientists can now directly compare the genes of living species. The more genes different species share in common, the more closely related the species are presumed to be. Consider humans and chimpanzees. They share about 98% of their genes. This means that they shared a common ancestor in the not-too-distant past. This is just one of many pieces of evidence that show we are part of the evolution of life on Earth.

Misconceptions About Evolution

Today, evolution is still questioned by some people. Often, people who disagree with the theory of evolution do not really understand it. For example, some people think that the theory of evolution explains how life on Earth first began. In fact, the theory explains only how life changed after it first appeared. Some people think the theory of evolution means that humans evolved from modern apes. In fact, the theory suggests humans and modern apes have a common ancestor that lived several million years ago. These and other misconceptions about evolution contribute to the controversy that still surrounds this fundamental principle of biology.

Summary

- Life began on Earth at least 3.5 to 4 billion years ago, and it has been evolving ever since.
- Darwin stated the theory of evolution by natural selection, presenting a great deal of evidence to support his theory.
- Evolution is a change in the characteristics of living things over time. Evolution occurs by natural selection.
- Characteristics of organisms are passed from one generation to the next through their genes.

Making Connections

403 ERROR

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Explore More

Use this resource to answer the questions that follow.

- **Natural Selection** at evolution.berkeley.edu/evosit...election.shtml.

1. What is meant by differential reproduction?
2. What is the end result of this process?
3. What three things are necessary for evolution by natural selection?

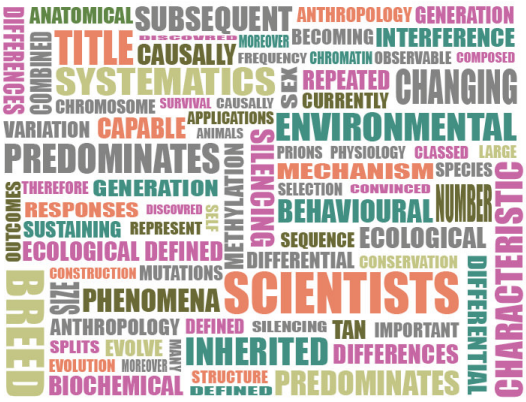
Review

1. What is evolution?
2. What is natural selection?
3. Briefly, explain the theory of evolution.

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1.3.2: Scientific Theories



Theory vs. theory. Is a scientific *theory* different from the everyday use of the word *theory*?

A scientific theory is accepted as a scientific *truth*, supported by evidence collected by many scientists. The theory of evolution by natural selection is a classic scientific theory.

Scientific Theories

With repeated testing, some hypotheses may eventually become scientific theories. Keep in mind, a hypothesis is a possible answer to a scientific question. A **scientific theory** is a broad explanation for events that is widely accepted as true. To become a theory, a hypothesis must be tested over and over again, and it must be supported by a great deal of evidence.

People commonly use the word *theory* to describe a guess about how or why something happens. For example, you might say, "I think a woodchuck dug this hole in the ground, but it's just a theory." Using the word *theory* in this way is different from the way it is used in science. A scientific theory is more like a fact than a guess because it is so well-supported. There are several well-known theories in biology, including the theory of evolution, cell theory, and germ theory.

Two videos explaining scientific theories can be seen at http://www.youtube.com/watch?v=S5YGhprR6KE and http://www.youtube.com/watch?v=jdWMcMW54fA.



> *As you view Know the Difference (Between Hypothesis and Theory), focus on these concepts:*
>
> 1. *the controversy surrounding the words "hypothesis" and "theory",*
> 2. *the scientific use of the words "hypothesis" and "theory",*
> 3. *the criteria for a "hypothesis,"*

> *4. the National Academy of Sciences definition of "theory",*
> *5. the meaning of the statement, "theories are the bedrock of our understanding of nature".*

The Theory of Evolution

The theory of evolution by natural selection is a scientific theory. **Evolution** is a change in the characteristics of living things over time. Evolution occurs by a process called **natural selection**. In natural selection, some living things produce more offspring than others, so they pass more genes to the next generation than others do. Over many generations, this can lead to major changes in the characteristics of living things. The theory of evolution by natural selection explains how living things are changing today and how modern living things have descended from ancient life forms that no longer exist on Earth. No evidence has been identified that proves this theory is incorrect. More on the theory of evolution will be presented in additional concepts.

The Cell Theory

The cell theory is another important scientific theory of biology. According to the **cell theory**, the cell is the smallest unit of structure and function of all living organisms, all living organisms are made up of at least one cell, and living cells always come from other living cells. Once again, no evidence has been identified that proves this theory is incorrect. More on the cell theory will be presented in additional concepts.

The Germ Theory

The **germ theory** of disease, also called the pathogenic theory of medicine, is a scientific theory that proposes that microorganisms are the cause of many diseases. Like the other scientific theories, lots of evidence has been identified that supports this theory, and no evidence has been identified that proves the theory is incorrect.

Summary

- With repeated testing, some hypotheses may eventually become scientific theories. A scientific theory is a broad explanation for events that is widely accepted as true.
- Evolution is a change species over time. Evolution occurs by natural selection.
- The cell theory states that all living things are made up of cells, and living cells always come from other living cells.
- The germ theory proposes that microorganisms are the cause of many diseases.

Explore More

Use these resources to answer the questions that follow.

Explore More I

- **Darwinian Evolution** - *Science and Theory* at Non-Majors Biology: http://www.hippocampus.org/Biology.

1. How is the word ''theory'' used in common language?
2. How is the word ''theory'' used in science?
3. Provide a detailed definition for a ''scientific theory''.

Explore More II

- **Concepts and Methods in Biology** -*Theories and Laws* at Non-Majors Biology: http://www.hippocampus.org/Biology.

1. What is a scientific law?
2. What is a scientific theory?
3. Give two examples of scientific theories.
4. Can a scientific theory become a law? Why or why not?

Review

1. Contrast how the term theory is used in science and in everyday language.
2. Explain how a hypothesis could become a theory.
3. Describe the evidence that proves the cell theory is incorrect.

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1.4: Core Concepts in Biology

Skills to Develop

- Identify and describe the properties of life
- Describe the levels of organization among living things
- Recognize and interpret a phylogenetic tree
- List examples of different sub disciplines in biology

Biology is the science that studies life, but what exactly is life? This may sound like a silly question with an obvious response, but it is not always easy to define life. For example, a branch of biology called virology studies viruses, which exhibit some of the characteristics of living entities but lack others. It turns out that although viruses can attack living organisms, cause diseases, and even reproduce, they do not meet the criteria that biologists use to define life. Consequently, virologists are not biologists, strictly speaking. Similarly, some biologists study the early molecular evolution that gave rise to life; since the events that preceded life are not biological events, these scientists are also excluded from biology in the strict sense of the term.

From its earliest beginnings, biology has wrestled with three questions: What are the shared properties that make something "alive"? And once we know something is alive, how do we find meaningful levels of organization in its structure? And, finally, when faced with the remarkable diversity of life, how do we organize the different kinds of organisms so that we can better understand them? As new organisms are discovered every day, biologists continue to seek answers to these and other questions.

Properties of Life

All living organisms share several key characteristics or functions: order, sensitivity or response to the environment, reproduction, adaptation, growth and development, regulation, homeostasis, energy processing, and evolution. When viewed together, these nine characteristics serve to define life.

Order

Organisms are highly organized, coordinated structures that consist of one or more cells. Even very simple, single-celled organisms are remarkably complex: inside each cell, atoms make up molecules; these in turn make up cell organelles and other cellular inclusions. In multicellular organisms (Figure **1.4.1**), similar cells form tissues. Tissues, in turn, collaborate to create organs (body structures with a distinct function). Organs work together to form organ systems.



Figure **1.4.1**: A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems. (credit: "Ivengo"/Wikimedia Commons)

Sensitivity or Response to Stimuli

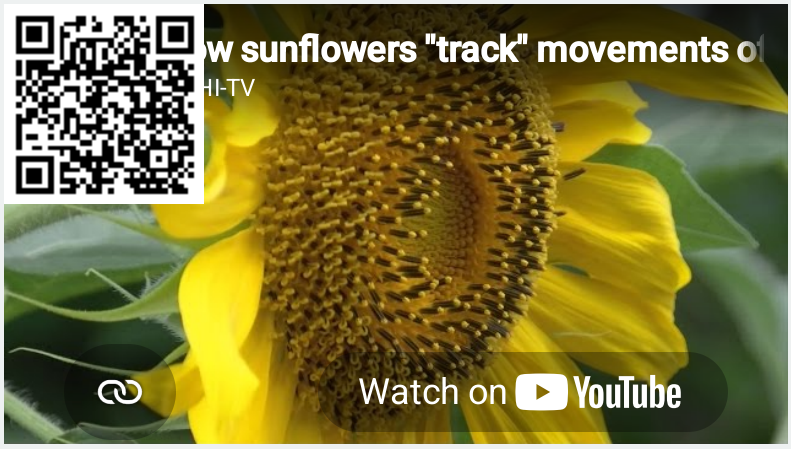
Organisms respond to diverse stimuli. For example, plants can bend toward a source of light, climb on fences and walls, or respond to touch (Figure **1.4.2**). Even tiny bacteria can move toward or away from chemicals (a process called *chemotaxis*) or light

(*phototaxis*). Movement toward a stimulus is considered a positive response, while movement away from a stimulus is considered a negative response.



Figure **1.4.2**: The leaves of this sensitive plant (*Mimosa pudica*) will instantly droop and fold when touched. After a few minutes, the plant returns to normal. (credit: Alex Lomas)

Link to Learning



Video: Watch this video to see how plants respond to a stimulus—from opening to light, to wrapping a tendril around a branch, to capturing prey.

Reproduction

Single-celled organisms reproduce by first duplicating their DNA, and then dividing it equally as the cell prepares to divide to form two new cells. Multicellular organisms often produce specialized reproductive germline cells that will form new individuals. When reproduction occurs, genes containing DNA are passed along to an organism's offspring. These genes ensure that the offspring will belong to the same species and will have similar characteristics, such as size and shape.

Growth and Development

Organisms grow and develop following specific instructions coded for by their genes. These genes provide instructions that will direct cellular growth and development, ensuring that a species' young (Figure **1.4.3**) will grow up to exhibit many of the same characteristics as its parents.



Figure **1.4.3**: Although no two look alike, these kittens have inherited genes from both parents and share many of the same characteristics. (credit: Rocky Mountain Feline Rescue)

Regulation

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, respond to stimuli, and cope with environmental stresses. Two examples of internal functions regulated in an organism are nutrient transport and blood flow. Organs (groups of tissues working together) perform specific functions, such as carrying oxygen throughout the body, removing wastes, delivering nutrients to every cell, and cooling the body.

Homeostasis

In order to function properly, cells need to have appropriate conditions such as proper temperature, pH, and appropriate concentration of diverse chemicals. These conditions may, however, change from one moment to the next. Organisms are able to maintain internal conditions within a narrow range almost constantly, despite environmental changes, through homeostasis (literally, “steady state”)—the ability of an organism to maintain constant internal conditions. For example, an organism needs to regulate body temperature through a process known as thermoregulation. Organisms that live in cold climates, such as the polar bear (Figure **1.4.4**), have body structures that help them withstand low temperatures and conserve body heat. Structures that aid in this type of insulation include fur, feathers, blubber, and fat. In hot climates, organisms have methods (such as perspiration in humans or panting in dogs) that help them to shed excess body heat.



Figure **1.4.4**: Polar bears (*Ursus maritimus*) and other mammals living in ice-covered regions maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin. (credit: “longhorndave”/Flickr)

Energy Processing

All organisms use a source of energy for their metabolic activities. Some organisms capture energy from the sun and convert it into chemical energy in food; others use chemical energy in molecules they take in as food (Figure **1.4.5**).



Figure **1.4.5**: The California condor (*Gymnogyps californianus*) uses chemical energy derived from food to power flight. California condors are an endangered species; this bird has a wing tag that helps biologists identify the individual. (credit: Pacific Southwest Region U.S. Fish and Wildlife Service)

Levels of Organization of Living Things

Living things are highly organized and structured, following a hierarchy that can be examined on a scale from small to large. The atom is the smallest and most fundamental unit of matter. It consists of a nucleus surrounded by electrons. Atoms form molecules. A molecule is a chemical structure consisting of at least two atoms held together by one or more chemical bonds. Many molecules that are biologically important are macromolecules, large molecules that are typically formed by polymerization (a polymer is a large molecule that is made by combining smaller units called monomers, which are simpler than macromolecules). An example of a macromolecule is deoxyribonucleic acid (DNA) (Figure **1.4.6**), which contains the instructions for the structure and functioning of all living organisms.

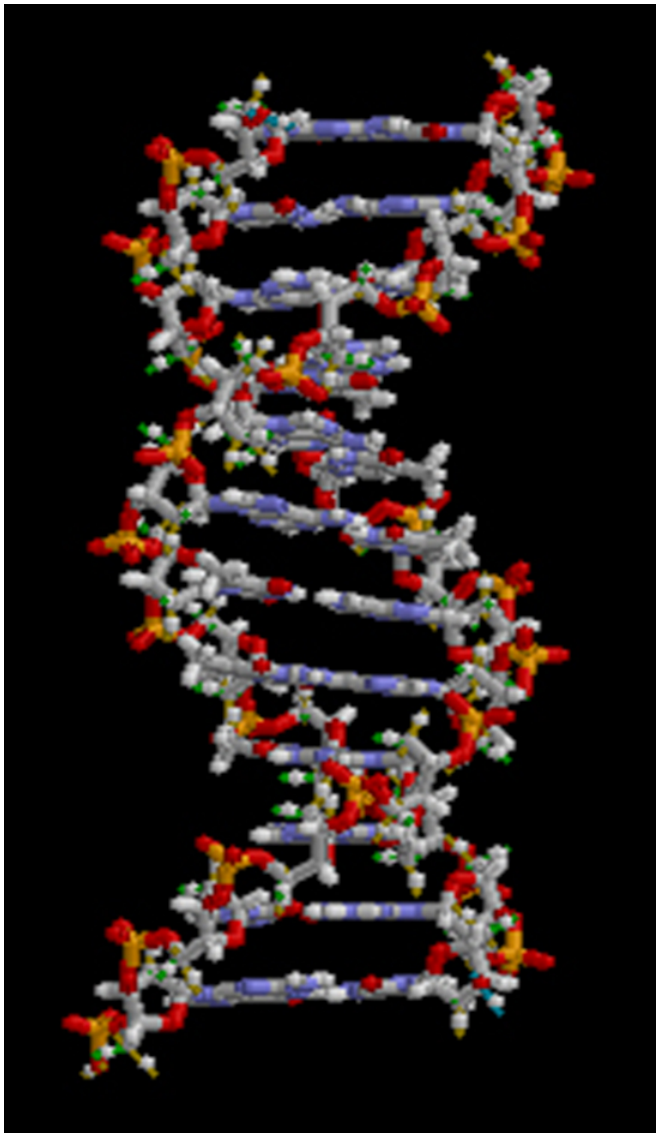


Figure 1.4.6: All molecules, including this DNA molecule, are composed of atoms. (credit: “brian0918”/Wikimedia Commons)

Link to Learning

Video: Watch this video that animates the three-dimensional structure of the DNA molecule shown in Figure 1.4.6.

Some cells contain aggregates of macromolecules surrounded by membranes; these are called organelles. Organelles are small structures that exist within cells. Examples of organelles include mitochondria and chloroplasts, which carry out indispensable functions: mitochondria produce energy to power the cell, while chloroplasts enable green plants to utilize the energy in sunlight to make sugars. All living things are made of cells; the cell itself is the smallest fundamental unit of structure and function in living organisms. (This requirement is why viruses are not considered living: they are not made of cells. To make new viruses, they have to invade and hijack the reproductive mechanism of a living cell; only then can they obtain the materials they need to reproduce.)

Some organisms consist of a single cell and others are multicellular. Cells are classified as prokaryotic or eukaryotic. Prokaryotes are single-celled or colonial organisms that do not have membrane-bound nuclei; in contrast, the cells of eukaryotes do have membrane-bound organelles and a membrane-bound nucleus.

In larger organisms, cells combine to make tissues, which are groups of similar cells carrying out similar or related functions. Organs are collections of tissues grouped together performing a common function. Organs are present not only in animals but also in plants. An organ system is a higher level of organization that consists of functionally related organs. Mammals have many organ systems. For instance, the circulatory system transports blood through the body and to and from the lungs; it includes organs such as the heart and blood vessels. Organisms are individual living entities. For example, each tree in a forest is an organism. Single-celled prokaryotes and single-celled eukaryotes are also considered organisms and are typically referred to as microorganisms.

All the individuals of a species living within a specific area are collectively called a population. For example, a forest may include many pine trees. All of these pine trees represent the population of pine trees in this forest. Different populations may live in the same specific area. For example, the forest with the pine trees includes populations of flowering plants and also insects and microbial populations. A community is the sum of populations inhabiting a particular area. For instance, all of the trees, flowers, insects, and other populations in a forest form the forest's community. The forest itself is an ecosystem. An ecosystem consists of all the living things in a particular area together with the abiotic, non-living parts of that environment such as nitrogen in the soil or rain water. At the highest level of organization (Figure 1.4.7), the biosphere is the collection of all ecosystems, and it represents the zones of life on earth. It includes land, water, and even the atmosphere to a certain extent.

Art Connection

https://bio.libretexts.org/@go/page/73992

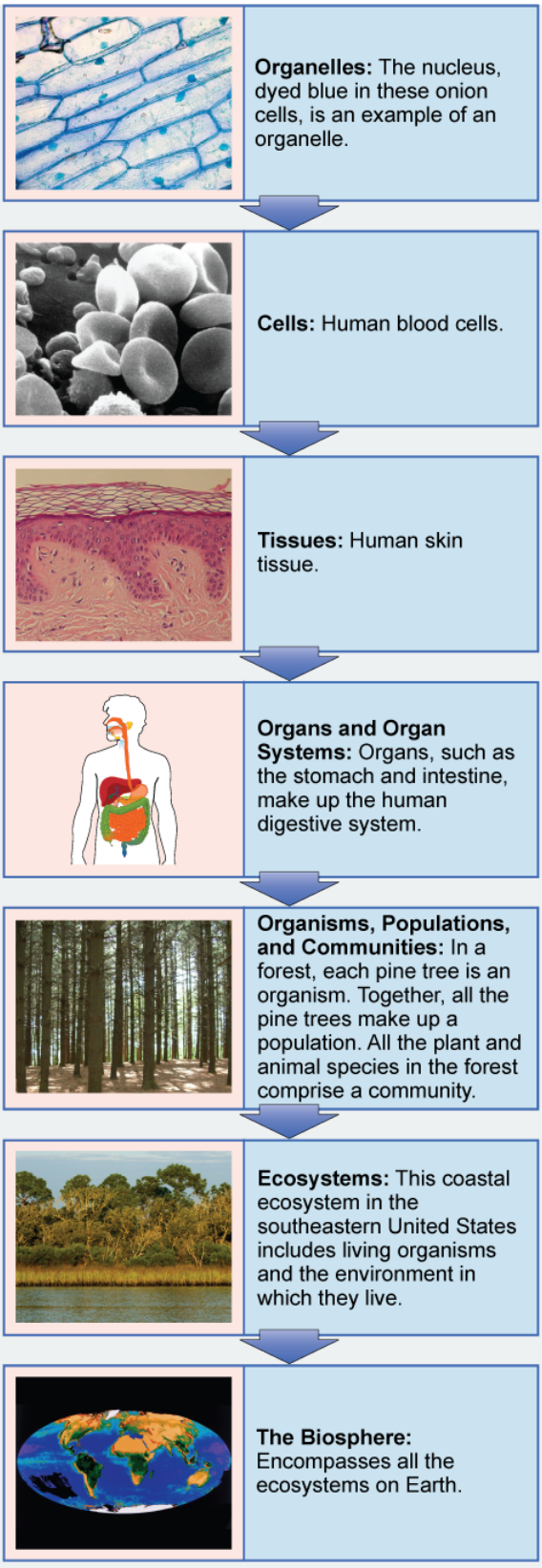

Organelles: The nucleus, dyed blue in these onion cells, is an example of an organelle.
Cells: Human blood cells.
Tissues: Human skin tissue.
Organs and Organ Systems: Organs, such as the stomach and intestine, make up the human digestive system.
Organisms, Populations, and Communities: In a forest, each pine tree is an organism. Together, all the pine trees make up a population. All the plant and animal species in the forest comprise a community.
Ecosystems: This coastal ecosystem in the southeastern United States includes living organisms and the environment in which they live.
The Biosphere: Encompasses all the ecosystems on Earth.

Figure 1.4.7: The biological levels of organization of living things are shown. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit “organelles”: modification of work by Umberto Salvagnin; credit “cells”: modification of work by Bruce Wetzel, Harry Schaefer/ National Cancer Institute; credit “tissues”: modification of work by Kilbad; Fama Clamosa; Mikael Häggström; credit “organs”: modification of work by Mariana Ruiz Villareal; credit “organisms”: modification of work by "Crystal"/Flickr; credit “ecosystems”: modification of work by US Fish and Wildlife Service Headquarters; credit “biosphere”: modification of work by NASA)

Which of the following statements is false?

A. Tissues exist within organs which exist within organ systems.
B. Communities exist within populations which exist within ecosystems.
C. Organelles exist within cells which exist within tissues.
D. Communities exist within ecosystems which exist in the biosphere.

The Diversity of Life

The fact that biology, as a science, has such a broad scope has to do with the tremendous diversity of life on earth. The source of this diversity is evolution, the process of gradual change during which new species arise from older species. Evolutionary biologists study the evolution of living things in everything from the microscopic world to ecosystems.

The evolution of various life forms on Earth can be summarized in a phylogenetic tree (Figure 1.4.8). A phylogenetic tree is a diagram showing the evolutionary relationships among biological species based on similarities and differences in genetic or physical traits or both. A phylogenetic tree is composed of nodes and branches. The internal nodes represent ancestors and are points in evolution when, based on scientific evidence, an ancestor is thought to have diverged to form two new species. The length of each branch is proportional to the time elapsed since the split.

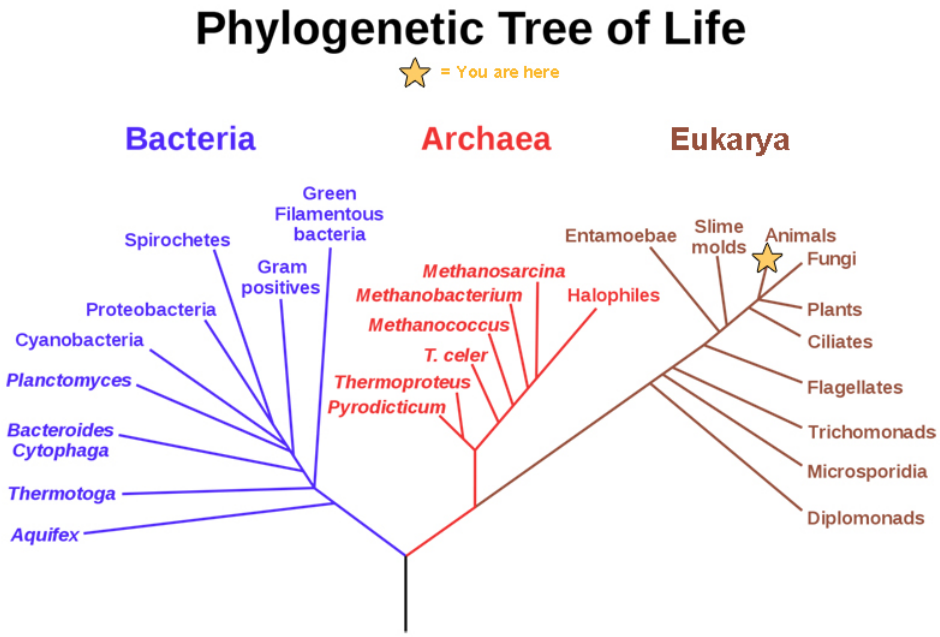


Figure 1.4.8: This phylogenetic tree was constructed by microbiologist Carl Woese using data obtained from sequencing ribosomal RNA genes. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are prokaryotes, single-celled organisms lacking intracellular organelles. (credit: Eric Gaba; NASA Astrobiology Institute)

Evolution Connection: Carl Woese and the Phylogenetic Tree

In the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists, and bacteria. The organizational scheme was based mainly on physical features, as opposed to physiology, biochemistry, or molecular biology, all of which are used by modern systematics. The pioneering work of American microbiologist Carl Woese in the early 1970s has shown, however, that life on Earth has evolved along three lineages, now called domains—Bacteria, Archaea, and Eukarya. The first two are prokaryotic cells with microbes that lack membrane-enclosed nuclei and organelles. The third domain contains the eukaryotes and includes unicellular microorganisms together with the four original kingdoms (excluding bacteria).

Woese defined Archaea as a new domain, and this resulted in a new taxonomic tree (Figure 1.4.8). Many organisms belonging to the Archaea domain live under extreme conditions and are called extremophiles. To construct his tree, Woese used genetic relationships rather than similarities based on morphology (shape).

Woese's tree was constructed from comparative sequencing of the genes that are universally distributed, present in every organism, and conserved (meaning that these genes have remained essentially unchanged throughout evolution). Woese's approach was revolutionary because comparisons of physical features are insufficient to differentiate between the prokaryotes that appear fairly similar in spite of their tremendous biochemical diversity and genetic variability (Figure 1.4.9). The comparison of homologous DNA and RNA sequences provided Woese with a sensitive device that revealed the extensive variability of prokaryotes, and which justified the separation of the prokaryotes into two domains: bacteria and archaea.

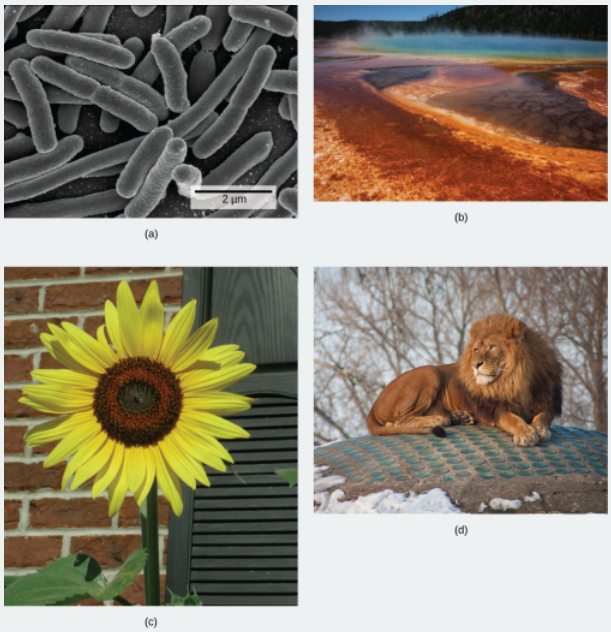


Figure 1.4.9: These images represent different domains. The (a) bacteria in this micrograph belong to Domain Bacteria, while the (b) extremophiles (not visible) living in this hot vent belong to Domain Archaea. Both the (c) sunflower and (d) lion are part of Domain Eukarya. (credit a: modification of work by Drew March; credit b: modification of work by Steve Jurvetson; credit c: modification of work by Michael Arrighi; credit d: modification of work by Leszek Leszcynski)

Branches of Biological Study

The scope of biology is broad and therefore contains many branches and subdisciplines. Biologists may pursue one of those subdisciplines and work in a more focused field. For instance, molecular biology and biochemistry study biological processes at the molecular and chemical level, including interactions among molecules such as DNA, RNA, and proteins, as well as the way they are regulated. Microbiology, the study of microorganisms, is the study of the structure and function of single-celled organisms. It is quite a broad branch itself, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

Career Connection: Forensic Scientist

Forensic science is the application of science to answer questions related to the law. Biologists as well as chemists and biochemists can be forensic scientists. Forensic scientists provide scientific evidence for use in courts, and their job involves examining trace materials associated with crimes. Interest in forensic science has increased in the last few years, possibly because of popular television shows that feature forensic scientists on the job. Also, the development of molecular techniques and the establishment of DNA databases have expanded the types of work that forensic scientists can do. Their job activities are primarily related to crimes against people such as murder, rape, and assault. Their work involves analyzing samples such as hair, blood, and other body fluids and also processing DNA (Figure 1.4.10) found in many different environments and materials. Forensic scientists also analyze other biological evidence left at crime scenes, such as insect larvae or pollen grains.

Students who want to pursue careers in forensic science will most likely be required to take chemistry and biology courses as well as some intensive math courses.



Figure **1.4.10**: This forensic scientist works in a DNA extraction room at the U.S. Army Criminal Investigation Laboratory at Fort Gillem, GA. (credit: United States Army CID Command Public Affairs)

Another field of biological study, neurobiology, studies the biology of the nervous system, and although it is considered a branch of biology, it is also recognized as an interdisciplinary field of study known as neuroscience. Because of its interdisciplinary nature, this subdiscipline studies different functions of the nervous system using molecular, cellular, developmental, medical, and computational approaches.



Figure **1.4.11**: Researchers work on excavating dinosaur fossils at a site in Castellón, Spain. (credit: Mario Modesto)

Paleontology, another branch of biology, uses fossils to study life's history (Figure **1.4.11**). Zoology and botany are the study of animals and plants, respectively. Biologists can also specialize as biotechnologists, ecologists, or physiologists, to name just a few areas. This is just a small sample of the many fields that biologists can pursue.

Biology is the culmination of the achievements of the natural sciences from their inception to today. Excitingly, it is the cradle of emerging sciences, such as the biology of brain activity, genetic engineering of custom organisms, and the biology of evolution that uses the laboratory tools of molecular biology to retrace the earliest stages of life on earth. A scan of news headlines—whether reporting on immunizations, a newly discovered species, sports doping, or a genetically-modified food—demonstrates the way biology is active in and important to our everyday world.

Summary

Biology is the science of life. All living organisms share several key properties such as order, sensitivity or response to stimuli, reproduction, growth and development, regulation, homeostasis, and energy processing. Living things are highly organized parts of

a hierarchy that includes atoms, molecules, organelles, cells, tissues, organs, and organ systems. Organisms, in turn, are grouped as populations, communities, ecosystems, and the biosphere. The great diversity of life today evolved from less-diverse ancestral organisms over billions of years. A diagram called a phylogenetic tree can be used to show evolutionary relationships among organisms.

Biology is very broad and includes many branches and subdisciplines. Examples include molecular biology, microbiology, neurobiology, zoology, and botany, among others.

Art Connections

Figure **1.4.7**: Which of the following statements is false?

A. Tissues exist within organs which exist within organ systems.
B. Communities exist within populations which exist within ecosystems.
C. Organelles exist within cells which exist within tissues.
D. Communities exist within ecosystems which exist in the biosphere.

Answer

Communities exist within populations which exist within ecosystems.

Glossary

atom
smallest and most fundamental unit of matter

biochemistry
study of the chemistry of biological organisms

biosphere
collection of all the ecosystems on Earth

botany
study of plants

cell
smallest fundamental unit of structure and function in living things

community
set of populations inhabiting a particular area

ecosystem
all the living things in a particular area together with the abiotic, nonliving parts of that environment

eukaryote
organism with cells that have nuclei and membrane-bound organelles

evolution
process of gradual change during which new species arise from older species and some species become extinct

homeostasis
ability of an organism to maintain constant internal conditions

macromolecule
large molecule, typically formed by the joining of smaller molecules

microbiology
study of the structure and function of microorganisms

molecule
chemical structure consisting of at least two atoms held together by one or more chemical bonds

molecular biology
study of biological processes and their regulation at the molecular level, including interactions among molecules such as DNA, RNA, and proteins

neurobiology
study of the biology of the nervous system

organ
collection of related tissues grouped together performing a common function

organ system
level of organization that consists of functionally related interacting organs

organelle
small structures that exist within cells and carry out cellular functions

organism
individual living entity

paleontology
study of life's history by means of fossils

phylogenetic tree
diagram showing the evolutionary relationships among various biological species based on similarities and differences in genetic or physical traits or both; in essence, a hypothesis concerning evolutionary connections

population
all of the individuals of a species living within a specific area

prokaryote
single-celled organism that lacks organelles and does not have nuclei surrounded by a nuclear membrane

tissue
group of similar cells carrying out related functions

zoology
study of animals

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CHAPTER OVERVIEW

2: The Nature of Molecules and the Properties of Water

2.1: The Nature of Atoms

2.2: Elements Found in Living Systems

2.3: The Nature of Chemical Bonds

2.3.1: Electronegativity and types of Chemical Bonds

2.4: Water- A Vital Compound

2.5: Properties of Water

2.6: Acids and Bases

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2.1: The Nature of Atoms

At its most fundamental level, life is made up of matter. Matter occupies space and has mass. All matter is composed of elements, substances that cannot be broken down or transformed chemically into other substances. Each element is made of atoms, each with a constant number of protons and unique properties. A total of 118 elements have been defined; however, only 92 occur naturally, and fewer than 30 are found in living cells. The remaining 26 elements are unstable and, therefore, do not exist for very long or are theoretical and have yet to be detected.

Each element is designated by its chemical symbol (such as H, N, O, C, and Na), and possesses unique properties. These unique properties allow elements to combine and to bond with each other in specific ways.

Atoms

An atom is the smallest component of an element that retains all of the chemical properties of that element. For example, one hydrogen atom has all of the properties of the element hydrogen, such as it exists as a gas at room temperature, and it bonds with oxygen to create a water molecule. Hydrogen atoms cannot be broken down into anything smaller while still retaining the properties of hydrogen. If a hydrogen atom were broken down into subatomic particles, it would no longer have the properties of hydrogen.

At the most basic level, all organisms are made of a combination of elements. They contain atoms that combine together to form molecules. In multicellular organisms, such as animals, molecules can interact to form cells that combine to form tissues, which make up organs. These combinations continue until entire multicellular organisms are formed.

All atoms contain protons, electrons, and neutrons (Figure **2.1.1**). The only exception is hydrogen (H), which is made of one proton and one electron. A proton is a positively charged particle that resides in the nucleus (the core of the atom) of an atom and has a mass of 1 and a charge of +1. An electron is a negatively charged particle that travels in the space around the nucleus. In other words, it resides outside of the nucleus. It has a negligible mass and has a charge of –1.

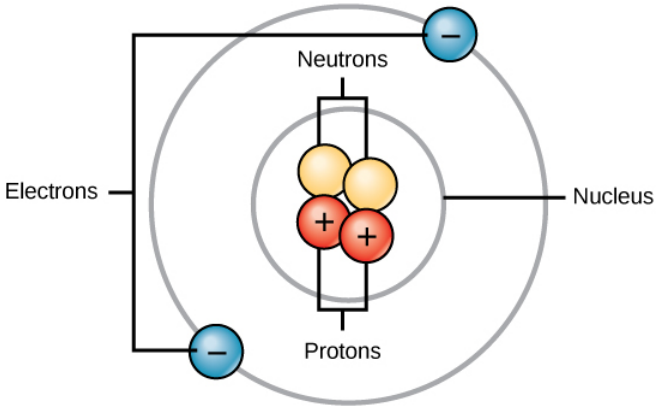


Figure 2.1.1: Atoms are made up of protons and neutrons located within the nucleus, and electrons surrounding the nucleus.

Neutrons, like protons, reside in the nucleus of an atom. They have a mass of 1 and no charge. The positive (protons) and negative (electrons) charges balance each other in a neutral atom, which has a net zero charge.

Because protons and neutrons each have a mass of 1, the mass of an atom is equal to the number of protons and neutrons of that atom. The number of electrons does not factor into the overall mass, because their mass is so small.

As stated earlier, each element has its own unique properties. Each contains a different number of protons and neutrons, giving it its own atomic number and mass number. The atomic number of an element is equal to the number of protons that element contains. The mass number, or atomic mass, is the number of protons plus the number of neutrons of that element. Therefore, it is possible to determine the number of neutrons by subtracting the atomic number from the mass number.

These numbers provide information about the elements and how they will react when combined. Different elements have different melting and boiling points, and are in different states (liquid, solid, or gas) at room temperature. They also combine in different ways. Some form specific types of bonds, whereas others do not. How they combine is based on the number of electrons present.

Because of these characteristics, the elements are arranged into the periodic table of elements, a chart of the elements that includes the atomic number and relative atomic mass of each element. The periodic table also provides key information about the properties of elements (Figure **2.1.2**)—often indicated by color-coding. The arrangement of the table also shows how the electrons in each element are organized and provides important details about how atoms will react with each other to form molecules.

Isotopes are different forms of the same element that have the same number of protons, but a different number of neutrons. Some elements, such as carbon, potassium, and uranium, have naturally occurring isotopes. Carbon-12, the most common isotope of carbon, contains six protons and six neutrons. Therefore, it has a mass number of 12 (six protons and six neutrons) and an atomic number of 6 (which makes it carbon). Carbon-14 contains six protons and eight neutrons. Therefore, it has a mass number of 14 (six protons and eight neutrons) and an atomic number of 6, meaning it is still the element carbon. These two alternate forms of carbon are isotopes. Some isotopes are unstable and will lose protons, other subatomic particles, or energy to form more stable elements. These are called radioactive isotopes or radioisotopes.

ART CONNECTION

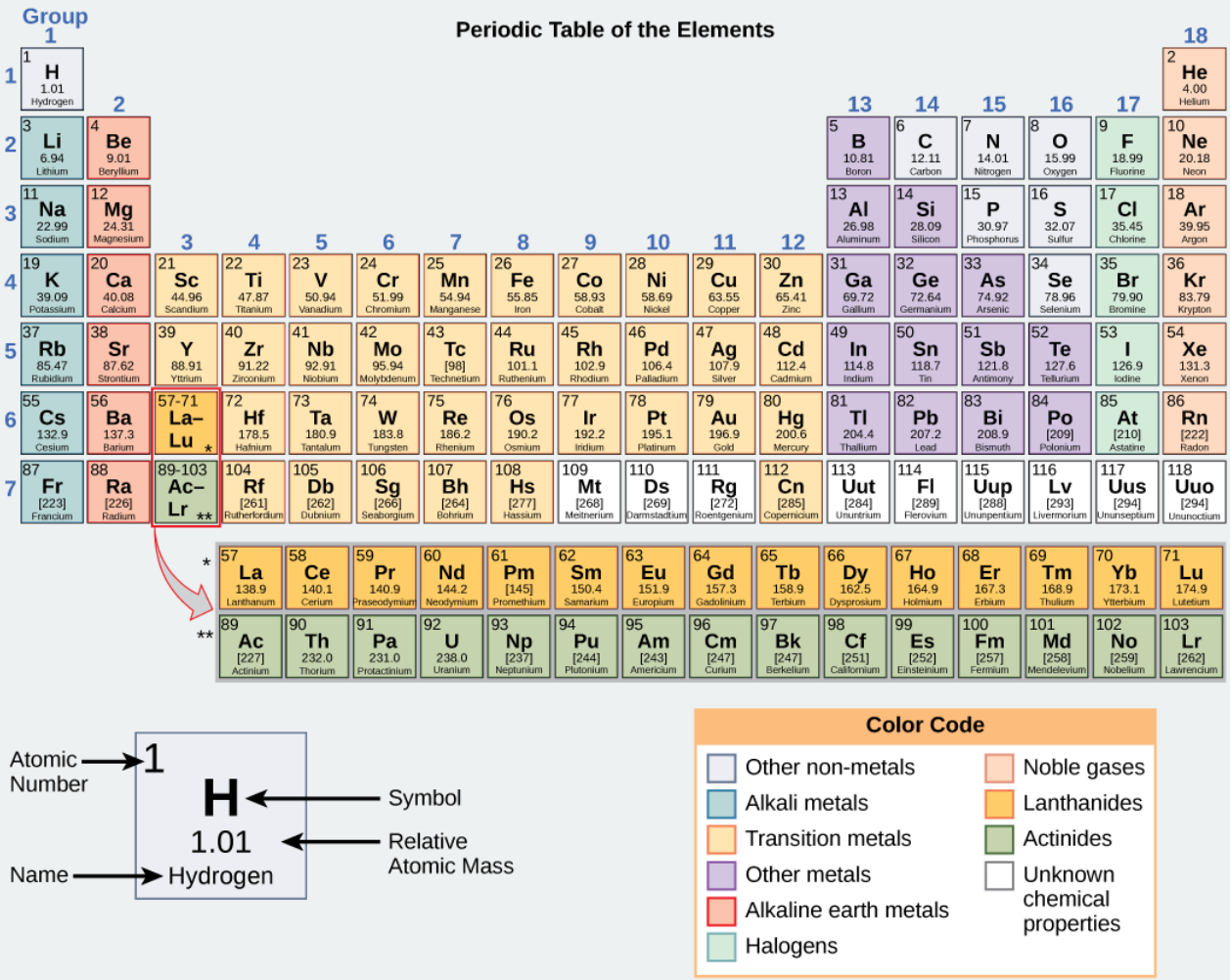


Figure 2.1.2: Arranged in columns and rows based on the characteristics of the elements, the periodic table provides key information about the elements and how they might interact with each other to form molecules. Most periodic tables provide a key or legend to the information they contain.

How many neutrons do (K) potassium-39 and potassium-40 have, respectively?

EVOLUTION IN ACTION: Carbon Dating

Carbon-14 (^{14}C) is a naturally occurring radioisotope that is created in the atmosphere by cosmic rays. This is a continuous process, so more ^{14}C is always being created. As a living organism develops, the relative level of ^{14}C in its body is equal to the concentration of ^{14}C in the atmosphere. When an organism dies, it is no longer ingesting ^{14}C, so the ratio will decline. ^{14}C decays to ^{14}N by a process called beta decay; it gives off energy in this slow process.

After approximately 5,730 years, only one-half of the starting concentration of ^{14}C will have been converted to ^{14}N. The time it takes for half of the original concentration of an isotope to decay to its more stable form is called its half-life. Because the half-life of ^{14}C is long, it is used to age formerly living objects, such as fossils. Using the ratio of the ^{14}C concentration found in an object to the amount of ^{14}C detected in the atmosphere, the amount of the isotope that has not yet decayed can be determined. Based on this amount, the age of the fossil can be calculated to about 50,000 years (Figure **2.1.3**). Isotopes with longer half-lives, such as potassium-40, are used to calculate the ages of older fossils. Through the use of carbon dating, scientists can reconstruct the ecology and biogeography of organisms living within the past 50,000 years.



Figure 2.1.3: The age of remains that contain carbon and are less than about 50,000 years old, such as this pygmy mammoth, can be determined using carbon dating. (credit: Bill Faulkner/NPS)

CONCEPT IN ACTION

To learn more about atoms and isotopes, and how you can tell one isotope from another, visit this site and run the simulation.

Chemical Bonds

How elements interact with one another depends on how their electrons are arranged and how many openings for electrons exist at the outermost region where electrons are present in an atom. Electrons exist at energy levels that form shells around the nucleus. The closest shell can hold up to two electrons. The closest shell to the nucleus is always filled first, before any other shell can be filled. Hydrogen has one electron; therefore, it has only one spot occupied within the lowest shell. Helium has two electrons; therefore, it can completely fill the lowest shell with its two electrons. If you look at the periodic table, you will see that hydrogen and helium are the only two elements in the first row. This is because they only have electrons in their first shell. Hydrogen and helium are the only two elements that have the lowest shell and no other shells.

The second and third energy levels can hold up to eight electrons. The eight electrons are arranged in four pairs and one position in each pair is filled with an electron before any pairs are completed.

Looking at the periodic table again (Figure **2.1.2**), you will notice that there are seven rows. These rows correspond to the number of shells that the elements within that row have. The elements within a particular row have increasing numbers of electrons as the columns proceed from left to right. Although each element has the same number of shells, not all of the shells are completely filled with electrons. If you look at the second row of the periodic table, you will find lithium (Li), beryllium (Be), boron (B), carbon (C), nitrogen (N), oxygen (O), fluorine (F), and neon (Ne). These all have electrons that occupy only the first and second shells. Lithium

has only one electron in its outermost shell, beryllium has two electrons, boron has three, and so on, until the entire shell is filled with eight electrons, as is the case with neon.

Not all elements have enough electrons to fill their outermost shells, but an atom is at its most stable when all of the electron positions in the outermost shell are filled. Because of these vacancies in the outermost shells, we see the formation of chemical bonds, or interactions between two or more of the same or different elements that result in the formation of molecules. To achieve greater stability, atoms will tend to completely fill their outer shells and will bond with other elements to accomplish this goal by sharing electrons, accepting electrons from another atom, or donating electrons to another atom. Because the outermost shells of the elements with low atomic numbers (up to calcium, with atomic number 20) can hold eight electrons, this is referred to as the octet rule. An element can donate, accept, or share electrons with other elements to fill its outer shell and satisfy the octet rule.

When an atom does not contain equal numbers of protons and electrons, it is called an ion. Because the number of electrons does not equal the number of protons, each ion has a net charge. Positive ions are formed by losing electrons and are called cations. Negative ions are formed by gaining electrons and are called anions.

For example, sodium only has one electron in its outermost shell. It takes less energy for sodium to donate that one electron than it does to accept seven more electrons to fill the outer shell. If sodium loses an electron, it now has 11 protons and only 10 electrons, leaving it with an overall charge of +1. It is now called a sodium ion.

The chlorine atom has seven electrons in its outer shell. Again, it is more energy-efficient for chlorine to gain one electron than to lose seven. Therefore, it tends to gain an electron to create an ion with 17 protons and 18 electrons, giving it a net negative (–1) charge. It is now called a chloride ion. This movement of electrons from one element to another is referred to as electron transfer. As Figure **2.1.4** illustrates, a sodium atom (Na) only has one electron in its outermost shell, whereas a chlorine atom (Cl) has seven electrons in its outermost shell. A sodium atom will donate its one electron to empty its shell, and a chlorine atom will accept that electron to fill its shell, becoming chloride. Both ions now satisfy the octet rule and have complete outermost shells. Because the number of electrons is no longer equal to the number of protons, each is now an ion and has a +1 (sodium) or –1 (chloride) charge.

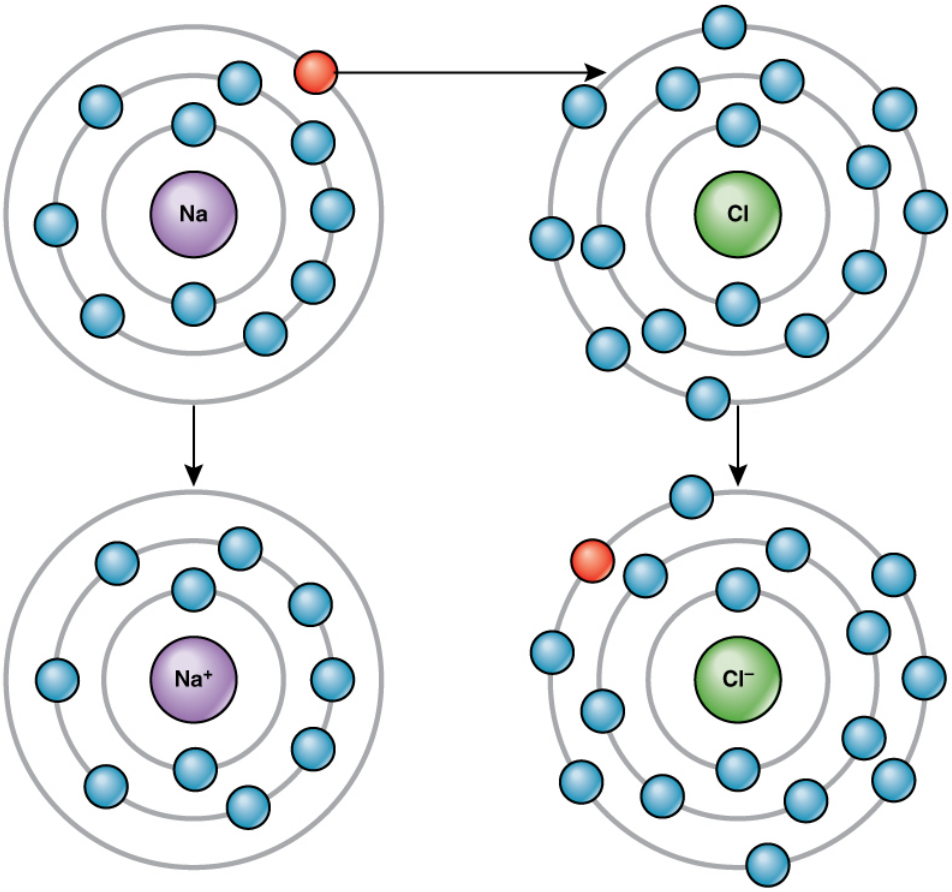


Figure 2.1.4: Elements tend to fill their outermost shells with electrons. To do this, they can either donate or accept electrons from other elements.

Ionic Bonds

There are four types of bonds or interactions: ionic, covalent, hydrogen bonds, and van der Waals interactions. Ionic and covalent bonds are strong interactions that require a larger energy input to break apart. When an element donates an electron from its outer shell, as in the sodium atom example above, a positive ion is formed. The element accepting the electron is now negatively charged. Because positive and negative charges attract, these ions stay together and form an ionic bond, or a bond between ions. The elements bond together with the electron from one element staying predominantly with the other element. When Na^+ and Cl^- ions combine to produce NaCl, an electron from a sodium atom stays with the other seven from the chlorine atom, and the sodium and chloride ions attract each other in a lattice of ions with a net zero charge.

Covalent Bonds

Another type of strong chemical bond between two or more atoms is a covalent bond. These bonds form when an electron is shared between two elements and are the strongest and most common form of chemical bond in living organisms. Covalent bonds form between the elements that make up the biological molecules in our cells. Unlike ionic bonds, covalent bonds do not dissociate in water.

The hydrogen and oxygen atoms that combine to form water molecules are bound together by covalent bonds. The electron from the hydrogen atom divides its time between the outer shell of the hydrogen atom and the incomplete outer shell of the oxygen atom. To completely fill the outer shell of an oxygen atom, two electrons from two hydrogen atoms are needed, hence the subscript “2” in H_2O. The electrons are shared between the atoms, dividing their time between them to “fill” the outer shell of each. This sharing is a lower energy state for all of the atoms involved than if they existed without their outer shells filled.

There are two types of covalent bonds: polar and nonpolar. Nonpolar covalent bonds form between two atoms of the same element or between different elements that share the electrons equally. For example, an oxygen atom can bond with another oxygen atom to fill their outer shells. This association is nonpolar because the electrons will be equally distributed between each oxygen atom. Two

covalent bonds form between the two oxygen atoms because oxygen requires two shared electrons to fill its outermost shell. Nitrogen atoms will form three covalent bonds (also called triple covalent) between two atoms of nitrogen because each nitrogen atom needs three electrons to fill its outermost shell. Another example of a nonpolar covalent bond is found in the methane (CH_4) molecule. The carbon atom has four electrons in its outermost shell and needs four more to fill it. It gets these four from four hydrogen atoms, each atom providing one. These elements all share the electrons equally, creating four nonpolar covalent bonds (Figure **2.1.5**).

In a polar covalent bond, the electrons shared by the atoms spend more time closer to one nucleus than to the other nucleus. Because of the unequal distribution of electrons between the different nuclei, a slightly positive (δ+) or slightly negative (δ–) charge develops. The covalent bonds between hydrogen and oxygen atoms in water are polar covalent bonds. The shared electrons spend more time near the oxygen nucleus, giving it a small negative charge, than they spend near the hydrogen nuclei, giving these molecules a small positive charge.

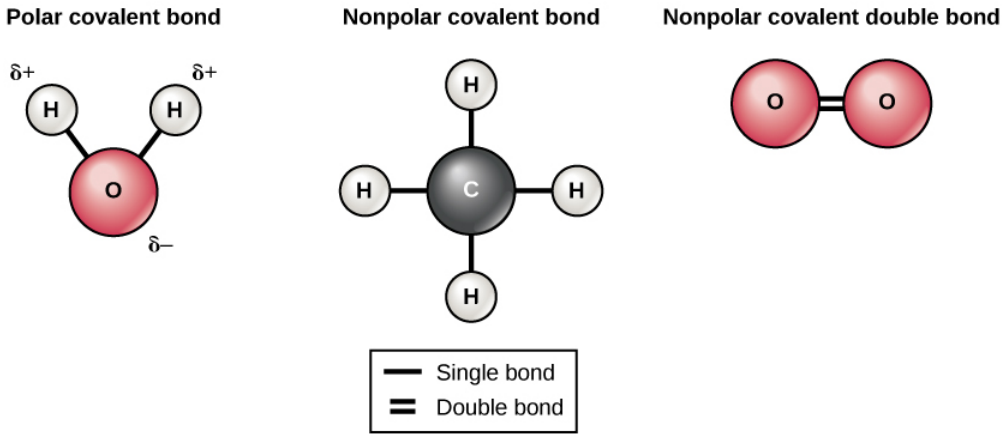


Figure 2.1.5: The water molecule (left) depicts a polar bond with a slightly positive charge on the hydrogen atoms and a slightly negative charge on the oxygen. Examples of nonpolar bonds include methane (middle) and oxygen (right).

Hydrogen Bonds

Ionic and covalent bonds are strong bonds that require considerable energy to break. However, not all bonds between elements are ionic or covalent bonds. Weaker bonds can also form. These are attractions that occur between positive and negative charges that do not require much energy to break. Two weak bonds that occur frequently are hydrogen bonds and van der Waals interactions. These bonds give rise to the unique properties of water and the unique structures of DNA and proteins.

When polar covalent bonds containing a hydrogen atom form, the hydrogen atom in that bond has a slightly positive charge. This is because the shared electron is pulled more strongly toward the other element and away from the hydrogen nucleus. Because the hydrogen atom is slightly positive (δ+), it will be attracted to neighboring negative partial charges (δ–). When this happens, a weak interaction occurs between the δ+ charge of the hydrogen atom of one molecule and the δ– charge of the other molecule. This interaction is called a hydrogen bond. This type of bond is common; for example, the liquid nature of water is caused by the hydrogen bonds between water molecules (Figure **2.1.6**). Hydrogen bonds give water the unique properties that sustain life. If it were not for hydrogen bonding, water would be a gas rather than a liquid at room temperature.

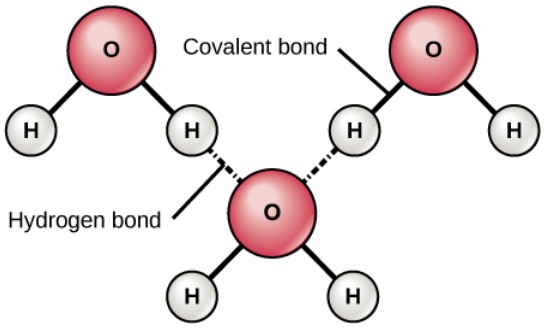


Figure 2.1.6: Hydrogen bonds form between slightly positive (δ+) and slightly negative (δ–) charges of polar covalent molecules, such as water.

Hydrogen bonds can form between different molecules and they do not always have to include a water molecule. Hydrogen atoms in polar bonds within any molecule can form bonds with other adjacent molecules. For example, hydrogen bonds hold together two long strands of DNA to give the DNA molecule its characteristic double-stranded structure. Hydrogen bonds are also responsible for some of the three-dimensional structure of proteins.

van der Waals Interactions

Like hydrogen bonds, van der Waals interactions are weak attractions or interactions between molecules. They occur between polar, covalently bound, atoms in different molecules. Some of these weak attractions are caused by temporary partial charges formed when electrons move around a nucleus. These weak interactions between molecules are important in biological systems.

CAREERS IN ACTION: Radiography Technician

Have you or anyone you know ever had a magnetic resonance imaging (MRI) scan, a mammogram, or an X-ray? These tests produce images of your soft tissues and organs (as with an MRI or mammogram) or your bones (as happens in an X-ray) by using either radiowaves or special isotopes (radiolabeled or fluorescently labeled) that are ingested or injected into the body. These tests provide data for disease diagnoses by creating images of your organs or skeletal system.

MRI imaging works by subjecting hydrogen nuclei, which are abundant in the water in soft tissues, to fluctuating magnetic fields, which cause them to emit their own magnetic field. This signal is then read by sensors in the machine and interpreted by a computer to form a detailed image.

Some radiography technologists and technicians specialize in computed tomography, MRI, and mammography. They produce films or images of the body that help medical professionals examine and diagnose. Radiologists work directly with patients, explaining machinery, preparing them for exams, and ensuring that their body or body parts are positioned correctly to produce the needed images. Physicians or radiologists then analyze the test results.

Radiography technicians can work in hospitals, doctors' offices, or specialized imaging centers. Training to become a radiography technician happens at hospitals, colleges, and universities that offer certificates, associate's degrees, or bachelor's degrees in radiography.

Summary

Matter is anything that occupies space and has mass. It is made up of atoms of different elements. All of the 92 elements that occur naturally have unique qualities that allow them to combine in various ways to create compounds or molecules. Atoms, which consist of protons, neutrons, and electrons, are the smallest units of an element that retain all of the properties of that element. Electrons can be donated or shared between atoms to create bonds, including ionic, covalent, and hydrogen bonds, as well as van der Waals interactions.

Art Connections

Figure **2.1.2**: How many neutrons do (K) potassium-39 and potassium-40 have, respectively?

Answer

Potassium-39 has twenty neutrons. Potassium-40 has twenty one neutrons.

Glossary

anion
a negative ion formed by gaining electrons

atomic number
the number of protons in an atom

cation
a positive ion formed by losing electrons

chemical bond
an interaction between two or more of the same or different elements that results in the formation of molecules

covalent bond
a type of strong bond between two or more of the same or different elements; forms when electrons are shared between elements

electron
a negatively charged particle that resides outside of the nucleus in the electron orbital; lacks functional mass and has a charge of –1

electron transfer
the movement of electrons from one element to another

element
one of 118 unique substances that cannot be broken down into smaller substances and retain the characteristic of that substance; each element has a specified number of protons and unique properties

hydrogen bond
a weak bond between partially positively charged hydrogen atoms and partially negatively charged elements or molecules

ion
an atom or compound that does not contain equal numbers of protons and electrons, and therefore has a net charge

ionic bond
a chemical bond that forms between ions of opposite charges

isotope
one or more forms of an element that have different numbers of neutrons

mass number
the number of protons plus neutrons in an atom

matter
anything that has mass and occupies space

neutron
a particle with no charge that resides in the nucleus of an atom; has a mass of 1

nonpolar covalent bond
a type of covalent bond that forms between atoms when electrons are shared equally between atoms, resulting in no regions with partial charges as in polar covalent bonds

nucleus
(chemistry) the dense center of an atom made up of protons and (except in the case of a hydrogen atom) neutrons

octet rule
states that the outermost shell of an element with a low atomic number can hold eight electrons

periodic table of elements
an organizational chart of elements, indicating the atomic number and mass number of each element; also provides key information about the properties of elements

polar covalent bond

a type of covalent bond in which electrons are pulled toward one atom and away from another, resulting in slightly positive and slightly negative charged regions of the molecule

proton

a positively charged particle that resides in the nucleus of an atom; has a mass of 1 and a charge of +1

radioactive isotope

an isotope that spontaneously emits particles or energy to form a more stable element

van der Waals interaction

a weak attraction or interaction between molecules caused by slightly positively charged or slightly negatively charged atoms

Contributors and Attributions

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2.2: Elements Found in Living Systems

Elements

Elements consist of only one kind of atom and cannot be decomposed into simpler substances. Our planet is made up of some **90 elements**. (Tiny amounts — sometimes only a few atoms — of additional elements have been made in nuclear physics laboratories, but they play no role in our story). Of these 90, only **25 or so** are used to build **living things**. The table shows the 11 most prevalent elements in the lithosphere (the earth's crust) and in the human body.

Living matter

- uses only a fraction of the elements available to it
- but, as the table shows, the relative proportions of those it does acquire from its surroundings are quite different from the proportions in the environment

So,

- the composition of living things is not simply a reflection of the elements available to them
  - For example, hydrogen, carbon, and nitrogen together represent less than 1% of the atoms found in the earth's crust but some 74% of the atoms in living matter.
- one of the properties of life is to take up certain elements that are scarce in the nonliving world and concentrate them within living cells.

  Some sea animals accumulate elements like vanadium and iodine within their cells to concentrations a thousand or more times as great as in the surrounding sea water. It has even been proposed that uranium be "mined" from the sea by extracting it from certain algae that can take up uranium from sea water and concentrate it within their cells.

Elemental composition of the lithosphere and the human body. Each number represents the percent of the total **number** of atoms present. For example, 47 of every 100 atoms found in a representative sample of the lithosphere are oxygen while there are only 19 atoms of carbon in every 10,000 atoms of lithosphere.

Composition of the Lithosphere		**Composition of the Human Body**	
Oxygen	47	Hydrogen	63
Silicon	28	Oxygen	25.5
Aluminum	7.9	Carbon	9.5
Iron	4.5	Nitrogen	1.4
Calcium	3.5	Calcium	0.31
Sodium	2.5	Phosphorus	0.22
Potassium	2.5	Chlorine	0.03
Magnesium	2.2	Potassium	0.06
Titanium	0.46	Sulfur	0.05
Hydrogen	0.22	Sodium	0.03
Carbon	0.19	Magnesium	0.01
All others	<0.1	All others	<0.01

There is still some uncertainty about the exact number of elements required by living things. Some elements, e.g., aluminum, are found in tiny amounts in living tissue, but whether they are playing an essential role or are simply an accidental acquisition (aluminum probably is) is sometimes difficult to determine.

Atoms

Each element is made up of one kind of atom. We can define an atom as the smallest part of an element that can enter into combination with other elements.

Structure of the atom

Each atom consists of a small, dense, **positively-charged** nucleus surrounded by much lighter, **negatively-charged electrons**. The nucleus of the simplest atom, the **hydrogen atom** (**H**), consists of a single **positively-charged proton**. Because of its single proton, the atom of hydrogen is assigned an **atomic number** of **1 and a single electron.** The charge of the electron is the same magnitude as that of the proton, so the atom as a whole is electrically neutral. Its proton accounts for almost all the weight of the atom.

The nucleus of the atom of the element **helium** (**He**) has **two protons** (hence helium has an **atomic number** of **2**) and **two neutrons**. Neutrons have the same weight as protons but no electrical charge. The helium atom has **two electrons** so that, once again, the atom as a whole is neutral.

The structure of each of the other kinds of atoms follows the same plan. From Lithium (At. No. = 3) to uranium (At. No. = 92), the atoms of each element can be listed in order of increasing atomic number. There are no gaps in the list. Each element has a unique atomic number and its atoms have one more proton and one more electron than the atoms of the element that precedes it in the list.

Electrons

Electrons are confined to relatively discrete regions around the nucleus. The two electrons of helium, for example, are confined to a spherical zone surrounding the nucleus called the **K shell** or **K energy level**.

Atomic Number	Element	Energy Levels or "shells"				
		K	L	M	N	O
1	Hydrogen (**H**)	1				
2	Helium (**He**)	2				
3	Lithium (**Li**)	2	1			
4	Beryllium (**Be**)	2	2			
5	Boron (**B**)	2	3			
6	Carbon (**C**)	2	4			
7	Nitrogen (**N**)	2	5			
8	Oxygen (**O**)	2	6			
9	Fluorine (**F**)	2	7			
10	Neon (**Ne**)	2	8			
11	Sodium (**Na**)	2	8	1		
12	Magnesium (**Mg**)	2	8	2		
13	Aluminum (**Al**)	2	8	3		
14	Silicon (**Si**)	2	8	4		
15	Phosphorus (**P**)	2	8	5		
16	Sulfur (**S**)	2	8	6		
17	Chlorine (**Cl**)	2	8	7		
18	Argon (**Ar**)	2	8	8		
19	Potassium (**K**)	2	8	8	1	
20	Calcium (**Ca**)	2	8	8	2	
21	Scandium (**Sc**)	2	8	9	2	
22	Titanium (**Ti**)	2	8	10	2	
23	Vanadium (**V**)	2	8	11	2	
24	Chromium (**Cr**)	2	8	13	1	
25	Manganese (**Mn**)	2	8	13	2	
26	Iron (**Fe**)	2	8	14	2	
27	Cobalt (**Co**)	2	8	15	2	
28	Nickel (**Ni**)	2	8	16	2	
29	Copper (**Cu**)	2	8	18	1	
30	Zinc (**Zn**)	2	8	18	2	

Atomic Number	Element	Energy Levels or "shells"				
31	Gallium (**Ga**)	2	8	18	3	
32	Germanium (**Ge**)	2	8	18	4	
33	Arsenic (**As**)	2	8	18	5	
34	Selenium (**Se**)	2	8	18	6	
35	Bromine (**Br**)	2	8	18	7	
36	Krypton (**Kr**)	2	8	18	8	
42	Molybdenum (**Mo**)	2	8	18	13	1
48	Cadmium (**Cd**)	2	8	18	18	2
50	Tin (**Sn**)	2	8	18	18	4
53	Iodine (**I**)	2	8	18	18	7

Lithium (At. No. = 3) has three electrons, two in the K shell and one located farther from the nucleus in the **L shell**. Being farther away from the opposite (+) charges of the nucleus, this third electron is held less tightly.

Each of the following elements, in order of increasing atomic number, adds one more electron to the L shell until we reach neon (At. No. = 10) which has eight electrons in the L shell.

Sodium places its eleventh electron in a still higher energy level, the **M shell**.

From sodium to **argon**, this shell is gradually filled with electrons until, once again, a maximum of eight is reached.

Note that after the K shell with its maximum of two electrons, the maximum number of electrons in any other **outermost** shell is **eight**.

As we shall see, the **chemical properties** of each element are strongly influenced by the **number of electrons in its outermost energy level** (shell).

This table shows the electronic structure of the atoms of elements 1 – 36 with those that have been demonstrated to be used by living things **shown in red**. Four elements of still higher atomic numbers that have been shown to be used by living things are also included.

The electronic structure of an atom plays the major role in its chemistry.

The pattern of electrons in an atom — especially those in the outermost shell — determines

- the **valence** of the atom; that is, the ratios with which it interacts with other atoms, and to a large degree,
- the **electronegativity** of the atom; that is, the strength with which it attracts other electrons.

Elements with the same number of electrons in their outermost shell show similar chemical properties.

Example 1: Fluorine, **chlorine**, **bromine**, and **iodine** each have 7 electrons in their outermost shell. These so-called **halogens** are also quite similar in their chemical behavior. When dissolved in water, for example, they all produce germicidal solutions.

Example 2: Those elements with 1, 2, or 3 electrons in their outermost shell are the **metals**.

Example 3: Those elements with 4, 5, 6, or 7 in their outermost shell are the **nonmetals**.

Example 4: Helium (with its 2), **neon**, **argon**, and **krypton** (each with 8) have "filled" their outermost shells. They are the so-called inert or "noble" gases. They have no chemistry at all. Under normal conditions they do not interact with other atoms. So, it is the number and arrangement of the electrons in the atoms of an element that establish the chemical behavior of that element.

This is how it works:

The atoms of an element interact with other atoms in such ways and ratios that they can "fill" their outermost shell with **8 electrons** (2 for hydrogen). They may do this by

- acquiring more electrons from another atom
- losing electrons to another atom
- sharing electrons with another atom

The number of electrons that an atom must acquire, or lose, or share to reach a stable configuration of 8 (2 for hydrogen) is called its **valence**.

Hydrogen, lithium, sodium, and potassium atoms all have a single electron in their outermost shell. Fluorine, chlorine, bromine, and iodine atoms all have 7. Any atom of the first group will interact with a single atom of any of the second group forming, HCl, NaCl, KI, etc. The result of all of these interactions is a pair of atoms each with an outermost shell like that of one of the inert gases: 2 for hydrogen, 8 for the others.

The elements with 2 electrons in their outermost shell interact with chlorine and the other halogens to form, e.g., $BeCl_2$, $MgCl_2$, $CaCl_2$. Again, the result is a pair of atoms each with a stable octet of electrons in its outermost shell.

The elements with 3 electrons in their outermost shell will interact with chlorine in a ratio of 1:3, forming BCl_3, $AlCl_3$.

Carbon atoms, with their 4 electrons in the L shell interact with chlorine to form CCl_4.

Nitrogen, with its 5 outermost electrons, interacts with hydrogen atoms in a ratio of 1:3, forming ammonia (NH_3).

Oxygen and **sulfur**, with their 6 outermost electrons react with hydrogen to form water (H_2O) and hydrogen sulfide (H_2S).

What determines whether a pair of atoms swap or share electrons?

The answer is their **relative electronegativities**. If two atoms differ greatly in their affinity for electrons; that is, in their electronegativity, then the strongly electronegative atom will take the electron away from the weakly electronegative one.

Example: Na (weakly electronegative) gives up its single electron to an atom of chlorine (strongly electronegative) to form NaCl. The sodium atom now has only 10 electrons but still 11 protons so there is a net positive charge of one on the atom. Similarly, chlorine now has one more electron than proton so its now has a net negative charge of 1. Electrically charged atoms are called **ions**. The mutual attraction of opposite electrical charges holds the ions together by **ionic bonds**.

Example: Carbon and hydrogen are both only weakly electronegative so neither can remove electrons from the other. Instead they achieve a stable configuration by sharing their outermost electrons forming **covalent bonds** of CH_4.

Isotopes

The number of protons in the nucleus of its atoms, which is its **atomic number**, defines each element. However, the nuclei of a given element may have varying numbers of neutrons. Because neutrons have weight (about the same as that of protons), such atoms differ in the **atomic weight**.

Atoms of the same element that differ in their atomic weight are called **isotopes**.

Atomic weights are expressed in terms of a standard atom: the isotope of carbon that has 6 protons and 6 neutrons in its nucleus. This atom is designated **carbon-12** or $\mathbf{^{12}C}$. It is arbitrarily assigned an atomic weight of 12 **daltons** (named after John Dalton, the pioneer in the study of atomic weights). Thus a dalton is 1/12 the weight of an atom of ^{12}C. Both protons and neutrons have weights very close to 1 dalton each. Carbon-12 is the most common isotope of carbon. Carbon-13 (^{13}C) with 6 protons and 7 neutrons, and carbon-14 (^{14}C) with 6 protons and 8 neutrons are found in much smaller quantities.

Isotopes as "tracers"

One can prepare, for example, a carbon compound used by living things that has many of its normal ^{12}C atoms replaced by ^{14}C atoms. Carbon-14 happens to be radioactive. By tracing the fate of radioactivity within the organism, one can learn the normal pathway of this carbon compound in that organism. Thus ^{14}C serves as an isotopic "label" or "tracer".

The basis of this technique is that the weight of the nucleus of an atom has little or no effect on the chemical properties of that atom. The chemistry of an element and the atoms of which it is made — whatever their atomic weight — is a function of the

atomic number of that element. As long as the atom had 6 protons, it is an atom of carbon irrespective of the number of neutrons. Thus while 6 protons and 8 neutrons produce an isotope of carbon, ^{14}C, 7 protons and 7 neutrons produce a totally-different element, nitrogen-14.

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SECTION OVERVIEW

2.3: The Nature of Chemical Bonds

At its most fundamental level, life is made up of matter. Matter occupies space and has mass. All matter is composed of elements, substances that cannot be broken down or transformed chemically into other substances. Each element is made of atoms, each with a constant number of protons and unique properties. A total of 118 elements have been defined; however, only 92 occur naturally, and fewer than 30 are found in living cells. The remaining 26 elements are unstable and, therefore, do not exist for very long or are theoretical and have yet to be detected.

Each element is designated by its chemical symbol (such as H, N, O, C, and Na), and possesses unique properties. These unique properties allow elements to combine and to bond with each other in specific ways.

Atoms

An atom is the smallest component of an element that retains all of the chemical properties of that element. For example, one hydrogen atom has all of the properties of the element hydrogen, such as it exists as a gas at room temperature, and it bonds with oxygen to create a water molecule. Hydrogen atoms cannot be broken down into anything smaller while still retaining the properties of hydrogen. If a hydrogen atom were broken down into subatomic particles, it would no longer have the properties of hydrogen.

At the most basic level, all organisms are made of a combination of elements. They contain atoms that combine together to form molecules. In multicellular organisms, such as animals, molecules can interact to form cells that combine to form tissues, which make up organs. These combinations continue until entire multicellular organisms are formed.

All atoms contain protons, electrons, and neutrons (Figure **2.3.1**). The only exception is hydrogen (H), which is made of one proton and one electron. A proton is a positively charged particle that resides in the nucleus (the core of the atom) of an atom and has a mass of 1 and a charge of +1. An electron is a negatively charged particle that travels in the space around the nucleus. In other words, it resides outside of the nucleus. It has a negligible mass and has a charge of –1.

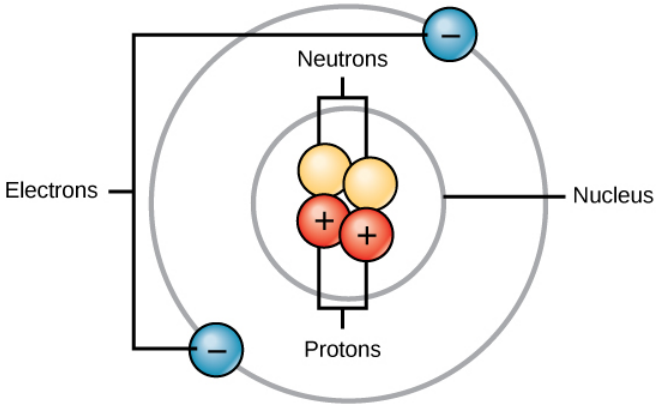


Figure 2.3.1: Atoms are made up of protons and neutrons located within the nucleus, and electrons surrounding the nucleus.

Neutrons, like protons, reside in the nucleus of an atom. They have a mass of 1 and no charge. The positive (protons) and negative (electrons) charges balance each other in a neutral atom, which has a net zero charge.

Because protons and neutrons each have a mass of 1, the mass of an atom is equal to the number of protons and neutrons of that atom. The number of electrons does not factor into the overall mass, because their mass is so small.

As stated earlier, each element has its own unique properties. Each contains a different number of protons and neutrons, giving it its own atomic number and mass number. The atomic number of an element is equal to the number of protons that element contains. The mass number, or atomic mass, is the number of protons plus the number of neutrons of that element. Therefore, it is possible to determine the number of neutrons by subtracting the atomic number from the mass number.

These numbers provide information about the elements and how they will react when combined. Different elements have different melting and boiling points, and are in different states (liquid, solid, or gas) at room temperature. They also combine in different ways. Some form specific types of bonds, whereas others do not. How they combine is based on the number of electrons present. Because of these characteristics, the elements are arranged into the periodic table of elements, a chart of the elements that includes the atomic number and relative atomic mass of each element. The periodic table also provides key information about the properties of elements (Figure **2.3.2**)—often indicated by color-coding. The arrangement of the table also shows how the electrons in each element are organized and provides important details about how atoms will react with each other to form molecules.

Isotopes are different forms of the same element that have the same number of protons, but a different number of neutrons. Some elements, such as carbon, potassium, and uranium, have naturally occurring isotopes. Carbon-12, the most common isotope of carbon, contains six protons and six neutrons. Therefore, it has a mass number of 12 (six protons and six neutrons) and an atomic number of 6 (which makes it carbon). Carbon-14 contains six protons and eight neutrons. Therefore, it has a mass number of 14 (six protons and eight neutrons) and an atomic number of 6, meaning it is still the element carbon. These two alternate forms of carbon are isotopes. Some isotopes are unstable and will lose protons, other subatomic particles, or energy to form more stable elements. These are called radioactive isotopes or radioisotopes.

ART CONNECTION

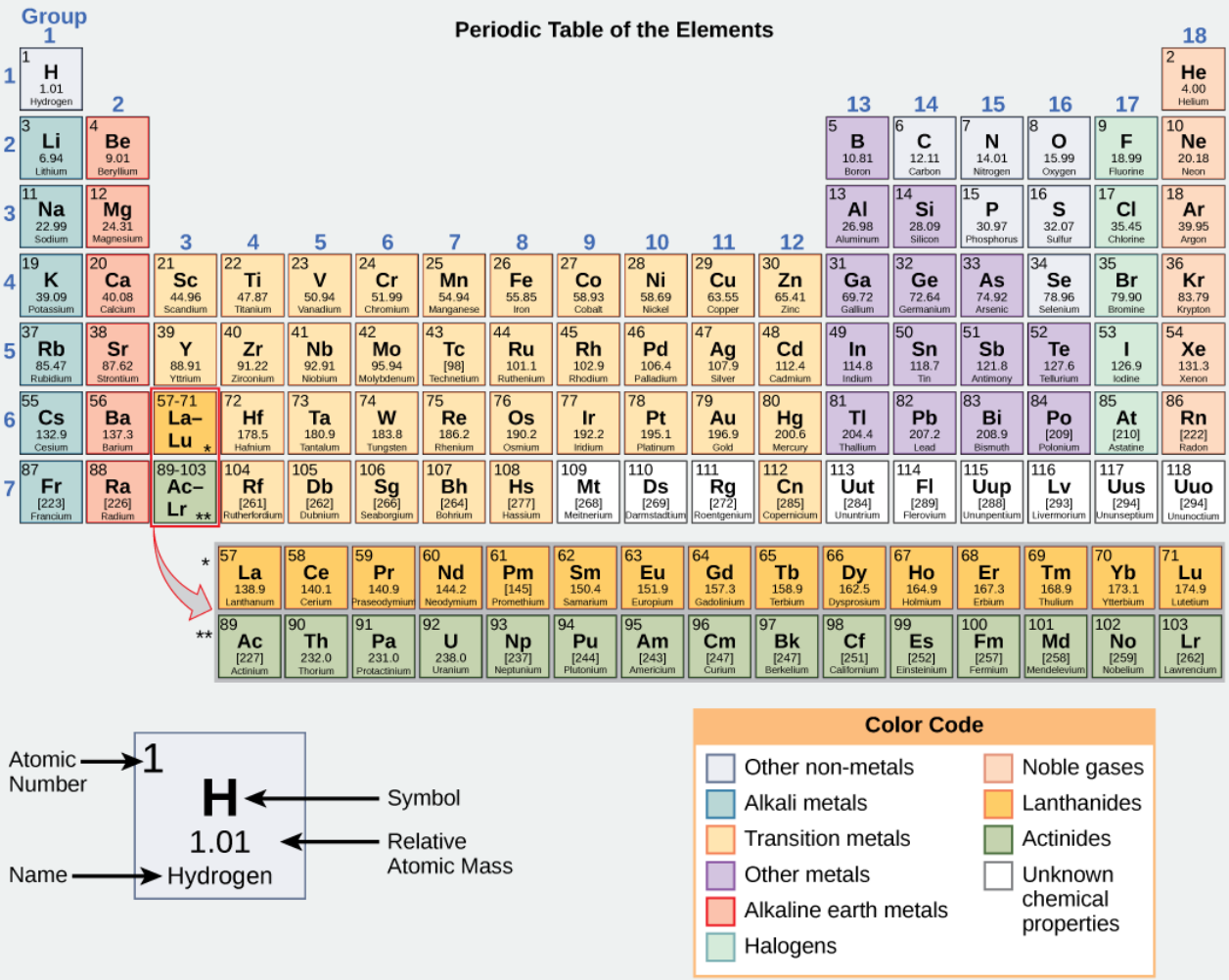


Figure 2.3.2: Arranged in columns and rows based on the characteristics of the elements, the periodic table provides key information about the elements and how they might interact with each other to form molecules. Most periodic tables provide a key or legend to the information they contain.

How many neutrons do (K) potassium-39 and potassium-40 have, respectively?

EVOLUTION IN ACTION: Carbon Dating

Carbon-14 (^{14}C) is a naturally occurring radioisotope that is created in the atmosphere by cosmic rays. This is a continuous process, so more ^{14}C is always being created. As a living organism develops, the relative level of ^{14}C in its body is equal to the concentration of ^{14}C in the atmosphere. When an organism dies, it is no longer ingesting ^{14}C, so the ratio will decline. ^{14}C decays to ^{14}N by a process called beta decay; it gives off energy in this slow process.

After approximately 5,730 years, only one-half of the starting concentration of ^{14}C will have been converted to ^{14}N. The time it takes for half of the original concentration of an isotope to decay to its more stable form is called its half-life. Because the half-life of ^{14}C is long, it is used to age formerly living objects, such as fossils. Using the ratio of the ^{14}C concentration found in an object to the amount of ^{14}C detected in the atmosphere, the amount of the isotope that has not yet decayed can be determined. Based on this amount, the age of the fossil can be calculated to about 50,000 years (Figure **2.3.3**). Isotopes with longer half-lives, such as potassium-40, are used to calculate the ages of older fossils. Through the use of carbon dating, scientists can reconstruct the ecology and biogeography of organisms living within the past 50,000 years.



Figure 2.3.3: The age of remains that contain carbon and are less than about 50,000 years old, such as this pygmy mammoth, can be determined using carbon dating. (credit: Bill Faulkner/NPS)

CONCEPT IN ACTION

To learn more about atoms and isotopes, and how you can tell one isotope from another, visit this site and run the simulation.

Chemical Bonds

How elements interact with one another depends on how their electrons are arranged and how many openings for electrons exist at the outermost region where electrons are present in an atom. Electrons exist at energy levels that form shells around the nucleus. The closest shell can hold up to two electrons. The closest shell to the nucleus is always filled first, before any other shell can be filled. Hydrogen has one electron; therefore, it has only one spot occupied within the lowest shell. Helium has two electrons; therefore, it can completely fill the lowest shell with its two electrons. If you look at the periodic table, you will see that hydrogen and helium are the only two elements in the first row. This is because they only have electrons in their first shell. Hydrogen and helium are the only two elements that have the lowest shell and no other shells.

The second and third energy levels can hold up to eight electrons. The eight electrons are arranged in four pairs and one position in each pair is filled with an electron before any pairs are completed.

Looking at the periodic table again (Figure **2.3.2**), you will notice that there are seven rows. These rows correspond to the number of shells that the elements within that row have. The elements within a particular row have increasing numbers of electrons as the columns proceed from left to right. Although each element has the same number of shells, not all of the shells are completely filled with electrons. If you look at the second row of the periodic table, you will find lithium (Li), beryllium (Be), boron (B), carbon (C), nitrogen (N), oxygen (O), fluorine (F), and neon (Ne). These all have electrons that occupy only the first and second shells. Lithium

has only one electron in its outermost shell, beryllium has two electrons, boron has three, and so on, until the entire shell is filled with eight electrons, as is the case with neon.

Not all elements have enough electrons to fill their outermost shells, but an atom is at its most stable when all of the electron positions in the outermost shell are filled. Because of these vacancies in the outermost shells, we see the formation of chemical bonds, or interactions between two or more of the same or different elements that result in the formation of molecules. To achieve greater stability, atoms will tend to completely fill their outer shells and will bond with other elements to accomplish this goal by sharing electrons, accepting electrons from another atom, or donating electrons to another atom. Because the outermost shells of the elements with low atomic numbers (up to calcium, with atomic number 20) can hold eight electrons, this is referred to as the octet rule. An element can donate, accept, or share electrons with other elements to fill its outer shell and satisfy the octet rule.

When an atom does not contain equal numbers of protons and electrons, it is called an ion. Because the number of electrons does not equal the number of protons, each ion has a net charge. Positive ions are formed by losing electrons and are called cations. Negative ions are formed by gaining electrons and are called anions.

For example, sodium only has one electron in its outermost shell. It takes less energy for sodium to donate that one electron than it does to accept seven more electrons to fill the outer shell. If sodium loses an electron, it now has 11 protons and only 10 electrons, leaving it with an overall charge of +1. It is now called a sodium ion.

The chlorine atom has seven electrons in its outer shell. Again, it is more energy-efficient for chlorine to gain one electron than to lose seven. Therefore, it tends to gain an electron to create an ion with 17 protons and 18 electrons, giving it a net negative (–1) charge. It is now called a chloride ion. This movement of electrons from one element to another is referred to as electron transfer. As Figure **2.3.4** illustrates, a sodium atom (Na) only has one electron in its outermost shell, whereas a chlorine atom (Cl) has seven electrons in its outermost shell. A sodium atom will donate its one electron to empty its shell, and a chlorine atom will accept that electron to fill its shell, becoming chloride. Both ions now satisfy the octet rule and have complete outermost shells. Because the number of electrons is no longer equal to the number of protons, each is now an ion and has a +1 (sodium) or –1 (chloride) charge.

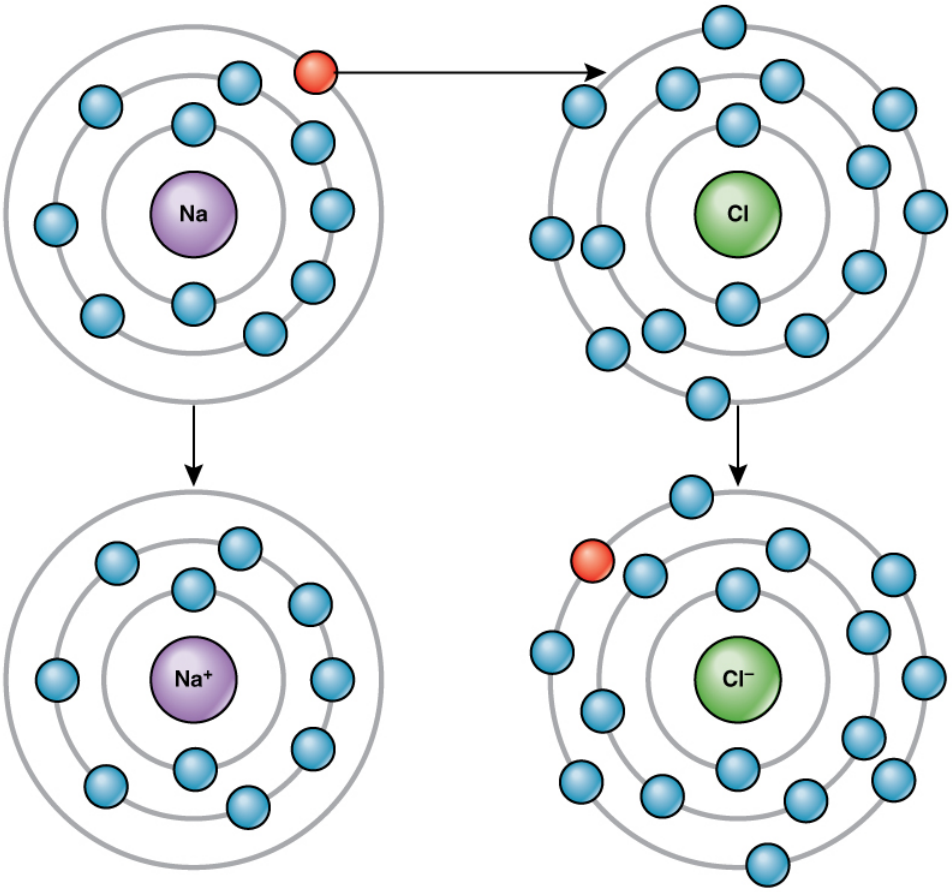


Figure 2.3.4: Elements tend to fill their outermost shells with electrons. To do this, they can either donate or accept electrons from other elements.

Ionic Bonds

There are four types of bonds or interactions: ionic, covalent, hydrogen bonds, and van der Waals interactions. Ionic and covalent bonds are strong interactions that require a larger energy input to break apart. When an element donates an electron from its outer shell, as in the sodium atom example above, a positive ion is formed. The element accepting the electron is now negatively charged. Because positive and negative charges attract, these ions stay together and form an ionic bond, or a bond between ions. The elements bond together with the electron from one element staying predominantly with the other element. When Na^+ and Cl^- ions combine to produce NaCl, an electron from a sodium atom stays with the other seven from the chlorine atom, and the sodium and chloride ions attract each other in a lattice of ions with a net zero charge.

Covalent Bonds

Another type of strong chemical bond between two or more atoms is a covalent bond. These bonds form when an electron is shared between two elements and are the strongest and most common form of chemical bond in living organisms. Covalent bonds form between the elements that make up the biological molecules in our cells. Unlike ionic bonds, covalent bonds do not dissociate in water.

The hydrogen and oxygen atoms that combine to form water molecules are bound together by covalent bonds. The electron from the hydrogen atom divides its time between the outer shell of the hydrogen atom and the incomplete outer shell of the oxygen atom. To completely fill the outer shell of an oxygen atom, two electrons from two hydrogen atoms are needed, hence the subscript “2” in H_2O. The electrons are shared between the atoms, dividing their time between them to “fill” the outer shell of each. This sharing is a lower energy state for all of the atoms involved than if they existed without their outer shells filled.

There are two types of covalent bonds: polar and nonpolar. Nonpolar covalent bonds form between two atoms of the same element or between different elements that share the electrons equally. For example, an oxygen atom can bond with another oxygen atom to fill their outer shells. This association is nonpolar because the electrons will be equally distributed between each oxygen atom. Two

covalent bonds form between the two oxygen atoms because oxygen requires two shared electrons to fill its outermost shell. Nitrogen atoms will form three covalent bonds (also called triple covalent) between two atoms of nitrogen because each nitrogen atom needs three electrons to fill its outermost shell. Another example of a nonpolar covalent bond is found in the methane (CH_4) molecule. The carbon atom has four electrons in its outermost shell and needs four more to fill it. It gets these four from four hydrogen atoms, each atom providing one. These elements all share the electrons equally, creating four nonpolar covalent bonds (Figure **2.3.5**).

In a polar covalent bond, the electrons shared by the atoms spend more time closer to one nucleus than to the other nucleus. Because of the unequal distribution of electrons between the different nuclei, a slightly positive (δ+) or slightly negative (δ–) charge develops. The covalent bonds between hydrogen and oxygen atoms in water are polar covalent bonds. The shared electrons spend more time near the oxygen nucleus, giving it a small negative charge, than they spend near the hydrogen nuclei, giving these molecules a small positive charge.

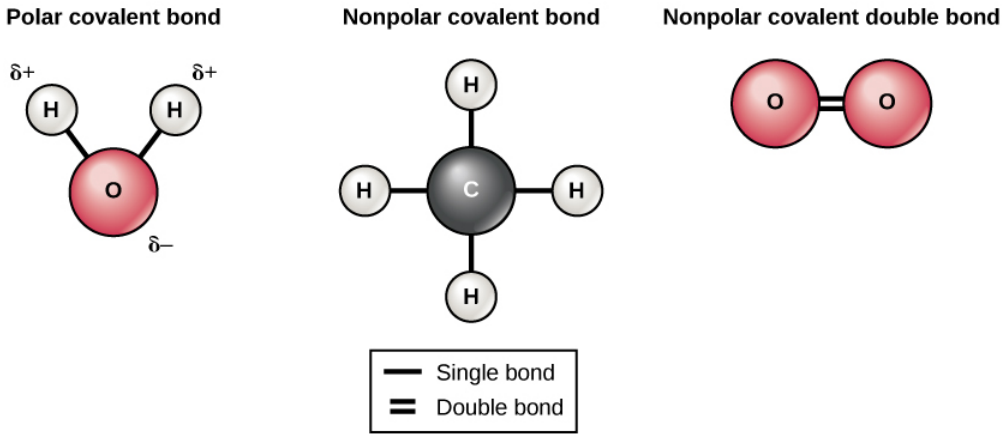


Figure 2.3.5: The water molecule (left) depicts a polar bond with a slightly positive charge on the hydrogen atoms and a slightly negative charge on the oxygen. Examples of nonpolar bonds include methane (middle) and oxygen (right).

Hydrogen Bonds

Ionic and covalent bonds are strong bonds that require considerable energy to break. However, not all bonds between elements are ionic or covalent bonds. Weaker bonds can also form. These are attractions that occur between positive and negative charges that do not require much energy to break. Two weak bonds that occur frequently are hydrogen bonds and van der Waals interactions. These bonds give rise to the unique properties of water and the unique structures of DNA and proteins.

When polar covalent bonds containing a hydrogen atom form, the hydrogen atom in that bond has a slightly positive charge. This is because the shared electron is pulled more strongly toward the other element and away from the hydrogen nucleus. Because the hydrogen atom is slightly positive (δ+), it will be attracted to neighboring negative partial charges (δ–). When this happens, a weak interaction occurs between the δ+ charge of the hydrogen atom of one molecule and the δ– charge of the other molecule. This interaction is called a hydrogen bond. This type of bond is common; for example, the liquid nature of water is caused by the hydrogen bonds between water molecules (Figure **2.3.6**). Hydrogen bonds give water the unique properties that sustain life. If it were not for hydrogen bonding, water would be a gas rather than a liquid at room temperature.

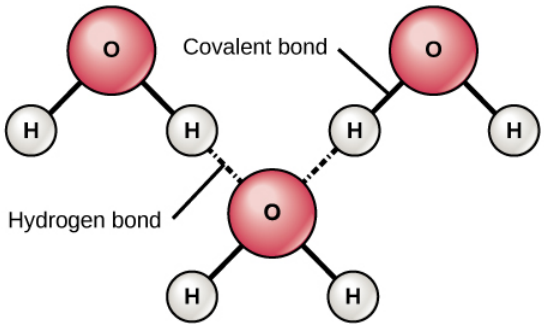


Figure 2.3.6: Hydrogen bonds form between slightly positive (δ+) and slightly negative (δ–) charges of polar covalent molecules, such as water.

Hydrogen bonds can form between different molecules and they do not always have to include a water molecule. Hydrogen atoms in polar bonds within any molecule can form bonds with other adjacent molecules. For example, hydrogen bonds hold together two long strands of DNA to give the DNA molecule its characteristic double-stranded structure. Hydrogen bonds are also responsible for some of the three-dimensional structure of proteins.

van der Waals Interactions

Like hydrogen bonds, van der Waals interactions are weak attractions or interactions between molecules. They occur between polar, covalently bound, atoms in different molecules. Some of these weak attractions are caused by temporary partial charges formed when electrons move around a nucleus. These weak interactions between molecules are important in biological systems.

CAREERS IN ACTION: Radiography Technician

Have you or anyone you know ever had a magnetic resonance imaging (MRI) scan, a mammogram, or an X-ray? These tests produce images of your soft tissues and organs (as with an MRI or mammogram) or your bones (as happens in an X-ray) by using either radiowaves or special isotopes (radiolabeled or fluorescently labeled) that are ingested or injected into the body. These tests provide data for disease diagnoses by creating images of your organs or skeletal system.

MRI imaging works by subjecting hydrogen nuclei, which are abundant in the water in soft tissues, to fluctuating magnetic fields, which cause them to emit their own magnetic field. This signal is then read by sensors in the machine and interpreted by a computer to form a detailed image.

Some radiography technologists and technicians specialize in computed tomography, MRI, and mammography. They produce films or images of the body that help medical professionals examine and diagnose. Radiologists work directly with patients, explaining machinery, preparing them for exams, and ensuring that their body or body parts are positioned correctly to produce the needed images. Physicians or radiologists then analyze the test results.

Radiography technicians can work in hospitals, doctors' offices, or specialized imaging centers. Training to become a radiography technician happens at hospitals, colleges, and universities that offer certificates, associate's degrees, or bachelor's degrees in radiography.

Summary

Matter is anything that occupies space and has mass. It is made up of atoms of different elements. All of the 92 elements that occur naturally have unique qualities that allow them to combine in various ways to create compounds or molecules. Atoms, which consist of protons, neutrons, and electrons, are the smallest units of an element that retain all of the properties of that element. Electrons can be donated or shared between atoms to create bonds, including ionic, covalent, and hydrogen bonds, as well as van der Waals interactions.

Art Connections

Figure 2.3.2: How many neutrons do (K) potassium-39 and potassium-40 have, respectively?

Answer

Potassium-39 has twenty neutrons. Potassium-40 has twenty one neutrons.

Glossary

anion
a negative ion formed by gaining electrons

atomic number
the number of protons in an atom

cation
a positive ion formed by losing electrons

chemical bond
an interaction between two or more of the same or different elements that results in the formation of molecules

covalent bond
a type of strong bond between two or more of the same or different elements; forms when electrons are shared between elements

electron
a negatively charged particle that resides outside of the nucleus in the electron orbital; lacks functional mass and has a charge of –1

electron transfer
the movement of electrons from one element to another

element
one of 118 unique substances that cannot be broken down into smaller substances and retain the characteristic of that substance; each element has a specified number of protons and unique properties

hydrogen bond
a weak bond between partially positively charged hydrogen atoms and partially negatively charged elements or molecules

ion
an atom or compound that does not contain equal numbers of protons and electrons, and therefore has a net charge

ionic bond
a chemical bond that forms between ions of opposite charges

isotope
one or more forms of an element that have different numbers of neutrons

mass number
the number of protons plus neutrons in an atom

matter
anything that has mass and occupies space

neutron
a particle with no charge that resides in the nucleus of an atom; has a mass of 1

nonpolar covalent bond
a type of covalent bond that forms between atoms when electrons are shared equally between atoms, resulting in no regions with partial charges as in polar covalent bonds

nucleus
(chemistry) the dense center of an atom made up of protons and (except in the case of a hydrogen atom) neutrons

octet rule
states that the outermost shell of an element with a low atomic number can hold eight electrons

periodic table of elements
an organizational chart of elements, indicating the atomic number and mass number of each element; also provides key information about the properties of elements

polar covalent bond

a type of covalent bond in which electrons are pulled toward one atom and away from another, resulting in slightly positive and slightly negative charged regions of the molecule

proton

a positively charged particle that resides in the nucleus of an atom; has a mass of 1 and a charge of +1

radioactive isotope

an isotope that spontaneously emits particles or energy to form a more stable element

van der Waals interaction

a weak attraction or interaction between molecules caused by slightly positively charged or slightly negatively charged atoms

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2.3.1: Electronegativity and types of Chemical Bonds

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SECTION OVERVIEW

2.3.1: Electronegativity and types of Chemical Bonds

Electronegativity

The electronegativity of an atom is a measure of its affinity for electrons. The atoms of the various elements differ in their affinity for electrons.

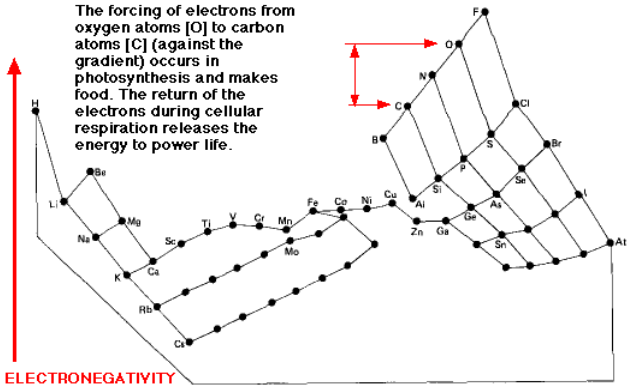


Figure **2.3.1.1**

This image distorts the conventional periodic table of the elements so that the greater the electronegativity of an atom, the higher its position in the table. Although fluorine (F) is the most electronegative element, it is the electronegativity of runner-up oxygen (O) that is exploited by life. The shuttling of electrons between carbon (C) and oxygen (O) atoms powers life.

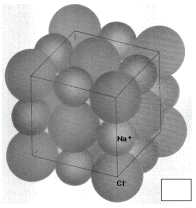
1. Moving electrons against the gradient (O to C) — as occurs in photosynthesis — requires energy (and stores it).
2. Moving electrons down the gradient (C to O) — as occurs in cellular respiration — releases energy.

The relative electronegativity of two interacting atoms also plays a major part in determining what kind of chemical bond forms between them.

Chemical Bonds

Three main types of chemical bonds:Ionic Bond, Covalent Bond, Polar Covalent Bond.

Ionic Bond



Example of an ionic bond is : Sodium (Na) and Chlorine (Cl) = Ionic Bond. There is a large difference in electronegativity between Na and Cl atoms, so

- the chlorine atom takes an electron from the sodium atom
- converting the atoms into **ions** (Na^{+}) and (Cl^{-})
- These are held together by their opposite electrical charge forming **ionic bonds**
- Each sodium ion is held by 6 chloride ions while each chloride ion is, in turn, held by 6 sodium ions
- Result: a **crystal lattice** (not molecules) of common table salt (NaCl)

Covalent Bond

Example of a covalent bond is: Carbon (C) and Hydrogen (H) = Covalent Bond. There is only a small difference in electronegativity between the C and H atoms, so

- the two atoms share the electrons
- Result: a **covalent bond** (depicted as C**:**H or C-H)
- The atoms are held together by their mutual affinity for their shared electrons
- An array of atoms held together by covalent bonds forms a true **molecule**

Polar Covalent Bond

Example of a polar covalent bond is: Hydrogen (H) and Oxygen (O) = Polar Covalent Bond. There is a moderate difference in electronegativity, causing the oxygen atom to pull the electron of the hydrogen atom closer to itself. This results in a **polar covalent bond. Oxygen does this with 2 hydrogen atoms to form a molecule of water**

Molecules, like water, with polar covalent bonds are themselves polar; that is, have partial electrical charges across the molecule and may be attracted to each other (as occurs with water molecules). These species are good solvents for polar and/or hydrophilic compounds may form hydrogen bonds.

Topic hierarchy

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2.4: Water- A Vital Compound

Do you ever wonder why scientists spend time looking for water on other planets? It is because water is essential to life; even minute traces of it on another planet can indicate that life could or did exist on that planet. Water is one of the more abundant molecules in living cells and the one most critical to life as we know it. Approximately 60–70 percent of your body is made up of water. Without it, life simply would not exist.

Water Is Polar

The hydrogen and oxygen atoms within water molecules form polar covalent bonds. The shared electrons spend more time associated with the oxygen atom than they do with hydrogen atoms. There is no overall charge to a water molecule, but there is a slight positive charge on each hydrogen atom and a slight negative charge on the oxygen atom. Because of these charges, the slightly positive hydrogen atoms repel each other and form the unique shape seen in Figure 2.1.6. Each water molecule attracts other water molecules because of the positive and negative charges in the different parts of the molecule. Water also attracts other polar molecules (such as sugars), forming hydrogen bonds. When a substance readily forms hydrogen bonds with water, it can dissolve in water and is referred to as hydrophilic ("water-loving"). Hydrogen bonds are not readily formed with nonpolar substances like oils and fats (Figure **2.4.1**). These nonpolar compounds are hydrophobic ("water-fearing") and will not dissolve in water.



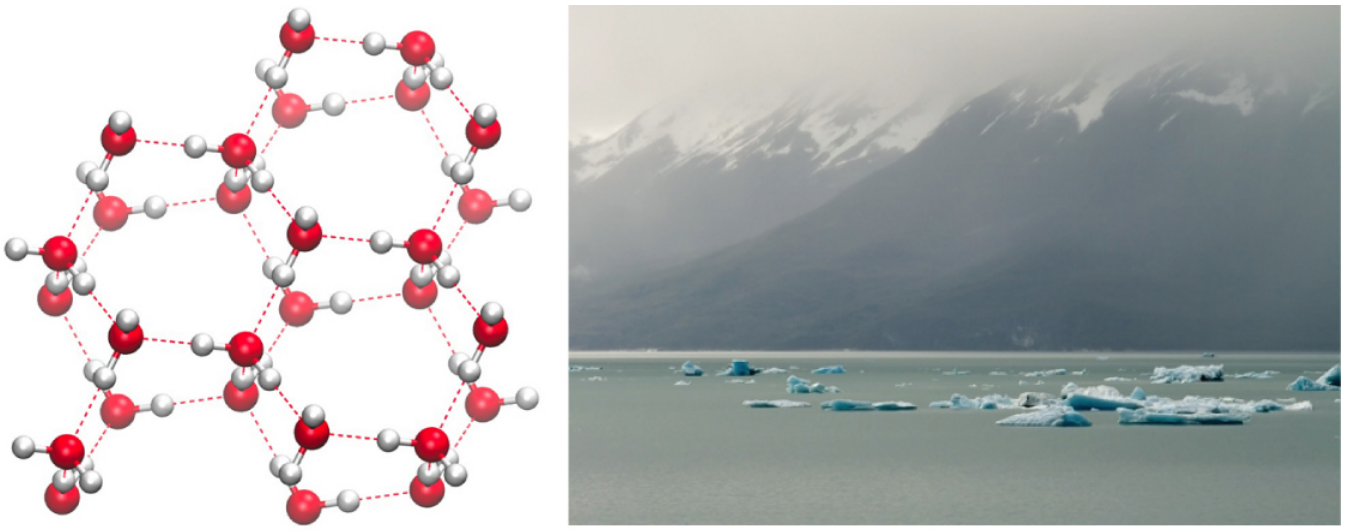
Figure 2.4.1: As this macroscopic image of oil and water show, oil is a nonpolar compound and, hence, will not dissolve in water. Oil and water do not mix. (credit: Gautam Dogra)

Water Stabilizes Temperature

The hydrogen bonds in water allow it to absorb and release heat energy more slowly than many other substances. Temperature is a measure of the motion (kinetic energy) of molecules. As the motion increases, energy is higher and thus temperature is higher. Water absorbs a great deal of energy before its temperature rises. Increased energy disrupts the hydrogen bonds between water molecules. Because these bonds can be created and disrupted rapidly, water absorbs an increase in energy and temperature changes only minimally. This means that water moderates temperature changes within organisms and in their environments. As energy input continues, the balance between hydrogen-bond formation and destruction swings toward the destruction side. More bonds are broken than are formed. This process results in the release of individual water molecules at the surface of the liquid (such as a body of water, the leaves of a plant, or the skin of an organism) in a process called evaporation. Evaporation of sweat, which is 90 percent water, allows for cooling of an organism, because breaking hydrogen bonds requires an input of energy and takes heat away from the body.

Conversely, as molecular motion decreases and temperatures drop, less energy is present to break the hydrogen bonds between water molecules. These bonds remain intact and begin to form a rigid, lattice-like structure (e.g., ice) (Figure **2.4.2a**). When frozen,

ice is less dense than liquid water (the molecules are farther apart). This means that ice floats on the surface of a body of water (Figure **2.4.2b**). In lakes, ponds, and oceans, ice will form on the surface of the water, creating an insulating barrier to protect the animal and plant life beneath from freezing in the water. If this did not happen, plants and animals living in water would freeze in a block of ice and could not move freely, making life in cold temperatures difficult or impossible.



(a) (b)

Figure 2.4.2: (a) The lattice structure of ice makes it less dense than the freely flowing molecules of liquid water. Ice's lower density enables it to (b) float on water. (credit a: modification of work by Jane Whitney; credit b: modification of work by Carlos Ponte)

CONCEPTS IN ACTION

Click here to see a 3-D animation of the structure of an ice lattice. (credit: image created by Jane Whitney using Visual Molecular Dynamics (VMD) software[1])

Water Is an Excellent Solvent

Because water is polar, with slight positive and negative charges, ionic compounds and polar molecules can readily dissolve in it. Water is, therefore, what is referred to as a solvent—a substance capable of dissolving another substance. The charged particles will form hydrogen bonds with a surrounding layer of water molecules. This is referred to as a sphere of hydration and serves to keep the particles separated or dispersed in the water. In the case of table salt (NaCl) mixed in water (Figure **2.4.3**), the sodium and chloride ions separate, or dissociate, in the water, and spheres of hydration are formed around the ions. A positively charged sodium ion is surrounded by the partially negative charges of oxygen atoms in water molecules. A negatively charged chloride ion is surrounded by the partially positive charges of hydrogen atoms in water molecules. These spheres of hydration are also referred to as hydration shells. The polarity of the water molecule makes it an effective solvent and is important in its many roles in living systems.

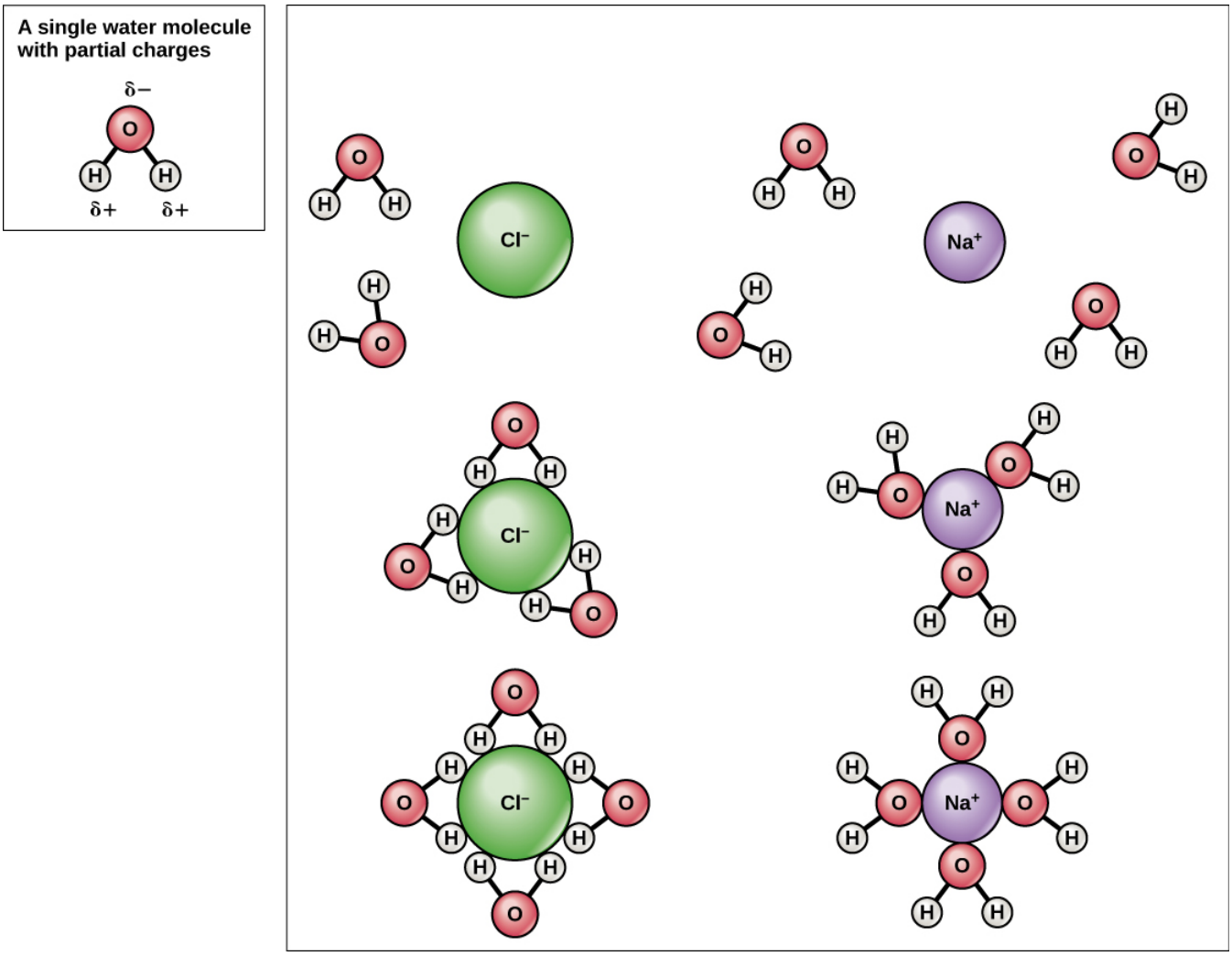


Figure 2.4.3: When table salt (NaCl) is mixed in water, spheres of hydration form around the ions.

Water Is Cohesive

Have you ever filled up a glass of water to the very top and then slowly added a few more drops? Before it overflows, the water actually forms a dome-like shape above the rim of the glass. This water can stay above the glass because of the property of cohesion. In cohesion, water molecules are attracted to each other (because of hydrogen bonding), keeping the molecules together at the liquid-air (gas) interface, although there is no more room in the glass. Cohesion gives rise to surface tension, the capacity of a substance to withstand rupture when placed under tension or stress. When you drop a small scrap of paper onto a droplet of water, the paper floats on top of the water droplet, although the object is denser (heavier) than the water. This occurs because of the surface tension that is created by the water molecules. Cohesion and surface tension keep the water molecules intact and the item floating on the top. It is even possible to "float" a steel needle on top of a glass of water if you place it gently, without breaking the surface tension (Figure **2.4.4**).



Figure 2.4.4: The weight of a needle on top of water pulls the surface tension downward; at the same time, the surface tension of the water is pulling it up, suspending the needle on the surface of the water and keeping it from sinking. Notice the indentation in the water around the needle. (credit: Cory Zanker)

These cohesive forces are also related to the water's property of adhesion, or the attraction between water molecules and other molecules. This is observed when water "climbs" up a straw placed in a glass of water. You will notice that the water appears to be higher on the sides of the straw than in the middle. This is because the water molecules are attracted to the straw and therefore adhere to it.

Cohesive and adhesive forces are important for sustaining life. For example, because of these forces, water can flow up from the roots to the tops of plants to feed the plant.

CONCEPT IN ACTION

To learn more about water, visit the U.S. Geological Survey Water Science for Schools: All About Water! website.

Buffers, pH, Acids, and Bases

The pH of a solution is a measure of its acidity or alkalinity. You have probably used litmus paper, paper that has been treated with a natural water-soluble dye so it can be used as a pH indicator, to test how much acid or base (alkalinity) exists in a solution. You might have even used some to make sure the water in an outdoor swimming pool is properly treated. In both cases, this pH test measures the amount of hydrogen ions that exists in a given solution. High concentrations of hydrogen ions yield a low pH, whereas low levels of hydrogen ions result in a high pH. The overall concentration of hydrogen ions is inversely related to its pH and can be measured on the pH scale (Figure **2.4.5**). Therefore, the more hydrogen ions present, the lower the pH; conversely, the fewer hydrogen ions, the higher the pH.

The pH scale ranges from 0 to 14. A change of one unit on the pH scale represents a change in the concentration of hydrogen ions by a factor of 10, a change in two units represents a change in the concentration of hydrogen ions by a factor of 100. Thus, small changes in pH represent large changes in the concentrations of hydrogen ions. Pure water is neutral. It is neither acidic nor basic, and has a pH of 7.0. Anything below 7.0 (ranging from 0.0 to 6.9) is acidic, and anything above 7.0 (from 7.1 to 14.0) is alkaline. The blood in your veins is slightly alkaline (pH = 7.4). The environment in your stomach is highly acidic (pH = 1 to 2). Orange juice is mildly acidic (pH = approximately 3.5), whereas baking soda is basic (pH = 9.0).

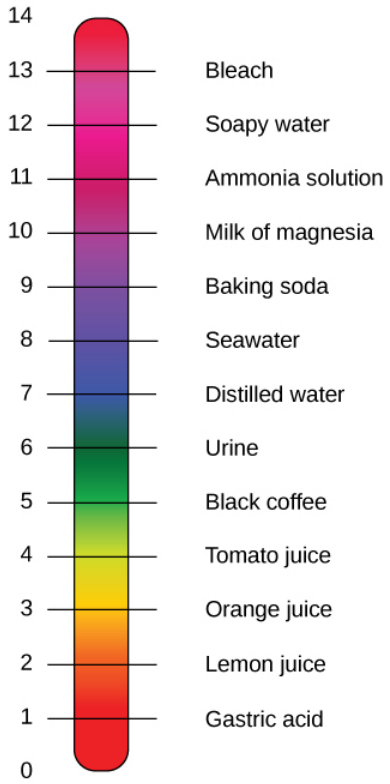


Figure 2.4.5: The pH scale measures the amount of hydrogen ions (H^+) in a substance. (credit: modification of work by Edward Stevens)

Acids are substances that provide hydrogen ions (H^+) and lower pH, whereas bases provide hydroxide ions (OH^-) and raise pH. The stronger the acid, the more readily it donates H^+. For example, hydrochloric acid and lemon juice are very acidic and readily give up H^+ when added to water. Conversely, bases are those substances that readily donate OH^-. The OH^- ions combine with H^+ to produce water, which raises a substance's pH. Sodium hydroxide and many household cleaners are very alkaline and give up OH^- rapidly when placed in water, thereby raising the pH.

Most cells in our bodies operate within a very narrow window of the pH scale, typically ranging only from 7.2 to 7.6. If the pH of the body is outside of this range, the respiratory system malfunctions, as do other organs in the body. Cells no longer function properly, and proteins will break down. Deviation outside of the pH range can induce coma or even cause death.

So how is it that we can ingest or inhale acidic or basic substances and not die? Buffers are the key. Buffersreadily absorb excess H^+ or OH^-, keeping the pH of the body carefully maintained in the aforementioned narrow range. Carbon dioxide is part of a prominent buffer system in the human body; it keeps the pH within the proper range. This buffer system involves carbonic acid (H_2CO_3) and bicarbonate (HCO_3^-) anion. If too much H^+ enters the body, bicarbonate will combine with the H^+ to create carbonic acid and limit the decrease in pH. Likewise, if too much OH^- is introduced into the system, carbonic acid will rapidly dissociate into bicarbonate and H^+ ions. The H^+ ions can combine with the OH^- ions, limiting the increase in pH. While carbonic acid is an important product in this reaction, its presence is fleeting because the carbonic acid is released from the body as carbon dioxide gas each time we breathe. Without this buffer system, the pH in our bodies would fluctuate too much and we would fail to survive.

Summary

Water has many properties that are critical to maintaining life. It is polar, allowing for the formation of hydrogen bonds, which allow ions and other polar molecules to dissolve in water. Therefore, water is an excellent solvent. The hydrogen bonds between water molecules give water the ability to hold heat better than many other substances. As the temperature rises, the hydrogen bonds between water continually break and reform, allowing for the overall temperature to remain stable, although increased energy is added to the system. Water's cohesive forces allow for the property of surface tension. All of these unique properties of water are important in the chemistry of living organisms.

The pH of a solution is a measure of the concentration of hydrogen ions in the solution. A solution with a high number of hydrogen ions is acidic and has a low pH value. A solution with a high number of hydroxide ions is basic and has a high pH value. The pH scale ranges from 0 to 14, with a pH of 7 being neutral. Buffers are solutions that moderate pH changes when an acid or base is added to the buffer system. Buffers are important in biological systems because of their ability to maintain constant pH conditions.

Footnotes

1. 1 Humphrey, W., Dalke, A. and Schulten, K., "VMD—Visual Molecular Dynamics", *J. Molec. Graphics*, 1996, vol. 14, pp. 33-38. http://www.ks.uiuc.edu/Research/vmd/

Glossary

acid
a substance that donates hydrogen ions and therefore lowers pH

adhesion
the attraction between water molecules and molecules of a different substance

base
a substance that absorbs hydrogen ions and therefore raises pH

buffer
a solution that resists a change in pH by absorbing or releasing hydrogen or hydroxide ions

cohesion
the intermolecular forces between water molecules caused by the polar nature of water; creates surface tension

evaporation
the release of water molecules from liquid water to form water vapor

hydrophilic
describes a substance that dissolves in water; water-loving

hydrophobic
describes a substance that does not dissolve in water; water-fearing

litmus paper
filter paper that has been treated with a natural water-soluble dye so it can be used as a pH indicator

pH scale
a scale ranging from 0 to 14 that measures the approximate concentration of hydrogen ions of a substance

solvent
a substance capable of dissolving another substance

surface tension
the cohesive force at the surface of a body of liquid that prevents the molecules from separating

temperature
a measure of molecular motion

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2.5: Properties of Water

Skills to Develop

- Describe the properties of water that are critical to maintaining life
- Explain why water is an excellent solvent
- Provide examples of water's cohesive and adhesive properties
- Discuss the role of acids, bases, and buffers in homeostasis

Why do scientists spend time looking for water on other planets? Why is water so important? It is because water is essential to life as we know it. Water is one of the more abundant molecules and the one most critical to life on Earth. Approximately 60–70 percent of the human body is made up of water. Without it, life as we know it simply would not exist.

The polarity of the water molecule and its resulting hydrogen bonding make water a unique substance with special properties that are intimately tied to the processes of life. Life originally evolved in a watery environment, and most of an organism's cellular chemistry and metabolism occur inside the watery contents of the cell's cytoplasm. Special properties of water are its high heat capacity and heat of vaporization, its ability to dissolve polar molecules, its cohesive and adhesive properties, and its dissociation into ions that leads to the generation of pH. Understanding these characteristics of water helps to elucidate its importance in maintaining life.

Water's Polarity

One of water's important properties is that it is composed of polar molecules: the hydrogen and oxygen within water molecules (H_2O) form polar covalent bonds. While there is no net charge to a water molecule, the polarity of water creates a slightly positive charge on hydrogen and a slightly negative charge on oxygen, contributing to water's properties of attraction. Water's charges are generated because oxygen is more electronegative than hydrogen, making it more likely that a shared electron would be found near the oxygen nucleus than the hydrogen nucleus, thus generating the partial negative charge near the oxygen.

As a result of water's polarity, each water molecule attracts other water molecules because of the opposite charges between water molecules, forming hydrogen bonds. Water also attracts or is attracted to other polar molecules and ions. A polar substance that interacts readily with or dissolves in water is referred to as hydrophilic (hydro- = "water"; -philic = "loving"). In contrast, nonpolar molecules such as oils and fats do not interact well with water, as shown in Figure **2.5.1** and separate from it rather than dissolve in it, as we see in salad dressings containing oil and vinegar (an acidic water solution). These nonpolar compounds are called hydrophobic (hydro- = "water"; -phobic = "fearing").

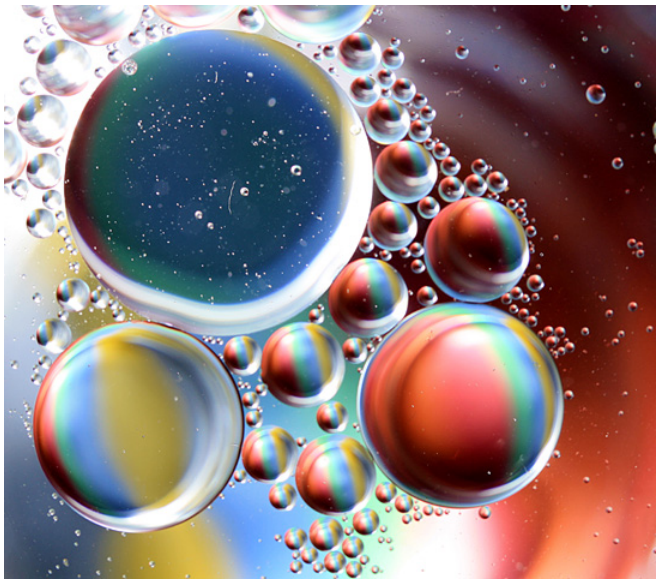


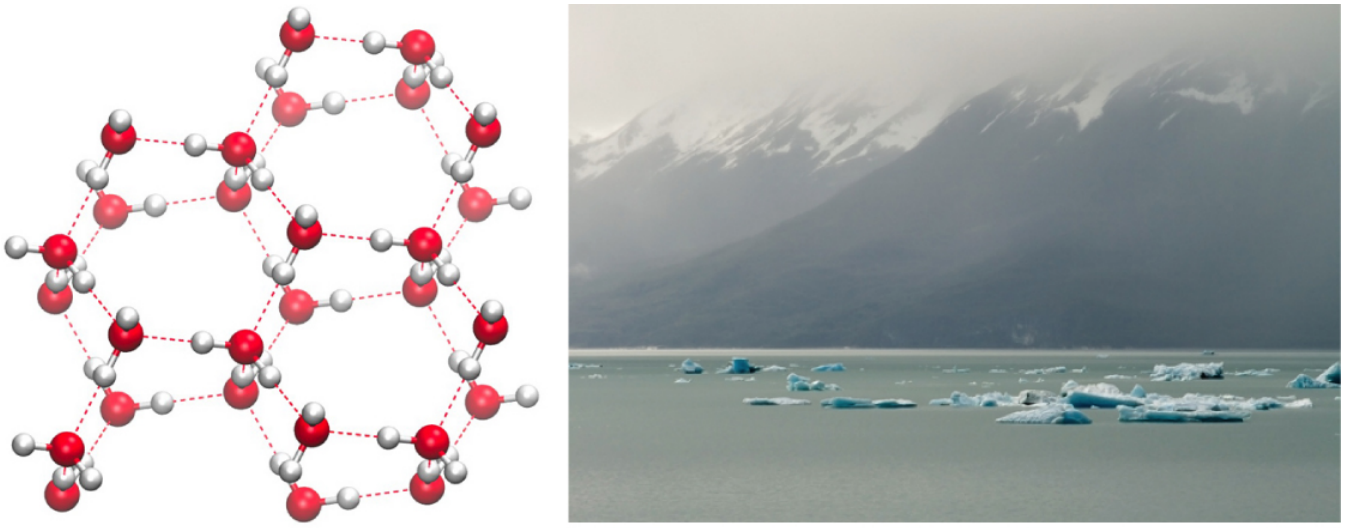
Figure **2.5.1**: Oil and water do not mix. As this macro image of oil and water shows, oil does not dissolve in water but forms droplets instead. This is due to it being a nonpolar compound. (credit: Gautam Dogra).

Water's States: Gas, Liquid, and Solid

The formation of hydrogen bonds is an important quality of the liquid water that is crucial to life as we know it. As water molecules make hydrogen bonds with each other, water takes on some unique chemical characteristics compared to other liquids and, since living things have a high water content, understanding these chemical features is key to understanding life. In liquid water, hydrogen bonds are constantly formed and broken as the water molecules slide past each other. The breaking of these bonds is caused by the motion (kinetic energy) of the water molecules due to the heat contained in the system. When the heat is raised as water is boiled, the higher kinetic energy of the water molecules causes the hydrogen bonds to break completely and allows water molecules to escape into the air as gas (steam or water vapor). On the other hand, when the temperature of water is reduced and water freezes, the water molecules form a crystalline structure maintained by hydrogen bonding (there is not enough energy to break the hydrogen bonds) that makes ice less dense than liquid water, a phenomenon not seen in the solidification of other liquids.

Water's lower density in its solid form is due to the way hydrogen bonds are oriented as it freezes: the water molecules are pushed farther apart compared to liquid water. With most other liquids, solidification when the temperature drops includes the lowering of kinetic energy between molecules, allowing them to pack even more tightly than in liquid form and giving the solid a greater density than the liquid.

The lower density of ice, illustrated and pictured in Figure **2.5.2**, an anomaly, causes it to float at the surface of liquid water, such as in an iceberg or in the ice cubes in a glass of ice water. In lakes and ponds, ice will form on the surface of the water creating an insulating barrier that protects the animals and plant life in the pond from freezing. Without this layer of insulating ice, plants and animals living in the pond would freeze in the solid block of ice and could not survive. The detrimental effect of freezing on living organisms is caused by the expansion of ice relative to liquid water. The ice crystals that form upon freezing rupture the delicate membranes essential for the function of living cells, irreversibly damaging them. Cells can only survive freezing if the water in them is temporarily replaced by another liquid like glycerol.



(a) (b)

Figure **2.5.2**: Hydrogen bonding makes ice less dense than liquid water. The (a) lattice structure of ice makes it less dense than the freely flowing molecules of liquid water, enabling it to (b) float on water. (credit a: modification of work by Jane Whitney, image created using Visual Molecular Dynamics (VMD) software[1]; credit b: modification of work by Carlos Ponte)

Link to Learning



Video: Click here to see a 3-D animation of the structure of an ice lattice. (Image credit: Jane Whitney. Image created using Visual Molecular Dynamics VMD software.[2])

Water's High Heat Capacity

Water's high heat capacity is a property caused by hydrogen bonding among water molecules. Water has the highest specific heat capacity of any liquids. Specific heat is defined as the amount of heat one gram of a substance must absorb or lose to change its temperature by one degree Celsius. For water, this amount is one calorie. It therefore takes water a long time to heat and long time to cool. In fact, the specific heat capacity of water is about five times more than that of sand. This explains why the land cools faster than the sea. Due to its high heat capacity, water is used by warm blooded animals to more evenly disperse heat in their bodies: it acts in a similar manner to a car's cooling system, transporting heat from warm places to cool places, causing the body to maintain a more even temperature.

Water's Heat of Vaporization

Water also has a high heat of vaporization, the amount of energy required to change one gram of a liquid substance to a gas. A considerable amount of heat energy (586 cal) is required to accomplish this change in water. This process occurs on the surface of water. As liquid water heats up, hydrogen bonding makes it difficult to separate the liquid water molecules from each other, which is required for it to enter its gaseous phase (steam). As a result, water acts as a heat sink or heat reservoir and requires much more heat to boil than does a liquid such as ethanol (grain alcohol), whose hydrogen bonding with other ethanol molecules is weaker than water's hydrogen bonding. Eventually, as water reaches its boiling point of 100° Celsius (212° Fahrenheit), the heat is able to break the hydrogen bonds between the water molecules, and the kinetic energy (motion) between the water molecules allows them to escape from the liquid as a gas. Even when below its boiling point, water's individual molecules acquire enough energy from other water molecules such that some surface water molecules can escape and vaporize: this process is known as evaporation.

The fact that hydrogen bonds need to be broken for water to evaporate means that a substantial amount of energy is used in the process. As the water evaporates, energy is taken up by the process, cooling the environment where the evaporation is taking place. In many living organisms, including in humans, the evaporation of sweat, which is 90 percent water, allows the organism to cool so that homeostasis of body temperature can be maintained.

Water's Solvent Properties

Since water is a polar molecule with slightly positive and slightly negative charges, ions and polar molecules can readily dissolve in it. Therefore, water is referred to as a solvent, a substance capable of dissolving other polar molecules and ionic compounds. The charges associated with these molecules will form hydrogen bonds with water, surrounding the particle with water molecules. This is referred to as a sphere of hydration, or a hydration shell, as illustrated in Figure **2.5.3** and serves to keep the particles separated or dispersed in the water.

When ionic compounds are added to water, the individual ions react with the polar regions of the water molecules and their ionic bonds are disrupted in the process of dissociation. Dissociation occurs when atoms or groups of atoms break off from molecules and form ions. Consider table salt (NaCl, or sodium chloride): when NaCl crystals are added to water, the molecules of NaCl dissociate into Na^+ and Cl^- ions, and spheres of hydration form around the ions, illustrated in Figure **2.5.3**. The positively charged sodium ion is surrounded by the partially negative charge of the water molecule's oxygen. The negatively charged chloride ion is surrounded by the partially positive charge of the hydrogen on the water molecule.

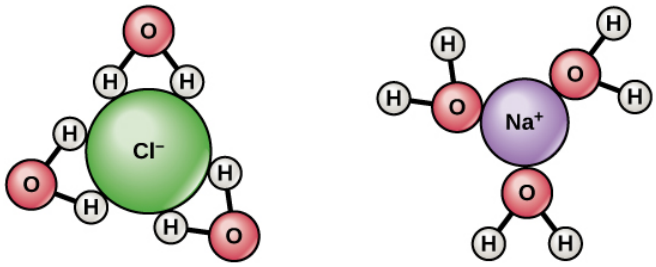


Figure **2.5.3**: When table salt (NaCl) is mixed in water, spheres of hydration are formed around the ions.

Water's Cohesive and Adhesive Properties

Have you ever filled a glass of water to the very top and then slowly added a few more drops? Before it overflows, the water forms a dome-like shape above the rim of the glass. This water can stay above the glass because of the property of cohesion. In cohesion, water molecules are attracted to each other (because of hydrogen bonding), keeping the molecules together at the liquid-gas (water-air) interface, although there is no more room in the glass.

Cohesion allows for the development of surface tension, the capacity of a substance to withstand being ruptured when placed under tension or stress. This is also why water forms droplets when placed on a dry surface rather than being flattened out by gravity. When a small scrap of paper is placed onto the droplet of water, the paper floats on top of the water droplet even though paper is denser (heavier) than the water. Cohesion and surface tension keep the hydrogen bonds of water molecules intact and support the item floating on the top. It's even possible to "float" a needle on top of a glass of water if it is placed gently without breaking the surface tension, as shown in Figure **2.5.4**.

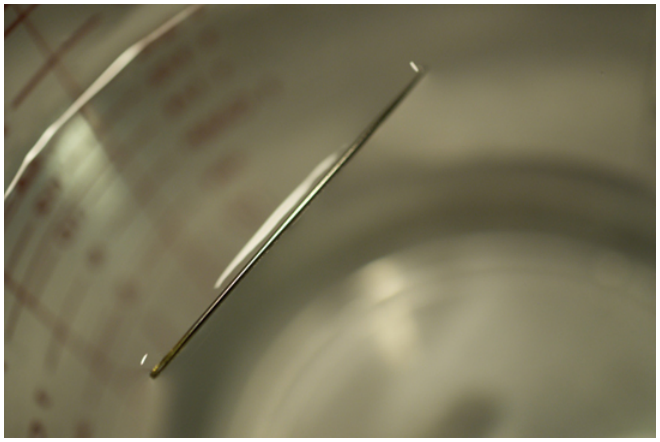


Figure **2.5.4**: The weight of the needle is pulling the surface downward; at the same time, the surface tension is pulling it up, suspending it on the surface of the water and keeping it from sinking. Notice the indentation in the water around the needle. (credit: Cory Zanker)

These cohesive forces are related to water's property of adhesion, or the attraction between water molecules and other molecules. This attraction is sometimes stronger than water's cohesive forces, especially when the water is exposed to charged surfaces such as those found on the inside of thin glass tubes known as capillary tubes. Adhesion is observed when water "climbs" up the tube placed in a glass of water: notice that the water appears to be higher on the sides of the tube than in the middle. This is because the water molecules are attracted to the charged glass walls of the capillary more than they are to each other and therefore adhere to it. This type of adhesion is called capillary action, and is illustrated in Figure **2.5.5**.

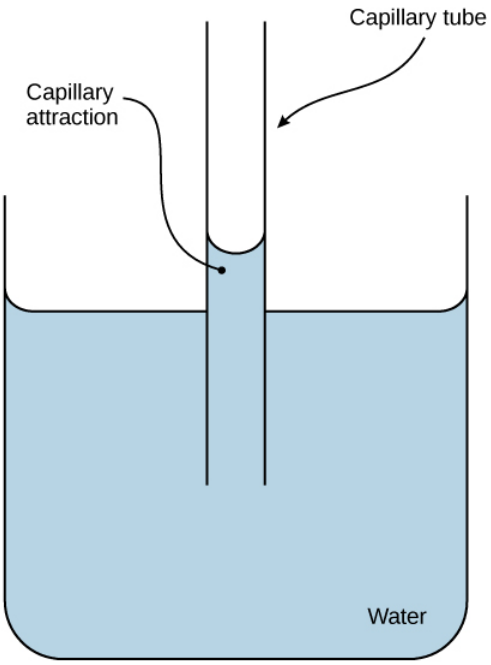


Figure **2.5.5**: Capillary action in a glass tube is caused by the adhesive forces exerted by the internal surface of the glass exceeding the cohesive forces between the water molecules themselves. (credit: modification of work by Pearson-Scott Foresman, donated to the Wikimedia Foundation)

Why are cohesive and adhesive forces important for life? Cohesive and adhesive forces are important for the transport of water from the roots to the leaves in plants. These forces create a "pull" on the water column. This pull results from the tendency of water molecules being evaporated on the surface of the plant to stay connected to water molecules below them, and so they are pulled along. Plants use this natural phenomenon to help transport water from their roots to their leaves. Without these properties of water, plants would be unable to receive the water and the dissolved minerals they require. In another example, insects such as the water strider, shown in Figure **2.5.6**, use the surface tension of water to stay afloat on the surface layer of water and even mate there.

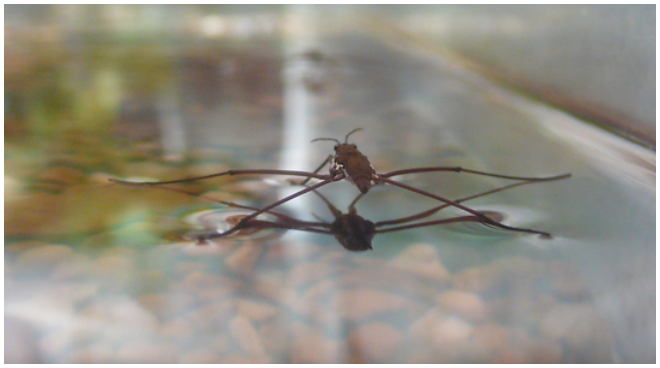


Figure **2.5.6**: Water's cohesive and adhesive properties allow this water strider (*Gerris* sp.) to stay afloat. (credit: Tim Vickers)

pH, Buffers, Acids, and Bases

The pH of a solution indicates its acidity or alkalinity.

$$H_2O(I) \leftrightharpoons H^+(aq) + O^-(aq)$$

litmus or pH paper, filter paper that has been treated with a natural water-soluble dye so it can be used as a pH indicator, to test how much acid (acidity) or base (alkalinity) exists in a solution. You might have even used some to test whether the water in a swimming pool is properly treated. In both cases, the pH test measures the concentration of hydrogen ions in a given solution.

Hydrogen ions are spontaneously generated in pure water by the dissociation (ionization) of a small percentage of water molecules into equal numbers of hydrogen (H^+) ions and hydroxide (OH^-) ions. While the hydroxide ions are kept in solution by their

hydrogen bonding with other water molecules, the hydrogen ions, consisting of naked protons, are immediately attracted to un-ionized water molecules, forming hydronium ions (H_30^+). Still, by convention, scientists refer to hydrogen ions and their concentration as if they were free in this state in liquid water.

The concentration of hydrogen ions dissociating from pure water is 1×10^{-7} moles H^+ ions per liter of water. Moles (mol) are a way to express the amount of a substance (which can be atoms, molecules, ions, etc), with one mole being equal to 6.02 x 10^{23} particles of the substance. Therefore, 1 mole of water is equal to 6.02 x 10^{23} water molecules. The pH is calculated as the negative of the base 10 logarithm of this concentration. The log10 of 1×10^{-7} is -7.0, and the negative of this number (indicated by the "p" of "pH") yields a pH of 7.0, which is also known as neutral pH. The pH inside of human cells and blood are examples of two areas of the body where near-neutral pH is maintained.

Non-neutral pH readings result from dissolving acids or bases in water. Using the negative logarithm to generate positive integers, high concentrations of hydrogen ions yield a low pH number, whereas low levels of hydrogen ions result in a high pH. An acid is a substance that increases the concentration of hydrogen ions (H^+) in a solution, usually by having one of its hydrogen atoms dissociate. A base provides either hydroxide ions ($OH^–$) or other negatively charged ions that combine with hydrogen ions, reducing their concentration in the solution and thereby raising the pH. In cases where the base releases hydroxide ions, these ions bind to free hydrogen ions, generating new water molecules.

The stronger the acid, the more readily it donates H^+. For example, hydrochloric acid (HCl) completely dissociates into hydrogen and chloride ions and is highly acidic, whereas the acids in tomato juice or vinegar do not completely dissociate and are considered weak acids. Conversely, strong bases are those substances that readily donate $OH^–$ or take up hydrogen ions. Sodium hydroxide (NaOH) and many household cleaners are highly alkaline and give up $OH^–$ rapidly when placed in water, thereby raising the pH. An example of a weak basic solution is seawater, which has a pH near 8.0, close enough to neutral pH that marine organisms adapted to this saline environment are able to thrive in it.

The pH scale is, as previously mentioned, an inverse logarithm and ranges from 0 to 14 (Figure **2.5.7**). Anything below 7.0 (ranging from 0.0 to 6.9) is acidic, and anything above 7.0 (from 7.1 to 14.0) is alkaline. Extremes in pH in either direction from 7.0 are usually considered inhospitable to life. The pH inside cells (6.8) and the pH in the blood (7.4) are both very close to neutral. However, the environment in the stomach is highly acidic, with a pH of 1 to 2. So how do the cells of the stomach survive in such an acidic environment? How do they homeostatically maintain the near neutral pH inside them? The answer is that they cannot do it and are constantly dying. New stomach cells are constantly produced to replace dead ones, which are digested by the stomach acids. It is estimated that the lining of the human stomach is completely replaced every seven to ten days.

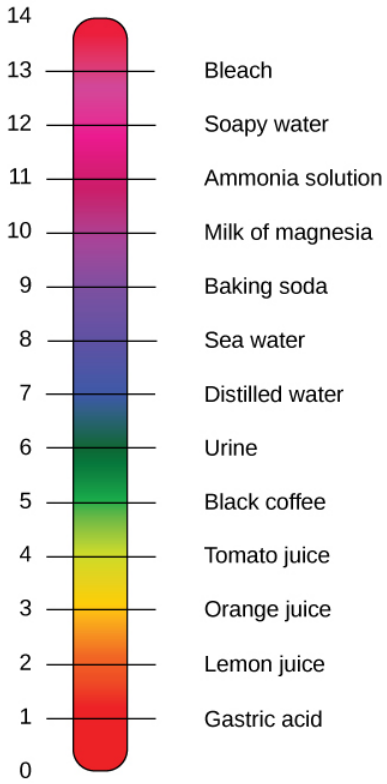


Figure **2.5.7**: The pH scale measures the concentration of hydrogen ions (H^+) in a solution. (credit: modification of work by Edward Stevens)

Link to Learning



Watch this video for a straightforward explanation of pH and its logarithmic scale.

So how can organisms whose bodies require a near-neutral pH ingest acidic and basic substances (a human drinking orange juice, for example) and survive? Buffers are the key. Buffers readily absorb excess H^+ or OH^-, keeping the pH of the body carefully maintained in the narrow range required for survival. Maintaining a constant blood pH is critical to a person's well-being. The buffer maintaining the pH of human blood involves carbonic acid (H_2CO_3), bicarbonate ion (HCO_3^-), and carbon dioxide (CO_2). When bicarbonate ions combine with free hydrogen ions and become carbonic acid, hydrogen ions are removed, moderating pH

changes. Similarly, as shown in Figure **2.5.8**, excess carbonic acid can be converted to carbon dioxide gas and exhaled through the lungs. This prevents too many free hydrogen ions from building up in the blood and dangerously reducing the blood's pH. Likewise, if too much OH^- is introduced into the system, carbonic acid will combine with it to create bicarbonate, lowering the pH. Without this buffer system, the body's pH would fluctuate enough to put survival in jeopardy.

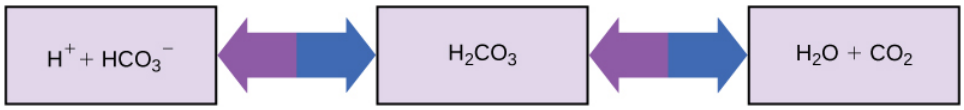


Figure **2.5.8**: This diagram shows the body's buffering of blood pH levels. The blue arrows show the process of raising pH as more CO_2 is made. The purple arrows indicate the reverse process: the lowering of pH as more bicarbonate is created.

Other examples of buffers are antacids used to combat excess stomach acid. Many of these over-the-counter medications work in the same way as blood buffers, usually with at least one ion capable of absorbing hydrogen and moderating pH, bringing relief to those that suffer "heartburn" after eating. The unique properties of water that contribute to this capacity to balance pH—as well as water's other characteristics—are essential to sustaining life on Earth.

Link to Learning

To learn more about water. Visit the U.S. Geological Survey Water Science for Schools All About Water! website.

Summary

Water has many properties that are critical to maintaining life. It is a polar molecule, allowing for the formation of hydrogen bonds. Hydrogen bonds allow ions and other polar molecules to dissolve in water. Therefore, water is an excellent solvent. The hydrogen bonds between water molecules cause the water to have a high heat capacity, meaning it takes a lot of added heat to raise its temperature. As the temperature rises, the hydrogen bonds between water continually break and form anew. This allows for the overall temperature to remain stable, although energy is added to the system. Water also exhibits a high heat of vaporization, which is key to how organisms cool themselves by the evaporation of sweat. Water's cohesive forces allow for the property of surface tension, whereas its adhesive properties are seen as water rises inside capillary tubes. The pH value is a measure of hydrogen ion concentration in a solution and is one of many chemical characteristics that is highly regulated in living organisms through homeostasis. Acids and bases can change pH values, but buffers tend to moderate the changes they cause. These properties of water are intimately connected to the biochemical and physical processes performed by living organisms, and life would be very different if these properties were altered, if it could exist at all.

Footnotes

1. 1 W. Humphrey W., A. Dalke, and K. Schulten, "VMD—Visual Molecular Dynamics," *Journal of Molecular Graphics* 14 (1996): 33-38.
2. 2 W. Humphrey W., A. Dalke, and K. Schulten, "VMD—Visual Molecular Dynamics," *Journal of Molecular Graphics* 14 (1996): 33-38.

Glossary

acid

molecule that donates hydrogen ions and increases the concentration of hydrogen ions in a solution

adhesion

attraction between water molecules and other molecules

base
molecule that donates hydroxide ions or otherwise binds excess hydrogen ions and decreases the concentration of hydrogen ions in a solution

buffer
substance that prevents a change in pH by absorbing or releasing hydrogen or hydroxide ions

calorie
amount of heat required to change the temperature of one gram of water by one degree Celsius

capillary action
occurs because water molecules are attracted to charges on the inner surfaces of narrow tubular structures such as glass tubes, drawing the water molecules to the sides of the tubes

cohesion
intermolecular forces between water molecules caused by the polar nature of water; responsible for surface tension

dissociation
release of an ion from a molecule such that the original molecule now consists of an ion and the charged remains of the original, such as when water dissociates into H^+ and OH^-

evaporation
separation of individual molecules from the surface of a body of water, leaves of a plant, or the skin of an organism

heat of vaporization of water
high amount of energy required for liquid water to turn into water vapor

hydrophilic
describes ions or polar molecules that interact well with other polar molecules such as water

hydrophobic
describes uncharged non-polar molecules that do not interact well with polar molecules such as water

litmus paper
(also, pH paper) filter paper that has been treated with a natural water-soluble dye that changes its color as the pH of the environment changes so it can be used as a pH indicator

pH paper
see litmus paper

pH scale
scale ranging from zero to 14 that is inversely proportional to the concentration of hydrogen ions in a solution

solvent
substance capable of dissolving another substance

specific heat capacity
the amount of heat one gram of a substance must absorb or lose to change its temperature by one degree Celsius

sphere of hydration
when a polar water molecule surrounds charged or polar molecules thus keeping them dissolved and in solution

surface tension

tension at the surface of a body of liquid that prevents the molecules from separating; created by the attractive cohesive forces between the molecules of the liquid

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2.6: Acids and Bases



Acids and bases. Why are these important in biology?

It comes back to a number of biological processes. For example, enzymes work best at specific levels of acids or bases. Take your stomach, a very acidic environment. The enzymes that work in that environment could not work in your mouth. What would your food taste like if your mouth was also a very acidic environment?

Acids and Bases

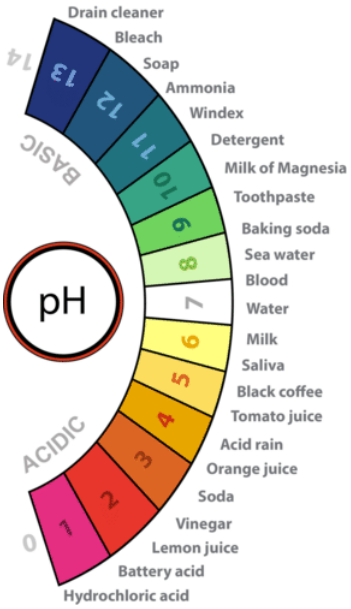
Water is the main ingredient of many solutions. A **solution** is a mixture of two or moresubstances that has the same composition throughout. Some solutions are acids and some are bases. To understand acids and bases, you need to know more about pure water. In pure water (such as distilled water), a tiny fraction of water molecules naturally breaks down to form ions. An **ion** is an electrically charged atom or molecule. The breakdown of water is represented by the chemical equation

$$2\ H_2O \rightarrow H_3O^+ + OH^-$$

The products of this reaction are a hydronium ion (H_3O^+) and a hydroxide ion (OH^-). The hydroxide ion, which has a negative charge, forms when a water molecule gives up a positively charged hydrogen ion (H^+). The hydronium ion, which has positive charge, forms when another water molecule accepts the hydrogen ion.

Acidity and pH

The concentration of hydronium ions in a solution is known as **acidity**. In pure water, the concentration of hydronium ions is very low; only about 1 in 10 million water molecules naturally breaks down to form a hydronium ion. As a result, pure water is essentially neutral. Acidity is measured on a scale called **pH**, as shown in **Figure** below. Pure water has a pH of 7, so the point of neutrality on the pH scale is 7.



Acidity and the pH Scale Water has a pH of 7, so this is the point of neutrality on the pH scale. Acids have a pH less than 7, and bases have a pH greater than 7. Approximate pHs of examples are shown.

Acids

If a solution has a higher concentration of hydronium ions than pure water, it has a pH lower than 7. A solution with a pH lower than 7 is called an **acid**. As the hydronium ion concentration increases, the pH value decreases. Therefore, the more acidic a solution is, the lower its pH value is. Did you ever taste vinegar? Like other acids, it tastes sour. Stronger acids can be harmful to organisms. For example, stomach acid would eat through the stomach if it were not lined with a layer of mucus. Strong acids can also damage materials, even hard materials such as glass.

Bases

If a solution has a lower concentration of hydronium ions than pure water, it has a pH higher than 7. A solution with a pH higher than 7 is called a **base**. Bases, such as baking soda, have a bitter taste. Like strong acids, strong bases can harm organisms and damage materials. For example, lye can burn the skin, and bleach can remove the color from clothing.

Acids and Bases in Organisms

Acids and bases are important in living things because most enzymes can do their job only at a certain level of acidity. Cells secrete acids and bases to maintain the proper pH for enzymes to work. For example, every time you digest food, acids and bases are at work in your digestive system. Consider the acidic environment of the stomach. The acidic environment helps with the digestion of food. The enzyme pepsin, which helps break down proteins in the stomach can only function optimally in the low pH environment. The stomach secretes a strong acid that allows pepsin to work, and the stomach to do its job. However, when stomach contents enter the small intestine, the acid must be neutralized. This is because enzymes in the small intestine need a basic environment in order to work. An organ called the pancreas secretes a strong base into the small intestine, and this base neutralizes the acid.

Summary

- A solution is a mixture of two or more substances that has the same composition throughout. Some solutions are acids, some are bases.
- Pure water has a pH of 7, so the point of neutrality on the pH scale is 7.
- Acids have a higher concentration of hydronium ions than pure water, and a pH lower than 7.
- Bases have a lower concentration of hydronium ions than pure water, and a pH higher than 7.
- Acids and bases are important in living organisms because most enzymes function best at a specific pH.

Explore More

Use these resources to answer the questions that follow.

Explore More I

- **pH** at http://johnkyrk.com/pH.html.

1. What is the definition of pH?
2. What is a strong acid?
3. What is the pH scale?
4. What is the pH range of most cellular processes?
5. Use the pH slider to find the pH of
    1. digestive juices.
    2. Windex.
    3. soapy water.
    4. sea water.
    5. beer.
    6. vinegar.

Explore More II

- **pH scale** at http://phet.colorado.edu/en/simulation/ph-scale.

Review

1. What is the pH of a neutral solution?
2. Distinguish between an acid and a base.
3. Describe an example of an acid or a base that is involved in human digestion.
4. Assume that you test an unknown solution and find that it has a pH of 7.2. What type of solution is it? How do you know?
5. Are the following acids or bases?
    1. milk
    2. coffee
    3. soap

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3.1.2: Synthesis of Biological Macromolecules

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3.1.1.1: The Chemical Basis for Life

Learning Objectives

- Explain the properties of carbon that allow it to serve as a building block for biomolecules

Carbon is the fourth most abundant element in the universe and is the building block of life on earth. On earth, carbon circulates through the land, ocean, and atmosphere, creating what is known as the Carbon Cycle. This global carbon cycle can be divided further into two separate cycles: the geological carbon cycles takes place over millions of years, whereas the biological or physical carbon cycle takes place from days to thousands of years. In a nonliving environment, carbon can exist as carbon dioxide (CO_2), carbonate rocks, coal, petroleum, natural gas, and dead organic matter. Plants and algae convert carbon dioxide to organic matter through the process of photosynthesis, the energy of light.



Figure **3.1.1.1.1**: Carbon is present in all life: All living things contain carbon in some form, and carbon is the primary component of macromolecules, including proteins, lipids, nucleic acids, and carbohydrates. Carbon exists in many forms in this leaf, including in the cellulose to form the leaf's structure and in chlorophyll, the pigment which makes the leaf green.

Carbon is Important to Life

In its metabolism of food and respiration, an animal consumes glucose ($C_6H_{12}O_6$), which combines with oxygen (O_2) to produce carbon dioxide (CO_2), water (H_2O), and energy, which is given off as heat. The animal has no need for the carbon dioxide and releases it into the atmosphere. A plant, on the other hand, uses the opposite reaction of an animal through photosynthesis. It intakes carbon dioxide, water, and energy from sunlight to make its own glucose and oxygen gas. The glucose is used for chemical energy, which the plant metabolizes in a similar way to an animal. The plant then emits the remaining oxygen into the environment.

Cells are made of many complex molecules called macromolecules, which include proteins, nucleic acids (RNA and DNA), carbohydrates, and lipids. The macromolecules are a subset of organic molecules (any carbon-containing liquid, solid, or gas) that are especially important for life. The fundamental component for all of these macromolecules is carbon. The carbon atom has unique properties that allow it to form covalent bonds to as many as four different atoms, making this versatile element ideal to serve as the basic structural component, or "backbone," of the macromolecules.

Structure of Carbon

Individual carbon atoms have an incomplete outermost electron shell. With an atomic number of 6 (six electrons and six protons), the first two electrons fill the inner shell, leaving four in the second shell. Therefore, carbon atoms can form four covalent bonds with other atoms to satisfy the octet rule. The methane molecule provides an example: it has the chemical formula CH_4. Each of its four hydrogen atoms forms a single covalent bond with the carbon atom by sharing a pair of electrons. This results in a filled outermost shell.

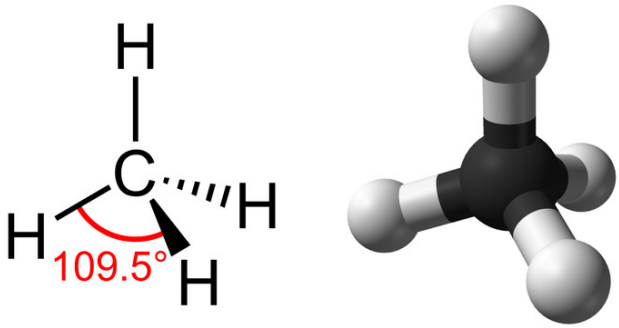


Figure 3.1.1.1.1: Structure of Methane: Methane has a tetrahedral geometry, with each of the four hydrogen atoms spaced 109.5° apart.

Key Points

- All living things contain carbon in some form.
- Carbon is the primary component of macromolecules, including proteins, lipids, nucleic acids, and carbohydrates.
- Carbon's molecular structure allows it to bond in many different ways and with many different elements.
- The carbon cycle shows how carbon moves through the living and non-living parts of the environment.

Key Terms

- **octet rule**: A rule stating that atoms lose, gain, or share electrons in order to have a full valence shell of 8 electrons (has some exceptions).
- **carbon cycle**: the physical cycle of carbon through the earth's biosphere, geosphere, hydrosphere, and atmosphere; includes such processes as photosynthesis, decomposition, respiration and carbonification
- **macromolecule**: a very large molecule, especially used in reference to large biological polymers (e.g., nucleic acids and proteins)

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3.1.1.2: Hydrocarbons

Learning Objectives

- Discuss the role of hydrocarbons in biomacromolecules

Hydrocarbons

Hydrocarbons are organic molecules consisting entirely of carbon and hydrogen, such as methane (CH_4). Hydrocarbons are often used as fuels: the propane in a gas grill or the butane in a lighter. The many covalent bonds between the atoms in hydrocarbons store a great amount of energy, which is released when these molecules are burned (oxidized). Methane, an excellent fuel, is the simplest hydrocarbon molecule, with a central carbon atom bonded to four different hydrogen atoms. The geometry of the methane molecule, where the atoms reside in three dimensions, is determined by the shape of its electron orbitals. The carbon and the four hydrogen atoms form a shape known as a tetrahedron, with four triangular faces; for this reason, methane is described as having tetrahedral geometry.

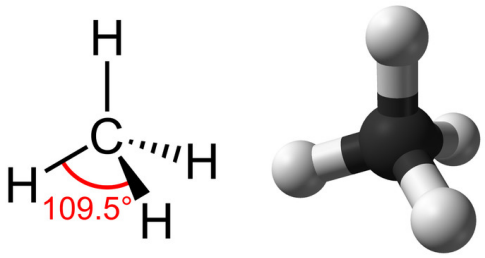


Figure **3.1.1.2.1**: Methane: Methane has a tetrahedral geometry, with each of the four hydrogen atoms spaced 109.5° apart.

As the backbone of the large molecules of living things, hydrocarbons may exist as linear carbon chains, carbon rings, or combinations of both. Furthermore, individual carbon-to-carbon bonds may be single, double, or triple covalent bonds; each type of bond affects the geometry of the molecule in a specific way. This three-dimensional shape or conformation of the large molecules of life (macromolecules) is critical to how they function.

Hydrocarbon Chains

Hydrocarbon chains are formed by successive bonds between carbon atoms and may be branched or unbranched. The overall geometry of the molecule is altered by the different geometries of single, double, and triple covalent bonds. The hydrocarbons ethane, ethene, and ethyne serve as examples of how different carbon-to-carbon bonds affect the geometry of the molecule. The names of all three molecules start with the prefix “eth-,” which is the prefix for two carbon hydrocarbons. The suffixes “-ane,” “-ene,” and “-yne” refer to the presence of single, double, or triple carbon-carbon bonds, respectively. Thus, propane, propene, and propyne follow the same pattern with three carbon molecules, butane, butene, and butyne for four carbon molecules, and so on. Double and triple bonds change the geometry of the molecule: single bonds allow rotation along the axis of the bond, whereas double bonds lead to a planar configuration and triple bonds to a linear one. These geometries have a significant impact on the shape a particular molecule can assume.

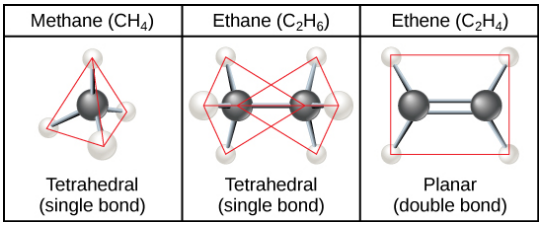


Figure **3.1.1.2.1**: Hydrocarbon Chains: When carbon forms single bonds with other atoms, the shape is tetrahedral. When two carbon atoms form a double bond, the shape is planar, or flat. Single bonds, like those found in ethane, are able to rotate. Double bonds, like those found in ethene cannot rotate, so the atoms on either side are locked in place.

Hydrocarbon Rings

The hydrocarbons discussed so far have been aliphatic hydrocarbons, which consist of linear chains of carbon atoms. Another type of hydrocarbon, aromatic hydrocarbons, consists of closed rings of carbon atoms. Ring structures are found in hydrocarbons, sometimes with the presence of double bonds, which can be seen by comparing the structure of cyclohexane to benzene. The benzene ring is present in many biological molecules including some amino acids and most steroids, which includes cholesterol and the hormones estrogen and testosterone. The benzene ring is also found in the herbicide 2,4-D. Benzene is a natural component of crude oil and has been classified as a carcinogen. Some hydrocarbons have both aliphatic and aromatic portions; beta-carotene is an example of such a hydrocarbon.

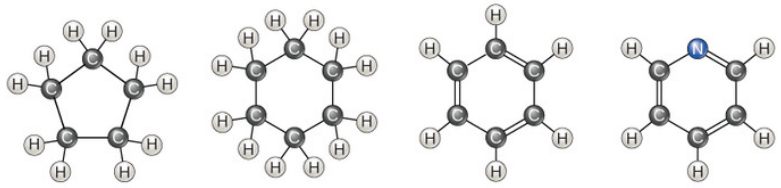


Figure **3.1.1.2.1**: Hydrocarbon Rings: Carbon can form five-and six membered rings. Single or double bonds may connect the carbons in the ring, and nitrogen may be substituted for carbon.

Key Points

- Hydrocarbons are molecules that contain only carbon and hydrogen.
- Due to carbon's unique bonding patterns, hydrocarbons can have single, double, or triple bonds between the carbon atoms.
- The names of hydrocarbons with single bonds end in "-ane," those with double bonds end in "-ene," and those with triple bonds end in "-yne".
- The bonding of hydrocarbons allows them to form rings or chains.

Key Terms

- **covalent bond**: A type of chemical bond where two atoms are connected to each other by the sharing of two or more electrons.
- **aliphatic**: Of a class of organic compounds in which the carbon atoms are arranged in an open chain.
- **aromatic**: Having a closed ring of alternate single and double bonds with delocalized electrons.

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3.1.1.3: Organic Isomers

Learning Objectives

- Give examples of isomers

The three-dimensional placement of atoms and chemical bonds within organic molecules is central to understanding their chemistry. Molecules that share the same chemical formula but differ in the placement (structure) of their atoms and/or chemical bonds are known as isomers.

Structural Isomers

Structural isomers (such as butane and isobutane) differ in the placement of their covalent bonds. Both molecules have four carbons and ten hydrogens (C_4H_{10}), but the different arrangement of the atoms within the molecules leads to differences in their chemical properties. For example, due to their different chemical properties, butane is suited for use as a fuel for cigarette lighters and torches, whereas isobutane is suited for use as a refrigerant and a propellant in spray cans.

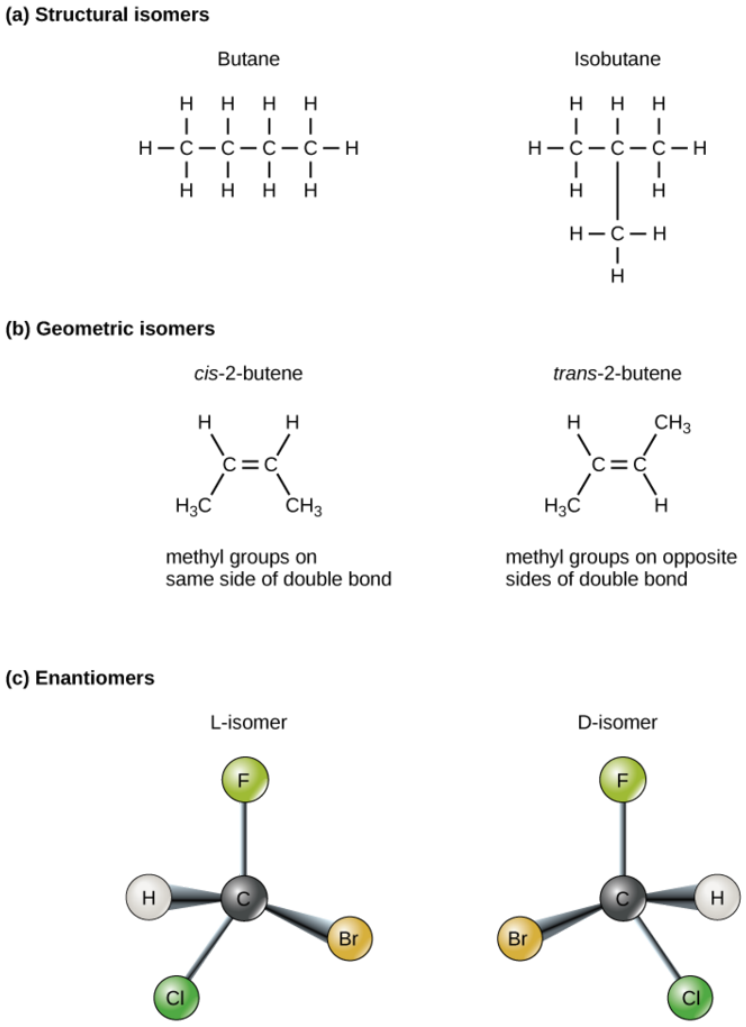


Figure **3.1.1.3.1**: Isomers: Molecules that have the same number and type of atoms arranged differently are called isomers. (a) Structural isomers have a different covalent arrangement of atoms. (b) Geometric isomers have a different arrangement of atoms around a double bond. (c) Enantiomers are mirror images of each other.

Geometric Isomers

Geometric isomers, on the other hand, have similar placements of their covalent bonds but differ in how these bonds are made to the surrounding atoms, especially in carbon-to-carbon double bonds. In the simple molecule butene (C_4H_8), the two methyl groups (CH_3) can be on either side of the double covalent bond central to the molecule. When the carbons are bound on the same side of the double bond, this is the cis configuration; if they are on opposite sides of the double bond, it is a trans configuration. In the trans configuration, the carbons form a more or less linear structure, whereas the carbons in the cis configuration make a bend (change in direction) of the carbon backbone.

Cis or Trans Configurations

In triglycerides (fats and oils), long carbon chains known as fatty acids may contain double bonds, which can be in either the cis or trans configuration. Fats with at least one double bond between carbon atoms are unsaturated fats. When some of these bonds are in the cis configuration, the resulting bend in the carbon backbone of the chain means that triglyceride molecules cannot pack tightly, so they remain liquid (oil) at room temperature. On the other hand, triglycerides with trans double bonds (popularly called trans fats), have relatively linear fatty acids that are able to pack tightly together at room temperature and form solid fats.

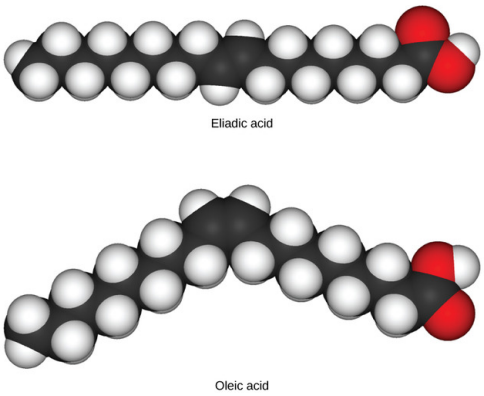


Figure **3.1.1.3.1**: Cis and Trans Fatty Acids: These space-filling models show a cis (oleic acid) and a trans (eliadic acid) fatty acid. Notice the bend in the molecule cause by the cis configuration.

In the human diet, trans fats are linked to an increased risk of cardiovascular disease, so many food manufacturers have reduced or eliminated their use in recent years. In contrast to unsaturated fats, triglycerides without double bonds between carbon atoms are called saturated fats, meaning that they contain all the hydrogen atoms available. Saturated fats are a solid at room temperature and usually of animal origin.

Key Points

- Isomers are molecules with the same chemical formula but have different structures.
- Isomers differ in how their bonds are positioned to surrounding atoms.
- When the carbons are bound on the same side of the double bond, this is the cis configuration; if they are on opposite sides of the double bond, it is a trans configuration.
- Triglycerides, which show both cis and trans configurations, can occur as either saturated or unsaturated, depending upon how many hydrogen atoms they have attached to them.

Key Terms

- **fatty acid**: Any of a class of aliphatic carboxylic acids, of general formula CnH2n+1COOH, that occur combined with glycerol as animal or vegetable oils and fats.
- **isomer**: Any of two or more compounds with the same molecular formula but with different structure.

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3.1.1.4: Organic Enantiomers

Learning Objectives

- Give examples of enantiomers

Stereoisomers are a type of isomer where the order of the atoms in the two molecules is the same but their arrangement in space is different. The two main types of stereoisomerism are diastereomerism (including 'cis-trans isomerism') and optical isomerism (also known as 'enantiomerism' and 'chirality'). Optical isomers are stereoisomers formed when asymmetric centers are present; for example, a carbon with four different groups bonded to it. Enantiomers are two optical isomers (i.e. isomers that are reflections of each other). Every stereocenter in one isomer has the opposite configuration in the other. They share the same chemical structure and chemical bonds, but differ in the three-dimensional placement of atoms so that they are mirror images, much as a person's left and right hands are. Compounds that are enantiomers of each other have the same physical properties except for the direction in which they rotate polarized light and how they interact with different optical isomers of other compounds.

The amino acid alanine is example of an entantiomer. The two structures, D-alanine and L-alanine, are non-superimposable. In nature, only the L-forms of amino acids are used to make proteins. Some D forms of amino acids are seen in the cell walls of bacteria, but never in their proteins. Similarly, the D-form of glucose is the main product of photosynthesis and the L-form of the molecule is rarely seen in nature.

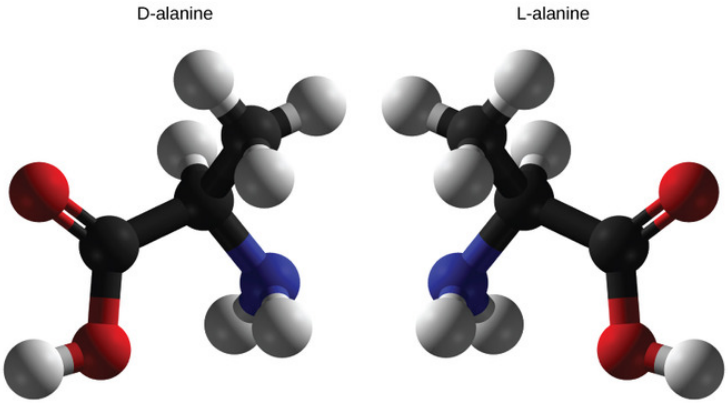


Figure **3.1.1.4.1**: Enantiomers: D-alanine and L-alanine are examples of enantiomers or mirror images. Only the L-forms of amino acids are used to make proteins.

Organic compounds that contain a chiral carbon usually have two non-superposable structures. These two structures are mirror images of each other and are, thus, commonly called enantiomorphs; hence, this structural property is now commonly referred to as enantiomerism. Enantiopure compounds refer to samples having, within the limits of detection, molecules of only one chirality.

Enantiomers of each other often show different chemical reactions with other substances that are also enantiomers. Since many molecules in the bodies of living beings are enantiomers themselves, there is sometimes a marked difference in the effects of two enantiomers on living beings. In drugs, for example, often only one of a drug's enantiomers is responsible for the desired physiologic effects, while the other enantiomer is less active, inactive, or sometimes even responsible for adverse effects. Owing to this discovery, drugs composed of only one enantiomer ("enantiopure") can be developed to enhance the pharmacological efficacy and sometimes do away with some side effects.

Key Points

- Enantiomers are stereoisomers, a type of isomer where the order of the atoms in the two molecules is the same but their arrangement in space is different.
- Many molecules in the bodies of living beings are enantiomers; there is sometimes a large difference in the effects of two enantiomers on organisms.
- Enantiopure compounds refer to samples having, within the limits of detection, molecules of only one chirality.

- Compounds that are enantiomers of each other have the same physical properties except for the direction in which they rotate polarized light and how they interact with different optical isomers of other compounds.

Key Terms

- **enantiomer**: One of a pair of stereoisomers that is the mirror image of the other, but may not be superimposed on this other stereoisomer.
- **chirality**: The phenomenon in chemistry, physics, and mathematics in which objects are mirror images of each other, but are not identical.
- **stereoisomer**: one of a set of the isomers of a compound in which atoms are arranged differently about a chiral center; they exhibit optical activity

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3.1.1.5: Organic Molecules and Functional Groups

Learning Objectives

- Describe the importance of functional groups to organic molecules

Location of Functional Groups

Functional groups are groups of atoms that occur within organic molecules and confer specific chemical properties to those molecules. When functional groups are shown, the organic molecule is sometimes denoted as “R.” Functional groups are found along the “carbon backbone” of macromolecules which is formed by chains and/or rings of carbon atoms with the occasional substitution of an element such as nitrogen or oxygen. Molecules with other elements in their carbon backbone are substituted hydrocarbons. Each of the four types of macromolecules—proteins, lipids, carbohydrates, and nucleic acids—has its own characteristic set of functional groups that contributes greatly to its differing chemical properties and its function in living organisms.

Properties of Functional Groups

A functional group can participate in specific chemical reactions. Some of the important functional groups in biological molecules include: hydroxyl, methyl, carbonyl, carboxyl, amino, phosphate, and sulfhydryl groups. These groups play an important role in the formation of molecules like DNA, proteins, carbohydrates, and lipids.

Classifying Functional Groups

Functional groups are usually classified as hydrophobic or hydrophilic depending on their charge or polarity. An example of a hydrophobic group is the non-polar methane molecule. Among the hydrophilic functional groups is the carboxyl group found in amino acids, some amino acid side chains, and the fatty acid heads that form triglycerides and phospholipids. This carboxyl group ionizes to release hydrogen ions (H^+) from the COOH group resulting in the negatively charged COO^- group; this contributes to the hydrophilic nature of whatever molecule it is found on. Other functional groups, such as the carbonyl group, have a partially negatively charged oxygen atom that may form hydrogen bonds with water molecules, again making the molecule more hydrophilic.

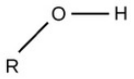
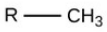
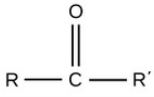
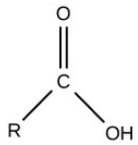
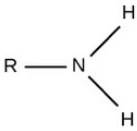
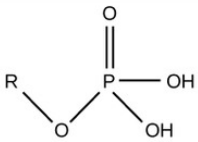
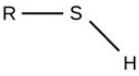
Functional Group	Structure	Properties
Hydroxyl		Polar
Methyl		Nonpolar
Carbonyl		Polar
Carboxyl		Charged, ionizes to release H^+. Since carboxyl groups can release H^+ ions into solution, they are considered acidic.
Amino		Charged, accepts H^+ to form NH_3^+. Since amino groups can remove H^+ from solution, they are considered basic.
Phosphate		Charged, ionizes to release H^+. Since phosphate groups can release H^+ ions into solution, they are considered acidic.
Sulfhydryl		Polar

Figure **3.1.1.5.1**: Examples of functional groups: The functional groups shown here are found in many different biological molecules, where "R" is the organic molecule.

Hydrogen Bonds between Functional Groups

Hydrogen bonds between functional groups (within the same molecule or between different molecules) are important to the function of many macromolecules and help them to fold properly and maintain the appropriate shape needed to function correctly. Hydrogen bonds are also involved in various recognition processes, such as DNA complementary base pairing and the binding of an enzyme to its substrate.

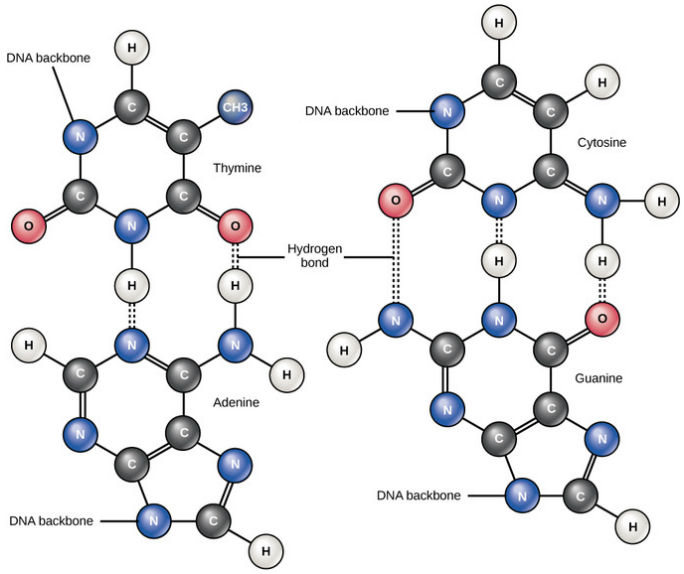


Figure **3.1.1.5.1**: Hydrogen bonds in DNA: Hydrogen bonds connect two strands of DNA together to create the double-helix structure.

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Key Points

- Functional groups are collections of atoms that attach the carbon skeleton of an organic molecule and confer specific properties.
- Each type of organic molecule has its own specific type of functional group.
- Functional groups in biological molecules play an important role in the formation of molecules like DNA, proteins, carbohydrates, and lipids.
- Functional groups include: hydroxyl, methyl, carbonyl, carboxyl, amino, phosphate, and sulfhydryl.

Key Terms

- **hydrophobic**: lacking an affinity for water; unable to absorb, or be wetted by water
- **hydrophilic**: having an affinity for water; able to absorb, or be wetted by water

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SECTION OVERVIEW

3.1.2: Synthesis of Biological Macromolecules

3.1.2.1: Types of Biological Macromolecules

3.1.2.2: Dehydration Synthesis

3.1.2.3: Hydrolysis

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3.1.2.1: Types of Biological Macromolecules

Learning Objectives

- Identify the four major classes of biological macromolecules

Nutrients are the molecules that living organisms require for survival and growth but that animals and plants cannot synthesize themselves. Animals obtain nutrients by consuming food, while plants pull nutrients from soil.



Figure **3.1.2.1.1**: Sources of biological macromolecules: Foods such as bread, fruit, and cheese are rich sources of biological macromolecules.

Many critical nutrients are biological macromolecules. The term “macromolecule” was first coined in the 1920s by Nobel laureate Hermann Staudinger. Staudinger was the first to propose that many large biological molecules are built by covalently linking smaller biological molecules together.

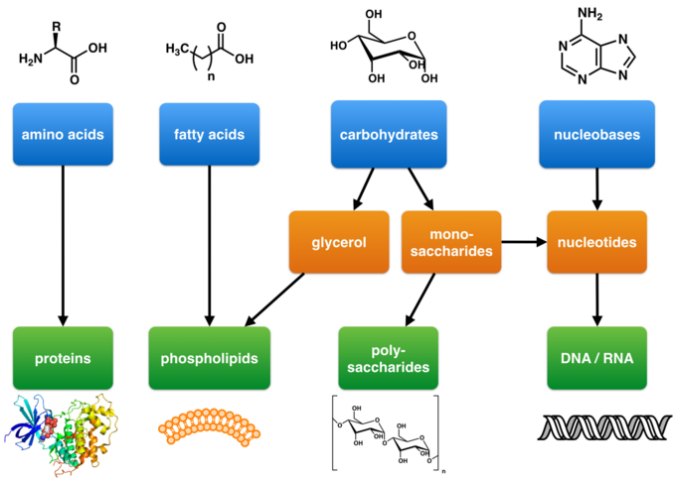
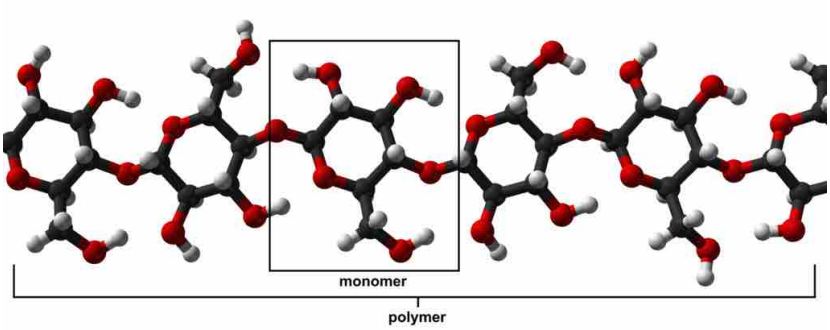


Figure **3.1.2.1.2**: Living organisms are made up of chemical building blocks: All organisms are composed of a variety of these biological macromolecules.

Monomers and Polymers

Biological macromolecules play a critical role in cell structure and function. Most (but not all) biological macromolecules are polymers, which are any molecules constructed by linking together many smaller molecules, called monomers. Typically all the monomers in a polymer tend to be the same, or at least very similar to each other, linked over and over again to build up the larger macromolecule. These simple monomers can be linked in many different combinations to produce complex biological polymers, just as a few types of Lego blocks can build anything from a house to a car.



Monomers and polymers: Many small monomer subunits combine to form this carbohydrate polymer.

Examples of these monomers and polymers can be found in the sugar you might put in your coffee or tea. Regular table sugar is the disaccharide sucrose (a polymer), which is composed of the monosaccharides fructose and glucose (which are monomers). If we were to string many carbohydrate monomers together we could make a polysaccharide like starch. The prefixes “mono-” (one), “di-” (two),and “poly-” (many) will tell you how many of the monomers have been joined together in a molecule.

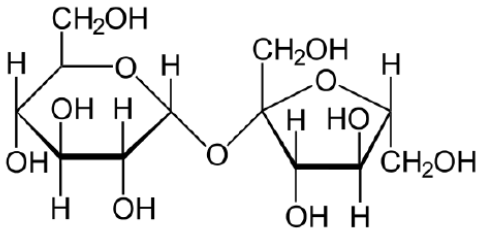


Figure **3.1.2.1.3**: The molecule sucrose (common table sugar): The carbohydrate monosaccharides (fructose and glucose) are joined to make the disaccharide sucrose.

Biological macromolecules all contain carbon in ring or chain form, which means they are classified as organic molecules. They usually also contain hydrogen and oxygen, as well as nitrogen and additional minor elements.

Four Classes of Biological Macromolecules

There are four major classes of biological macromolecules:

1. carbohydrates
2. lipids
3. proteins
4. nucleic acids

Each of these types of macromolecules performs a wide array of important functions within the cell; a cell cannot perform its role within the body without many different types of these crucial molecules. In combination, these biological macromolecules make up the majority of a cell’s dry mass. (Water molecules make up the majority of a cell’s total mass.) All the molecules both inside and outside of cells are situated in a water-based (i.e., aqueous) environment, and all the reactions of biological systems are occurring in that same environment.

Key Points

- Biological macromolecules are important cellular components and perform a wide array of functions necessary for the survival and growth of living organisms.
- The four major classes of biological macromolecules are carbohydrates, lipids, proteins, and nucleic acids.

Key Terms

- **polymer**: A relatively large molecule consisting of a chain or network of many identical or similar monomers chemically bonded to each other.
- **monomer**: A relatively small molecule that can form covalent bonds with other molecules of this type to form a polymer.

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3.1.2.2: Dehydration Synthesis

Learning Objectives

- Explain dehydration (or condensation) reactions

Dehydration Synthesis

Most macromolecules are made from single subunits, or building blocks, called monomers. The monomers combine with each other via covalent bonds to form larger molecules known as polymers. In doing so, monomers release water molecules as byproducts. This type of reaction is known as dehydration synthesis, which means “to put together while losing water. ” It is also considered to be a condensation reaction since two molecules are condensed into one larger molecule with the loss of a smaller molecule (the water.)

In a dehydration synthesis reaction between two un-ionized monomers, such as monosaccharide sugars, the hydrogen of one monomer combines with the hydroxyl group of another monomer, releasing a molecule of water in the process. The removal of a hydrogen from one monomer and the removal of a hydroxyl group from the other monomer allows the monomers to share electrons and form a covalent bond. Thus, the monomers that are joined together are being *dehydrated* to allow for *synthesis* of a larger molecule.

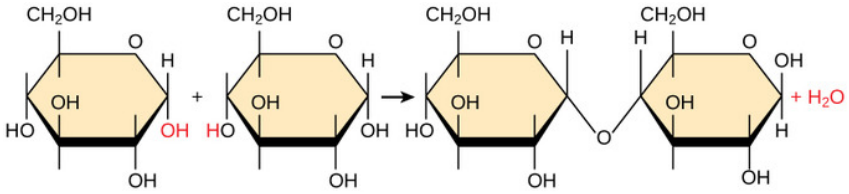


Figure **3.1.2.2.1**: A dehydration synthesis reaction involving un-ionized moners..: In the dehydration synthesis reaction between two molecules of glucose, a hydroxyl group from the first glucose is combined with a hydrogen from the second glucose, creating a covalent bond that links the two monomeric sugars (monosaccharides) together to form the dissacharide maltose. In the process, a water molecule is formed.

When the monomers are ionized, such as is the case with amino acids in an aqueous environment like cytoplasm, two hydrogens from the positively-charged end of one monomer are combined with an oxygen from the negatively-charged end of another monomer, again forming water, which is released as a side-product, and again joining the two monomers with a covalent bond.



Figure **3.1.2.2.1**: A dehydration synthesis reaction involving ionized monomers.: In the dehydration synthesis reaction between two amino acids, with are ionized in aqueous environments like the cell, an oxygen from the first amino acid is combined with two hydrogens from the second amino acid, creating a covalent bond that links the two monomers together to form a dipeptide. In the process a water molecule is formed.

As additional monomers join via multiple dehydration synthesis reactions, the chain of repeating monomers begins to form a polymer. Different types of monomers can combine in many configurations, giving rise to a diverse group of macromolecules.

Three of the four major classes of biological macromolecules (complex carbohydrates, nucleic acids, and proteins), are composed of monomers that join together via dehydration synthesis reactions. Complex carbohydrates are formed from monosaccharides, nucleic acids are formed from mononucleotides, and proteins are formed from amino acids.

There is great diversity in the manner by which monomers can combine to form polymers. For example, glucose monomers are the constituents of starch, glycogen, and cellulose. These three are polysaccharides, classified as carbohydrates, that have formed as a result of multiple dehydration synthesis reactions between glucose monomers. However, the manner by which glucose monomers join together, specifically locations of the covalent bonds between connected monomers and the orientation (stereochemistry) of the covalent bonds, results in these three different polysaccharides with varying properties and functions. In nucleic acids and proteins, the location and stereochemistry of the covalent linkages connecting the monomers do not vary from molecule to molecule, but instead the multiple kinds of monomers (five different monomers in nucleic acids, A, G, C, T, and U mononucleotides; 21 different amino acids monomers in proteins) are combined in a huge variety of sequences. Each protein or nucleic acid with a different sequence is a different molecule with different properties.

Key Points

- During dehydration synthesis, either the hydrogen of one monomer combines with the hydroxyl group of another monomer releasing a molecule of water, or two hydrogens from one monomer combine with one oxygen from the other monomer releasing a molecule of water.
- The monomers that are joined via dehydration synthesis reactions share electrons and form covalent bonds with each other.
- As additional monomers join via multiple dehydration synthesis reactions, this chain of repeating monomers begins to form a polymer.
- Complex carbohydrates, nucleic acids, and proteins are all examples of polymers that are formed by dehydration synthesis.
- Monomers like glucose can join together in different ways and produce a variety of polymers. Monomers like mononucleotides and amino acids join together in different sequences to produce a variety of polymers.

Key Terms

- **covalent bond**: A type of chemical bond where two atoms are connected to each other by the sharing of two or more electrons.
- **monomer**: A relatively small molecule which can be covalently bonded to other monomers to form a polymer.

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3.1.2.3: Hydrolysis

Learning Objectives

- Explain hydrolysis reactions

Polymers are broken down into monomers in a process known as hydrolysis, which means “to split water,” a reaction in which a water molecule is used during the breakdown. During these reactions, the polymer is broken into two components. If the components are un-ionized, one part gains a hydrogen atom (H-) and the other gains a hydroxyl group (OH–) from a split water molecule. This is what happens when monosaccharides are released from complex carbohydrates via hydrolysis.

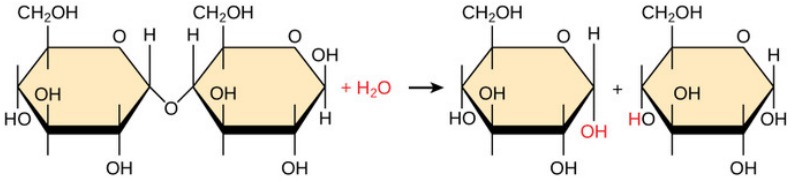


Figure **3.1.2.3.1**: Hydrolysis reaction generating un-ionized products.: In the hydrolysis reaction shown here, the disaccharide maltose is broken down to form two glucose monomers with the addition of a water molecule. One glucose gets a hydroxyl group at the site of the former covalent bond, the other glucose gets a hydrogen atom. This is the reverse of the dehydration synthesis reaction joining these two monomers.

If the components are ionized after the split, one part gains two hydrogen atoms and a positive charge, the other part gains an oxygen atom and a negative charge. This is what happens when amino acids are released from protein chains via hydrolysis.

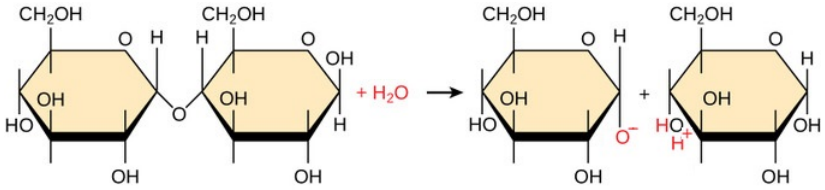


Figure **3.1.2.3.1**: Hydrolysis reaction generating ionized products.: In the hydrolysis reaction shown here, the dipeptide is broken down to form two ionized amino acids with the addition of a water molecule. One amino acid gets an oxygen atom and a negative charge, the other amino acid gets two hydrogen atoms and a positive charge. This is the reverse of the dehydration synthesis reaction joining these two monomers.

These reactions are in contrast to dehydration synthesis (also known as condensation) reactions. In dehydration synthesis reactions, a water molecule is formed as a result of generating a covalent bond between two monomeric components in a larger polymer. In hydrolysis reactions, a water molecule is consumed as a result of breaking the covalent bond holding together two components of a polymer.

Dehydration and hydrolysis reactions are chemical reactions that are catalyzed, or “sped up,” by specific enzymes; dehydration reactions involve the formation of new bonds, requiring energy, while hydrolysis reactions break bonds and release energy.

In our bodies, food is first hydrolyzed, or broken down, into smaller molecules by catalytic enzymes in the digestive tract. This allows for easy absorption of nutrients by cells in the intestine. Each macromolecule is broken down by a specific enzyme. For instance, carbohydrates are broken down by amylase, sucrase, lactase, or maltase. Proteins are broken down by the enzymes trypsin, pepsin, peptidase and others. Lipids are broken down by lipases. Once the smaller metabolites that result from these hydrolytic enzymezes are absorbed by cells in the body, they are further broken down by other enzymes. The breakdown of these macromolecules is an overall energy-releasing process and provides energy for cellular activities.

Exercise 3.1.2.3.1

1. What are biological macromolecules? Name the four major classes.
2. Biological macromolecules are organic. What does that mean?
3. What are monomers? What are polymer?
4. Explain the process “dehydration synthesis.” Is there another name for this process? Explain.
5. Explain Figure 1 in your own words.

6. Give an example of how condensation can form different carbohydrates.
7. Explain the process of Hydrolysis.
8. Explain Figure 2 in your own words.
9. What role do enzymes play in hydrolysis and condensation? Explain.
10. In our bodies, food is hydrolyzed, or broken down into smaller molecules. Explain why.
11. The breakdown of macromolecules provides...
12. Create a comparison chart to indicate the enzymes that break down carbohydrates, proteins, and lipids.

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Key Points

- Hydrolysis reactions use water to breakdown polymers into monomers and is the opposite of dehydration synthesis, which forms water when synthesizing a polymer from monomers.
- Hydrolysis reactions break bonds and release energy.
- Biological macromolecules are ingested and hydrolyzed in the digestive tract to form smaller molecules that can be absorbed by cells and then further broken down to release energy.

Key Terms

- **enzyme**: a globular protein that catalyses a biological chemical reaction
- **hydrolysis**: A chemical process of decomposition involving the splitting of a bond by the addition of water.

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SECTION OVERVIEW

3.2: Carbohydrates - Energy Storage and Structural Molecules

3.2.1.1: Carbohydrate Molecules

3.2.1.2: Importance of Carbohydrates

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3.2.1.1: Carbohydrate Molecules

Learning Objectives

- Describe the structure of mono-, di-, and poly-saccharides

Carbohydrates can be represented by the stoichiometric formula $(CH_2O)_n$, where n is the number of carbons in the molecule. Therefore, the ratio of carbon to hydrogen to oxygen is 1:2:1 in carbohydrate molecules. The origin of the term “carbohydrate” is based on its components: carbon (“carbo”) and water (“hydrate”). Carbohydrates are classified into three subtypes: monosaccharides, disaccharides, and polysaccharides.

Monosaccharides

Monosaccharides (mono- = “one”; sacchar- = “sweet”) are simple sugars. In monosaccharides, the number of carbons usually ranges from three to seven. If the sugar has an aldehyde group (the functional group with the structure R-CHO), it is known as an aldose, and if it has a ketone group (the functional group with the structure RC(=O)R’), it is known as a ketose. Depending on the number of carbons in the sugar, they also may be known as trioses (three carbons), pentoses (five carbons), and or hexoses (six carbons). Monosaccharides can exist as a linear chain or as ring-shaped molecules; in aqueous solutions they are usually found in ring forms.

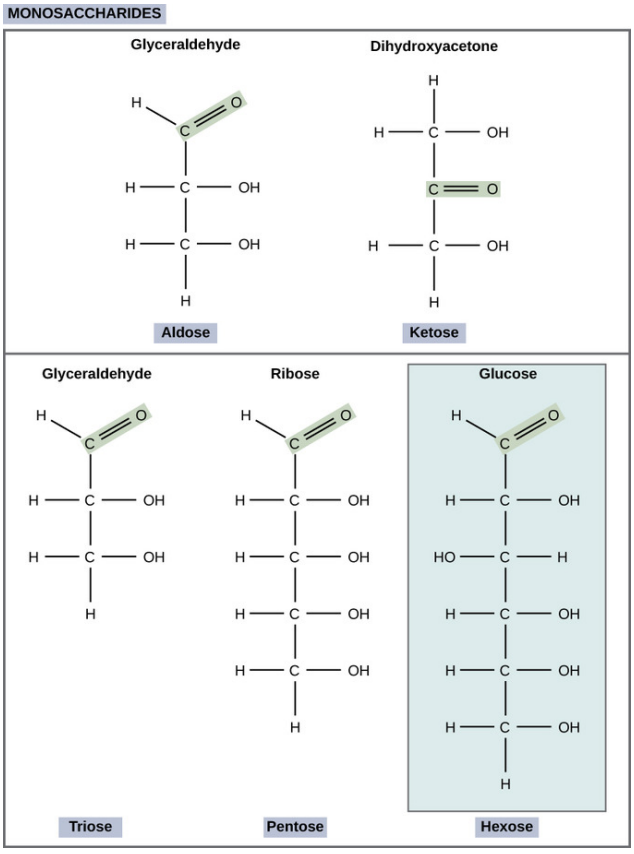


Figure **3.2.1.1.1**: Monosaccharides: Monosaccharides are classified based on the position of their carbonyl group and the number of carbons in the backbone. Aldoses have a carbonyl group (indicated in green) at the end of the carbon chain, and ketoses have a carbonyl group in the middle of the carbon chain. Trioses, pentoses, and hexoses have three, five, and six carbon backbones, respectively.

Common Monosaccharides

Glucose ($C_6H_{12}O_6$) is a common monosaccharide and an important source of energy. During cellular respiration, energy is released from glucose and that energy is used to help make adenosine triphosphate (ATP). Plants synthesize glucose using carbon dioxide

and water, and glucose, in turn, is used for energy requirements for the plant.

Galactose (a milk sugar) and fructose (found in fruit) are other common monosaccharides. Although glucose, galactose, and fructose all have the same chemical formula ($C_6H_{12}O_6$), they differ structurally and stereochemically. This makes them different molecules despite sharing the same atoms in the same proportions, and they are all isomers of one another, or isomeric monosaccharides. Glucose and galactose are aldoses, and fructose is a ketose.

Disaccharides

Disaccharides (di- = “two”) form when two monosaccharides undergo a dehydration reaction (also known as a condensation reaction or dehydration synthesis). During this process, the hydroxyl group of one monosaccharide combines with the hydrogen of another monosaccharide, releasing a molecule of water and forming a covalent bond. A covalent bond formed between a carbohydrate molecule and another molecule (in this case, between two monosaccharides) is known as a glycosidic bond. Glycosidic bonds (also called glycosidic linkages) can be of the alpha or the beta type.

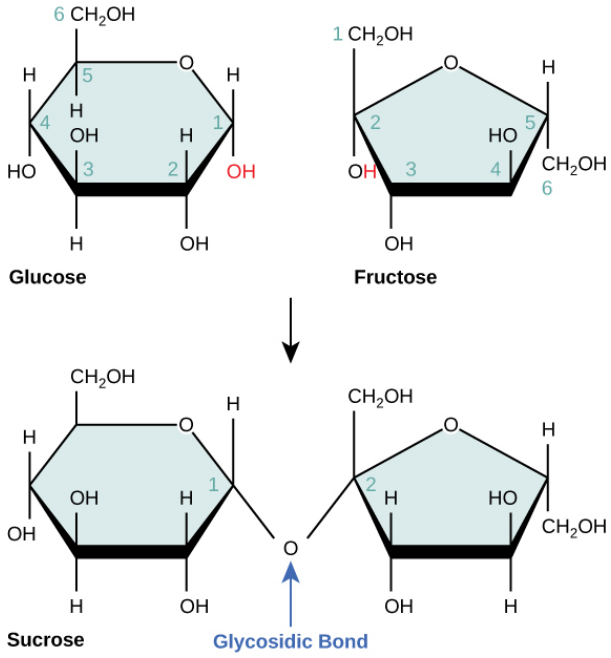


Figure **3.2.1.1.1**: Disaccharides: Sucrose is formed when a monomer of glucose and a monomer of fructose are joined in a dehydration reaction to form a glycosidic bond. In the process, a water molecule is lost. By convention, the carbon atoms in a monosaccharide are numbered from the terminal carbon closest to the carbonyl group. In sucrose, a glycosidic linkage is formed between carbon 1 in glucose and carbon 2 in fructose.

Common Disaccharides

Common disaccharides include lactose, maltose, and sucrose. Lactose is a disaccharide consisting of the monomers glucose and galactose. It is found naturally in milk. Maltose, or malt sugar, is a disaccharide formed by a dehydration reaction between two glucose molecules. The most common disaccharide is sucrose, or table sugar, which is composed of the monomers glucose and fructose.

Polysaccharides

A long chain of monosaccharides linked by glycosidic bonds is known as a polysaccharide (poly- = “many”). The chain may be branched or unbranched, and it may contain different types of monosaccharides. Starch, glycogen, cellulose, and chitin are primary examples of polysaccharides.

Plants are able to synthesize glucose, and the excess glucose is stored as starch in different plant parts, including roots and seeds. Starch is the stored form of sugars in plants and is made up of glucose monomers that are joined by α1-4 or 1-6 glycosidic bonds. The starch in the seeds provides food for the embryo as it germinates while the starch that is consumed by humans is broken down by enzymes into smaller molecules, such as maltose and glucose. The cells can then absorb the glucose.

Common Polysaccharides

Glycogen is the storage form of glucose in humans and other vertebrates. It is made up of monomers of glucose. Glycogen is the animal equivalent of starch and is a highly branched molecule usually stored in liver and muscle cells. Whenever blood glucose levels decrease, glycogen is broken down to release glucose in a process known as glycogenolysis.

Cellulose is the most abundant natural biopolymer. The cell wall of plants is mostly made of cellulose and provides structural support to the cell. Cellulose is made up of glucose monomers that are linked by β 1-4 glycosidic bonds. Every other glucose monomer in cellulose is flipped over, and the monomers are packed tightly as extended long chains. This gives cellulose its rigidity and high tensile strength—which is so important to plant cells.

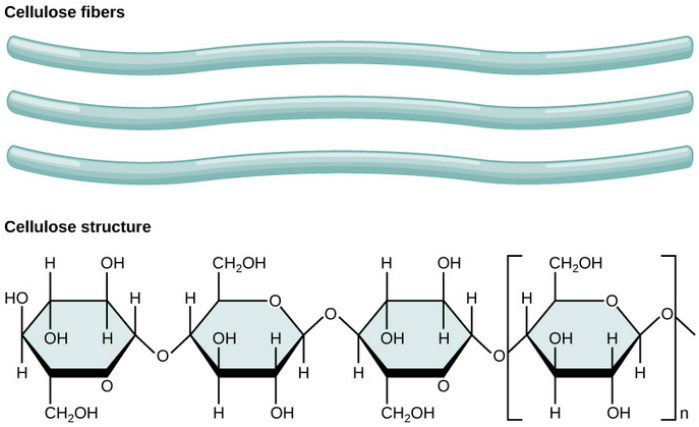


Figure **3.2.1.1.1**: Polysaccharides: In cellulose, glucose monomers are linked in unbranched chains by β 1-4 glycosidic linkages. Because of the way the glucose subunits are joined, every glucose monomer is flipped relative to the next one resulting in a linear, fibrous structure.

Carbohydrate Function

Carbohydrates serve various functions in different animals. Arthropods have an outer skeleton, the exoskeleton, which protects their internal body parts. This exoskeleton is made of chitin, which is a polysaccharide-containing nitrogen. It is made of repeating units of N-acetyl-β-d-glucosamine, a modified sugar. Chitin is also a major component of fungal cell walls.

Key Points

- Monosaccharides are simple sugars made up of three to seven carbons, and they can exist as a linear chain or as ring-shaped molecules.
- Glucose, galactose, and fructose are monosaccharide isomers, which means they all have the same chemical formula but differ structurally and chemically.
- Disaccharides form when two monosaccharides undergo a dehydration reaction (a condensation reaction); they are held together by a covalent bond.
- Sucrose (table sugar) is the most common disaccharide, which is composed of the monomers glucose and fructose.
- A polysaccharide is a long chain of monosaccharides linked by glycosidic bonds; the chain may be branched or unbranched and can contain many types of monosaccharides.

Key Terms

- **isomer**: Any of two or more compounds with the same molecular formula but with different structure.
- **dehydration reaction**: A chemical reaction in which two molecules are covalently linked in a reaction that generates H2O as a second product.
- **biopolymer**: Any macromolecule of a living organism that is formed from the polymerization of smaller entities; a polymer that occurs in a living organism or results from life.

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3.2.1.2: Importance of Carbohydrates

Learning Objectives

- Describe the benefits provided to organisms by carbohydrates

Benefits of Carbohydrates

Biological macromolecules are large molecules that are necessary for life and are built from smaller organic molecules. One major class of biological macromolecules are carbohydrates, which are further divided into three subtypes: monosaccharides, disaccharides, and polysaccharides. Carbohydrates are, in fact, an essential part of our diet; grains, fruits, and vegetables are all natural sources of carbohydrates. Importantly, carbohydrates provide energy to the body, particularly through glucose, a simple sugar that is a component of starch and an ingredient in many basic foods.

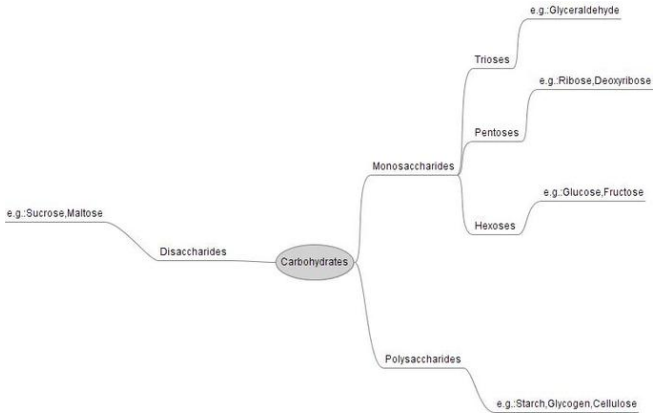


Figure 3.2.1.2.1: Carbohydrates: Carbohydrates are biological macromolecules that are further divided into three subtypes: monosaccharides, disaccharides, and polysaccharides. Like all macromolecules, carbohydrates are necessary for life and are built from smaller organic molecules.

Carbohydrates in Nutrition

Carbohydrates have been a controversial topic within the diet world. People trying to lose weight often avoid carbs, and some diets completely forbid carbohydrate consumption, claiming that a low-carb diet helps people to lose weight faster. However, carbohydrates have been an important part of the human diet for thousands of years; artifacts from ancient civilizations show the presence of wheat, rice, and corn in our ancestors' storage areas.

Carbohydrates should be supplemented with proteins, vitamins, and fats to be parts of a well-balanced diet. Calorie-wise, a gram of carbohydrate provides 4.3 Kcal. In comparison, fats provide 9 Kcal/g, a less desirable ratio. Carbohydrates contain soluble and insoluble elements; the insoluble part is known as fiber, which is mostly cellulose. Fiber has many uses; it promotes regular bowel movement by adding bulk, and it regulates the rate of consumption of blood glucose. Fiber also helps to remove excess cholesterol from the body. Fiber binds and attaches to the cholesterol in the small intestine and prevents the cholesterol particles from entering the bloodstream. Then cholesterol exits the body via the feces. Fiber-rich diets also have a protective role in reducing the occurrence of colon cancer. In addition, a meal containing whole grains and vegetables gives a feeling of fullness. As an immediate source of energy, glucose is broken down during the process of cellular respiration, which produces adenosine triphosphate (ATP), the energy currency of the cell. Without the consumption of carbohydrates, the availability of "instant energy" would be reduced. Eliminating carbohydrates from the diet is not the best way to lose weight. A low-calorie diet that is rich in whole grains, fruits, vegetables, and lean meat, together with plenty of exercise and plenty of water, is the more sensible way to lose weight.

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Key Points

- Carbohydrates provide energy to the body, particularly through glucose, a simple sugar that is found in many basic foods.
- Carbohydrates contain soluble and insoluble elements; the insoluble part is known as fiber, which promotes regular bowel movement, regulates the rate of consumption of blood glucose, and also helps to remove excess cholesterol from the body.
- As an immediate source of energy, glucose is broken down during the process of cellular respiration, which produces ATP, the energy currency of the cell.
- Since carbohydrates are an important part of the human nutrition, eliminating them from the diet is not the best way to lose weight.

Key Terms

- **carbohydrate**: A sugar, starch, or cellulose that is a food source of energy for an animal or plant; a saccharide.
- **glucose**: a simple monosaccharide (sugar) with a molecular formula of C6H12O6; it is a principal source of energy for cellular metabolism
- **ATP**: A nucleotide that occurs in muscle tissue, and is used as a source of energy in cellular reactions, and in the synthesis of nucleic acids. ATP is the abbreviation for adenosine triphosphate.

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SECTION OVERVIEW

3.3: Nucleic Acids- Information Molecules



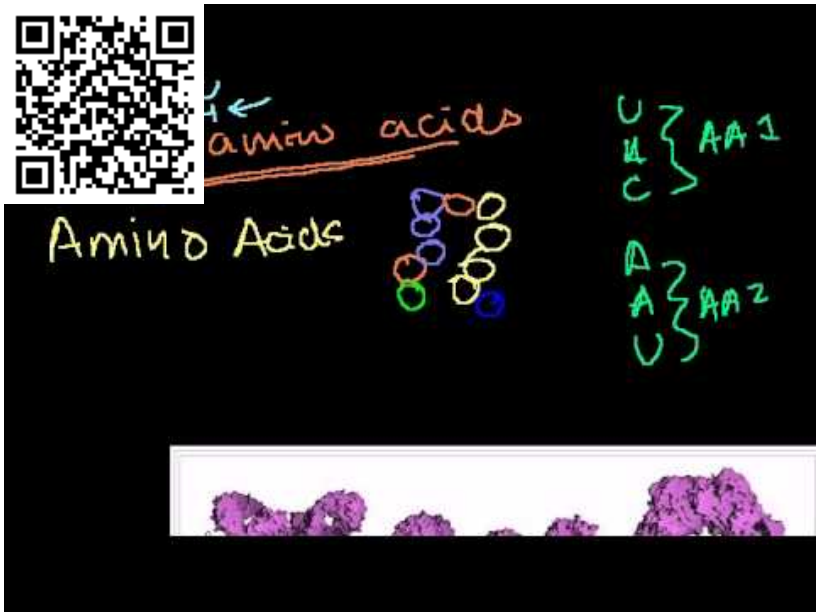
You may have heard that something is "encoded in your DNA." What does that mean?

Nucleic acids. Essentially the "instructions" or "blueprints" of life. Deoxyribonucleic acid, or DNA, is the unique blueprints to make the proteins that give you your traits. Half of these blueprints come from your mother, and half from your father. Therefore, every person that has ever lived - except for identical twins - has his or her own unique set of blueprints - or instructions - or DNA.

Nucleic Acids

A **nucleic acid** is an organic compound, such as DNA or RNA, that is built of small units called**nucleotides**. Many nucleotides bind together to form a chain called a **polynucleotide**. The nucleic acid **DNA** (deoxyribonucleic acid) consists of two polynucleotide chains. The nucleic acid **RNA** (ribonucleic acid) consists of just one polynucleotide chain.

An overview of DNA can be seen at http://www.youtube.com/watch?v=_-vZ_g7K6P0 (28:05).



> *As you view DNA, focus on the following concept:*
>
> *1. the structure and role of DNA.*

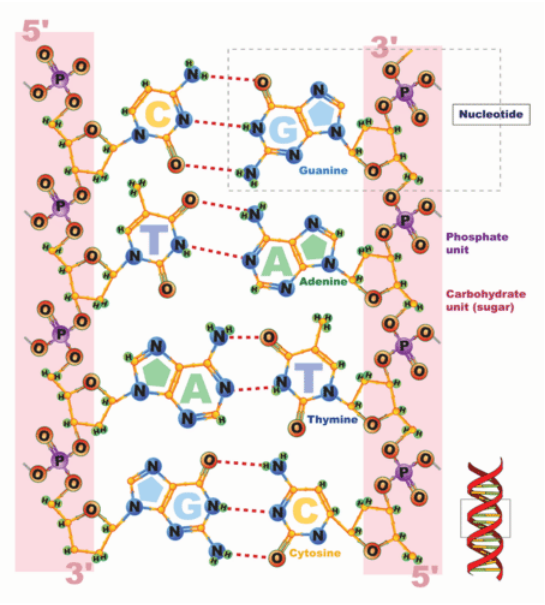
Structure of Nucleic Acids

Each nucleotide consists of three smaller molecules:

1. sugar
2. phosphate group
3. nitrogen base

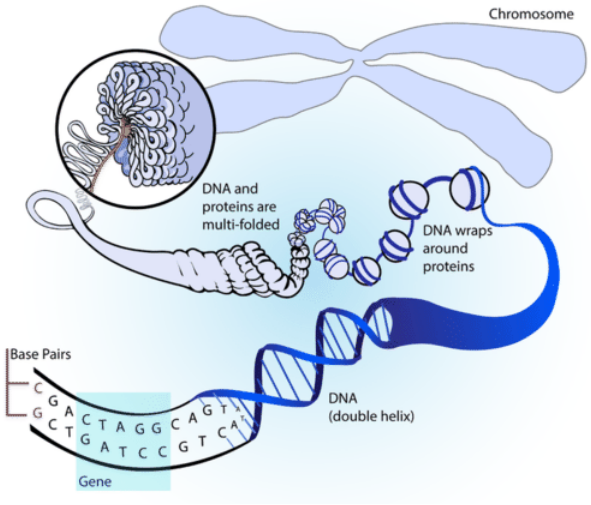
If you look at **Figure** below, you will see that the sugar of one nucleotide binds to the phosphate group of the next nucleotide. These two molecules alternate to form the backbone of the nucleotide chain. This backbone is known as the *sugar-phosphate backbone*.

The nitrogen bases in a nucleic acid stick out from the backbone. There are four different types of bases: cytosine (C), adenine (A), guanine (G), and either thymine (T) in DNA, or uracil (U) in RNA. In DNA, bonds form between bases on the two nucleotide chains and hold the chains together. Each type of base binds with just one other type of base: cytosine always binds with guanine, and adenine always binds with thymine. These pairs of bases are called**complementary base pairs**.



Nucleic Acid. Sugars and phosphate groups form the backbone of a polynucleotide chain. Hydrogen bonds between complementary bases hold two polynucleotide chains together.

The binding of complementary bases allows DNA molecules to take their well-known shape, called a **double helix**, which is shown in **Figure** below. A double helix is like a spiral staircase. The double helix shape forms naturally and is very strong, making the two polynucleotide chains difficult to break apart.

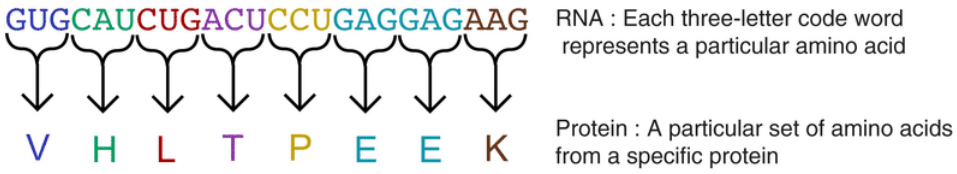


DNA Molecule. Bonds between complementary bases help form the double helix of a DNA molecule. The letters A, T, G, and C stand for the bases adenine, thymine, guanine, and cytosine. The sequence of these four bases in DNA is a code that carries instructions for making proteins. Shown is how the DNA winds into a chromosome.

An animation of DNA structure can be viewed at http://www.youtube.com/watch?v=qy8dk5iS1f0.

Roles of Nucleic Acids

DNA is also known as the hereditary material or genetic information. It is found in genes, and its sequence of bases makes up a code. Between "starts" and "stops," the code carries instructions for the correct sequence of amino acids in a protein (see **Figure** below). DNA and RNA have different functions relating to the genetic code and proteins. Like a set of blueprints, DNA contains the genetic instructions for the correct sequence of amino acids in proteins. RNA uses the information in DNA to assemble the correct amino acids and help make the protein. The information in DNA is passed from parent cells to daughter cells whenever cells divide. The information in DNA is also passed from parents to offspring when organisms reproduce. This is how inherited characteristics are passed from one generation to the next.



The letters G, U, C, and A stand for the bases in RNA. Each group of three bases makes up a code word, and each code word represents one amino acid (represented here by a single letter, such as V, H, or L). A string of code words specifies the sequence of amino acids in a protein.

Summary

- DNA and RNA are nucleic acids. Nucleic acids are built of small units called nucleotides.
- The bases of DNA are adenine, guanine, cytosine and thymine. In RNA, thymine is replaced by uracil.
- In DNA, A always binds to T, and G always binds to C.
- The shape of the DNA molecule is known as a double helix.
- DNA contains the genetic instructions for the correct sequence of amino acids in proteins. RNA uses the information in DNA to assemble the correct amino acids and help make the protein.

Explore More

Use this resource to answer the questions that follow.

- **What is DNA?** at learn.genetics.utah.edu/content/begin/dna/.

1. Why is DNA referred to as the "instructions"?
2. Where is DNA located in the cell?
3. What do A, C, G and T refer to? How can only four letters tell the cell what to do?
4. What is a gene?

Review

1. Identify the three parts of a nucleotide.
2. What is DNA?
3. What are complementary base pairs? Give an example.
4. Describe the shape of DNA.
5. How are DNA and RNA related to proteins?

3.3.1: DNA and RNA

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3.3.1: DNA and RNA

Learning Objectives

- Describe the structure of nucleic acids and the types of molecules that contain them

Types of Nucleic Acids

The two main types of nucleic acids are deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). DNA is the genetic material found in all living organisms, ranging from single-celled bacteria to multicellular mammals. It is found in the nucleus of eukaryotes and in the chloroplasts and mitochondria. In prokaryotes, the DNA is not enclosed in a membranous envelope, but rather free-floating within the cytoplasm.

The entire genetic content of a cell is known as its genome and the study of genomes is genomics. In eukaryotic cells, but not in prokaryotes, DNA forms a complex with histone proteins to form chromatin, the substance of eukaryotic chromosomes. A chromosome may contain tens of thousands of genes. Many genes contain the information to make protein products; other genes code for RNA products. DNA controls all of the cellular activities by turning the genes “on” or “off. ”

The other type of nucleic acid, RNA, is mostly involved in protein synthesis. In eukaryotes, the DNA molecules never leave the nucleus but instead use an intermediary to communicate with the rest of the cell. This intermediary is the messenger RNA (mRNA). Other types of RNA—like rRNA, tRNA, and microRNA—are involved in protein synthesis and its regulation.

Nucleotides

DNA and RNA are made up of monomers known as nucleotides. The nucleotides combine with each other to form a polynucleotide: DNA or RNA. Each nucleotide is made up of three components:

1. a nitrogenous base
2. a pentose (five-carbon) sugar
3. a phosphate group

Each nitrogenous base in a nucleotide is attached to a sugar molecule, which is attached to one or more phosphate groups.

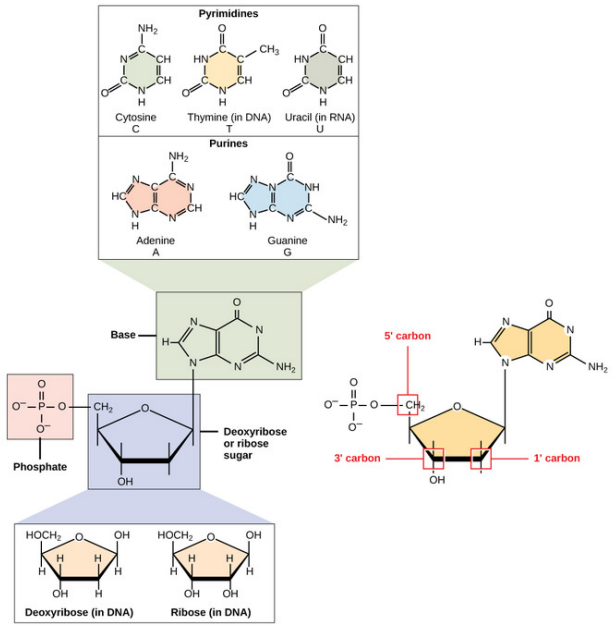


Figure **3.3.1.1**: DNA and RNA: A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and one or more phosphate groups. Carbon residues in the pentose are numbered 1′ through 5′ (the prime distinguishes these residues from those in the base, which are numbered without using a prime notation). The base is attached to the 1′ position of the ribose, and the phosphate is attached to the 5′ position. When a polynucleotide is formed, the 5′ phosphate of the incoming nucleotide attaches to the 3′ hydroxyl group at the end of the growing chain. Two types of pentose are found in nucleotides, deoxyribose (found in DNA) and ribose (found in RNA). Deoxyribose is similar in structure to ribose, but it has an H instead of an OH at the 2′ position. Bases can be divided into two categories: purines and pyrimidines. Purines have a double ring structure, and pyrimidines have a single ring.

Nitrogenous Base

The nitrogenous bases are organic molecules and are so named because they contain carbon and nitrogen. They are bases because they contain an amino group that has the potential of binding an extra hydrogen, and thus, decreasing the hydrogen ion concentration in its environment, making it more basic. Each nucleotide in DNA contains one of four possible nitrogenous bases: adenine (A), guanine (G) cytosine (C), and thymine (T).

Adenine and guanine are classified as purines. The primary structure of a purine consists of two carbon-nitrogen rings. Cytosine, thymine, and uracil are classified as pyrimidines which have a single carbon-nitrogen ring as their primary structure. Each of these basic carbon-nitrogen rings has different functional groups attached to it. In molecular biology shorthand, the nitrogenous bases are simply known by their symbols A, T, G, C, and U. DNA contains A, T, G, and C whereas RNA contains A, U, G, and C.

Five-Carbon Sugar

The pentose sugar in DNA is deoxyribose and in RNA it is ribose. The difference between the sugars is the presence of the hydroxyl group on the second carbon of the ribose and hydrogen on the second carbon of the deoxyribose. The carbon atoms of the sugar molecule are numbered as 1′, 2′, 3′, 4′, and 5′ (1′ is read as “one prime”).

Phosphate Group

The phosphate residue is attached to the hydroxyl group of the 5′ carbon of one sugar and the hydroxyl group of the 3′ carbon of the sugar of the next nucleotide, which forms a 5′3′ phosphodiester linkage. The phosphodiester linkage is not formed by simple dehydration reaction like the other linkages connecting monomers in macromolecules: its formation involves the removal of two phosphate groups. A polynucleotide may have thousands of such phosphodiester linkages.

Key Points

- The two main types of nucleic acids are DNA and RNA.
- Both DNA and RNA are made from nucleotides, each containing a five-carbon sugar backbone, a phosphate group, and a nitrogen base.

- DNA provides the code for the cell ‘s activities, while RNA converts that code into proteins to carry out cellular functions.
- The sequence of nitrogen bases (A, T, C, G) in DNA is what forms an organism’s traits.
- The nitrogen bases A and T (or U in RNA) always go together and C and G always go together, forming the 5′-3′ phosphodiester linkage found in the nucleic acid molecules.

Key Terms

- **nucleotide**: the monomer comprising DNA or RNA molecules; consists of a nitrogenous heterocyclic base that can be a purine or pyrimidine, a five-carbon pentose sugar, and a phosphate group
- **genome**: the cell’s complete genetic information packaged as a double-stranded DNA molecule
- **monomer**: A relatively small molecule which can be covalently bonded to other monomers to form a polymer.

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SECTION OVERVIEW

3.4: Proteins- Molecules with Diverse Structures and Functions

3.4.1: Types and Functions of Proteins

3.4.2: Amino Acids

3.4.3: Protein Structure

3.4.4: Denaturation and Protein Folding

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3.4.1: Types and Functions of Proteins

Learning Objectives

- Differentiate among the types and functions of proteins

Types and Functions of Proteins

Proteins perform essential functions throughout the systems of the human body. These long chains of amino acids are critically important for:

- catalyzing chemical reactions
- synthesizing and repairing DNA
- transporting materials across the cell
- receiving and sending chemical signals
- responding to stimuli
- providing structural support

Proteins (a polymer) are macromolecules composed of amino acid subunits (the monomers). These amino acids are covalently attached to one another to form long linear chains called polypeptides, which then fold into a specific three-dimensional shape. Sometimes these folded polypeptide chains are functional by themselves. Other times they combine with additional polypeptide chains to form the final protein structure. Sometimes non-polypeptide groups are also required in the final protein. For instance, the blood protein hemogobin is made up of four polypeptide chains, each of which also contains a heme molecule, which is ring structure with an iron atom in its center.

Proteins have different shapes and molecular weights, depending on the amino acid sequence. For example, hemoglobin is a globular protein, which means it folds into a compact globe-like structure, but collagen, found in our skin, is a fibrous protein, which means it folds into a long extended fiber-like chain. You probably look similar to your family members because you share similar proteins, but you look different from strangers because the proteins in your eyes, hair, and the rest of your body are different.

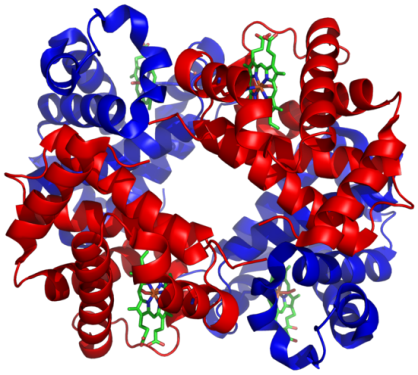


Figure **3.4.1.1**: Human Hemoglobin: Structure of human hemoglobin. The proteins' α and β subunits are in red and blue, and the iron-containing heme groups in green. From the protein data base.

Because form determines function, any slight change to a protein's shape may cause the protein to become dysfunctional. Small changes in the amino acid sequence of a protein can cause devastating genetic diseases such as Huntington's disease or sickle cell anemia.

Enzymes

Enzymes are proteins that catalyze biochemical reactions, which otherwise would not take place. These enzymes are essential for chemical processes like digestion and cellular metabolism. Without enzymes, most physiological processes would proceed so

slowly (or not at all) that life could not exist.

Because form determines function, each enzyme is specific to its substrates. The substrates are the reactants that undergo the chemical reaction catalyzed by the enzyme. The location where substrates bind to or interact with the enzyme is known as the active site, because that is the site where the chemistry occurs. When the substrate binds to its active site at the enzyme, the enzyme may help in its breakdown, rearrangement, or synthesis. By placing the substrate into a specific shape and microenvironment in the active site, the enzyme encourages the chemical reaction to occur. There are two basic classes of enzymes:

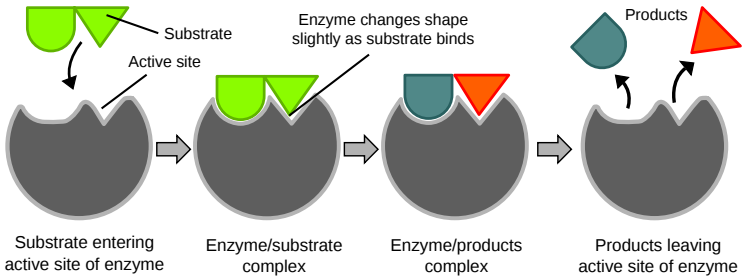


Figure **3.4.1.1**: Enzyme reaction: A catabolic enzyme reaction showing the substrate matching the exact shape of the active site.

- Catabolic enzymes: enzymes that break down their substrate
- Anabolic enzymes: enzymes that build more complex molecules from their substrates

Enzymes are essential for digestion: the process of breaking larger food molecules down into subunits small enough to diffuse through a cell membrane and to be used by the cell. These enzymes include amylase, which catalyzes the digestion carbohydrates in the mouth and small intestine; pepsin, which catalyzes the digestion of proteins in the stomach; lipase, which catalyzes reactions need to emulsify fats in the small intestine; and trypsin, which catalyzes the further digestion of proteins in the small intestine.

Enzymes are also essential for biosynthesis: the process of making new, complex molecules from the smaller subunits that are provided to or generated by the cell. These biosynthetic enzymes include DNA Polymerase, which catalyzes the synthesis of new strands of the genetic material before cell division; fatty acid synthetase, which the synthesis of new fatty acids for fat or membrane lipid formation; and components of the ribosome, which catalyzes the formation of new polypeptides from amino acid monomers.

Hormones

Some proteins function as chemical-signaling molecules called hormones. These proteins are secreted by endocrine cells that act to control or regulate specific physiological processes, which include growth, development, metabolism, and reproduction. For example, insulin is a protein hormone that helps to regulate blood glucose levels. Other proteins act as receptors to detect the concentrations of chemicals and send signals to respond. Some types of hormones, such as estrogen and testosterone, are lipid steroids, not proteins.

Other Protein Functions

Proteins perform essential functions throughout the systems of the human body. In the respiratory system, hemoglobin (composed of four protein subunits) transports oxygen for use in cellular metabolism. Additional proteins in the blood plasma and lymph carry nutrients and metabolic waste products throughout the body. The proteins actin and tubulin form cellular structures, while keratin forms the structural support for the dead cells that become fingernails and hair. Antibodies, also called immunoglobins, help recognize and destroy foreign pathogens in the immune system. Actin and myosin allow muscles to contract, while albumin nourishes the early development of an embryo or a seedling.

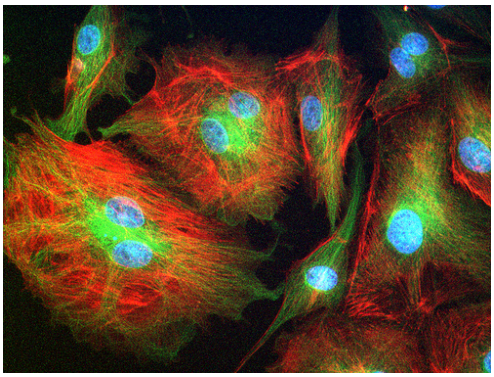


Figure **3.4.1.1**: Tubulin: The structural protein tubulin stained red in mouse cells.

Key Points

- Proteins are essential for the main physiological processes of life and perform functions in every system of the human body.
- A protein's shape determines its function.
- Proteins are composed of amino acid subunits that form polypeptide chains.
- Enzymes catalyze biochemical reactions by speeding up chemical reactions, and can either break down their substrate or build larger molecules from their substrate.
- The shape of an enzyme's active site matches the shape of the substrate.
- Hormones are a type of protein used for cell signaling and communication.

Key Terms

- **amino acid**: Any of 20 naturally occurring α-amino acids (having the amino, and carboxylic acid groups on the same carbon atom), and a variety of side chains, that combine, via peptide bonds, to form proteins.
- **polypeptide**: Any polymer of (same or different) amino acids joined via peptide bonds.
- **catalyze**: To accelerate a process.

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3.4.2: Amino Acids

Learning Objectives

- Describe the structure of an amino acid and the features that confer its specific properties

Structure of an Amino Acid

Amino acids are the monomers that make up proteins. Each amino acid has the same fundamental structure, which consists of a central carbon atom, also known as the alpha (α) carbon, bonded to an amino group (NH_2), a carboxyl group (COOH), and to a hydrogen atom. In the aqueous environment of the cell, the both the amino group and the carboxyl group are ionized under physiological conditions, and so have the structures $-NH_3^+$ and $-COO^-$, respectively. Every amino acid also has another atom or group of atoms bonded to the central atom known as the R group. This R group, or side chain, gives each amino acid proteins specific characteristics, including size, polarity, and pH.

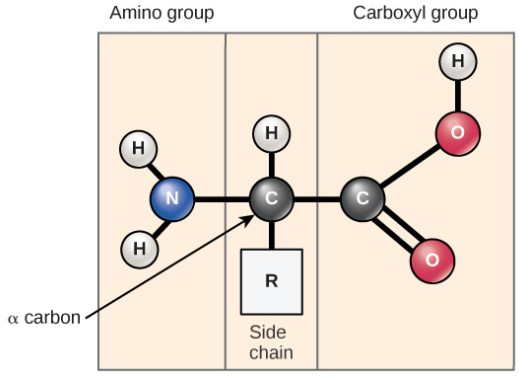


Figure **3.4.2.1**: Amino acid structure: Amino acids have a central asymmetric carbon to which an amino group, a carboxyl group, a hydrogen atom, and a side chain (R group) are attached. This amino acid is unionized, but if it were placed in water at pH 7, its amino group would pick up another hydrogen and a positive charge, and the hydroxyl in its carboxyl group would lose and a hydrogen and gain a negative charge.

Types of Amino Acids

The name “amino acid” is derived from the amino group and carboxyl-acid-group in their basic structure. There are 21 amino acids present in proteins, each with a specific R group or side chain. Ten of these are considered essential amino acids in humans because the human body cannot produce them and they must be obtained from the diet. All organisms have different essential amino acids based on their physiology.

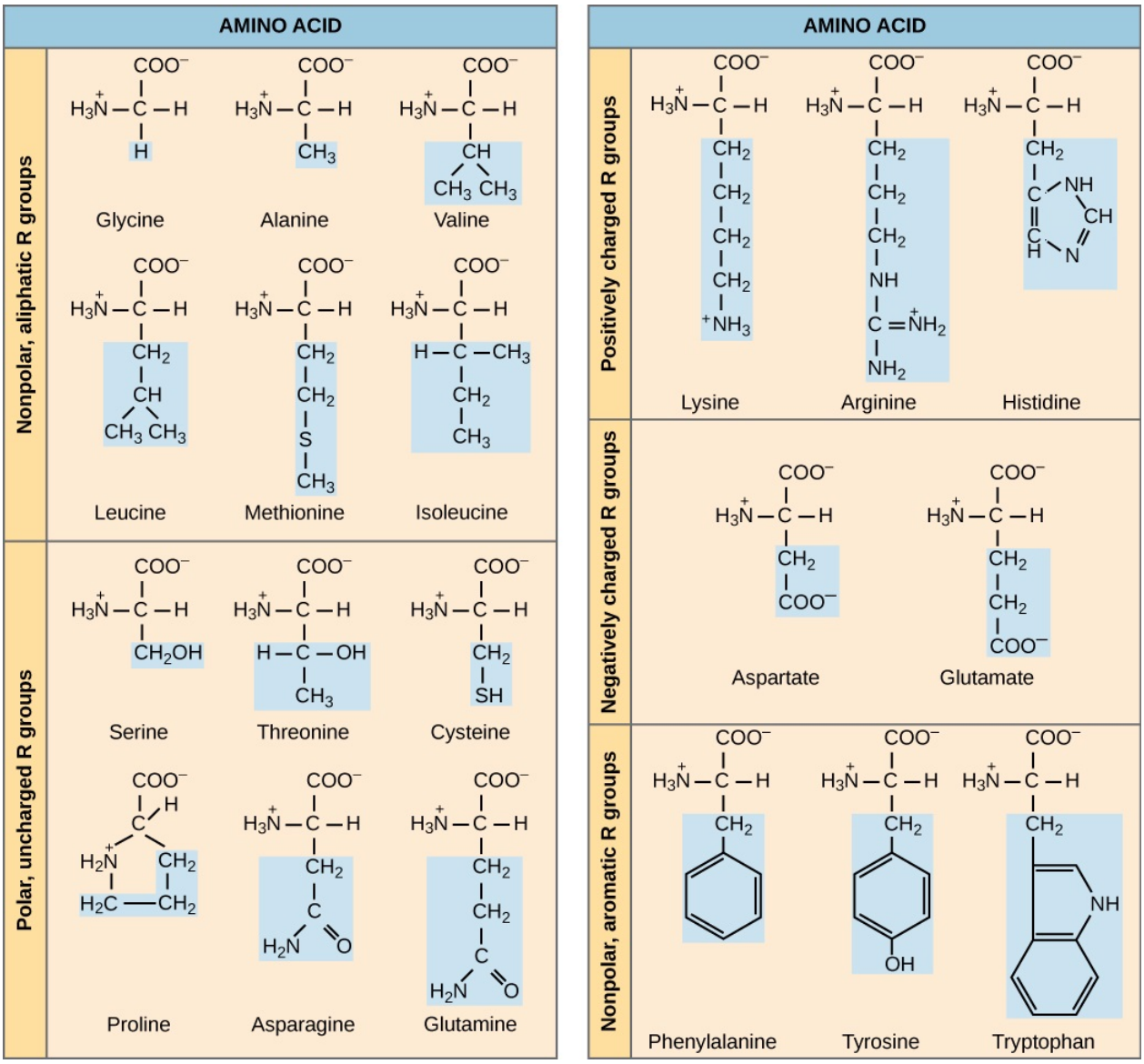


Figure **3.4.2.1**: Types of amino acids: There are 21 common amino acids commonly found in proteins, each with a different R group (variant group) that determines its chemical nature. The 21st amino acid, not shown here, is selenocysteine, with an R group of -CH_2-SeH.

Characteristics of Amino Acids

Which categories of amino acid would you expect to find on the surface of a soluble protein, and which would you expect to find in the interior? What distribution of amino acids would you expect to find in a protein embedded in a lipid bilayer?

The chemical composition of the side chain determines the characteristics of the amino acid. Amino acids such as valine, methionine, and alanine are nonpolar (hydrophobic), while amino acids such as serine, threonine, and cysteine are polar (hydrophilic). The side chains of lysine and arginine are positively charged so these amino acids are also known as basic (high pH) amino acids. Proline is an exception to the standard structure of an amino acid because its R group is linked to the amino group, forming a ring-like structure.

Amino acids are represented by a single upper case letter or a three-letter abbreviation. For example, valine is known by the letter V or the three-letter symbol val.

Peptide Bonds

The sequence and the number of amino acids ultimately determine the protein's shape, size, and function. Each amino acid is attached to another amino acid by a covalent bond, known as a peptide bond. When two amino acids are covalently attached by a peptide bond, the carboxyl group of one amino acid and the amino group of the incoming amino acid combine and release a molecule of water. Any reaction that combines two monomers in a reaction that generates H_2O as one of the products is known as a dehydration reaction, so peptide bond formation is an example of a dehydration reaction.

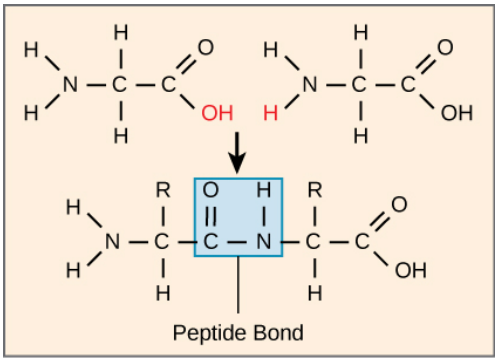


Figure **3.4.2.1**: Peptide bond formation: Peptide bond formation is a dehydration synthesis reaction. The carboxyl group of one amino acid is linked to the amino group of the incoming amino acid. In the process, a molecule of water is released.

Polypeptide Chains

The resulting chain of amino acids is called a polypeptide chain. Each polypeptide has a free amino group at one end. This end is called the N terminal, or the amino terminal, and the other end has a free carboxyl group, also known as the C or carboxyl terminal. When reading or reporting the amino acid sequence of a protein or polypeptide, the convention is to use the N-to-C direction. That is, the first amino acid in the sequence is assumed to the be one at the N terminal and the last amino acid is assumed to be the one at the C terminal.

Although the terms polypeptide and protein are sometimes used interchangeably, a polypeptide is technically any polymer of amino acids, whereas the term protein is used for a polypeptide or polypeptides that have folded properly, combined with any additional components needed for proper functioning, and is now functional.

Key Points

- Each amino acid contains a central C atom, an amino group (NH2), a carboxyl group (COOH), and a specific R group.
- The R group determines the characteristics (size, polarity, and pH) for each type of amino acid.
- Peptide bonds form between the carboxyl group of one amino acid and the amino group of another through dehydration synthesis.
- A chain of amino acids is a polypeptide.

Key Terms

- **amino acid**: Any of 20 naturally occurring α-amino acids (having the amino, and carboxylic acid groups on the same carbon atom), and a variety of side chains, that combine, via peptide bonds, to form proteins.
- **R group**: The R group is a side chain specific to each amino acid that confers particular chemical properties to that amino acid.
- **polypeptide**: Any polymer of (same or different) amino acids joined via peptide bonds.

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3.4.3: Protein Structure

Learning Objectives

- Summarize the four levels of protein structure

The shape of a protein is critical to its function because it determines whether the protein can interact with other molecules. Protein structures are very complex, and researchers have only very recently been able to easily and quickly determine the structure of complete proteins down to the atomic level. (The techniques used date back to the 1950s, but until recently they were very slow and laborious to use, so complete protein structures were very slow to be solved.) Early structural biochemists conceptually divided protein structures into four "levels" to make it easier to get a handle on the complexity of the overall structures. To determine how the protein gets its final shape or conformation, we need to understand these four levels of protein structure: primary, secondary, tertiary, and quaternary.

Primary Structure

A protein's primary structure is the unique sequence of amino acids in each polypeptide chain that makes up the protein. Really, this is just a list of which amino acids appear in which order in a polypeptide chain, not really a structure. But, because the final protein structure ultimately depends on this sequence, this was called the primary structure of the polypeptide chain. For example, the pancreatic hormone insulin has two polypeptide chains, A and B.

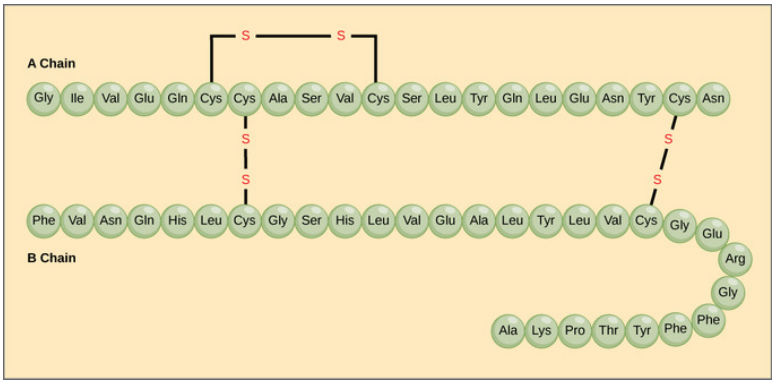


Figure **3.4.3.1**: Primary structure: The A chain of insulin is 21 amino acids long and the B chain is 30 amino acids long, and each sequence is unique to the insulin protein.

The gene, or sequence of DNA, ultimately determines the unique sequence of amino acids in each peptide chain. A change in nucleotide sequence of the gene's coding region may lead to a different amino acid being added to the growing polypeptide chain, causing a change in protein structure and therefore function.

The oxygen-transport protein hemoglobin consists of four polypeptide chains, two identical α chains and two identical β chains. In sickle cell anemia, a single amino substitution in the hemoglobin β chain causes a change the structure of the entire protein. When the amino acid glutamic acid is replaced by valine in the β chain, the polypeptide folds into an slightly-different shape that creates a dysfunctional hemoglobin protein. So, just one amino acid substitution can cause dramatic changes. These dysfunctional hemoglobin proteins, under low-oxygen conditions, start associating with one another, forming long fibers made from millions of aggregated hemoglobins that distort the red blood cells into crescent or "sickle" shapes, which clog arteries. People affected by the disease often experience breathlessness, dizziness, headaches, and abdominal pain.

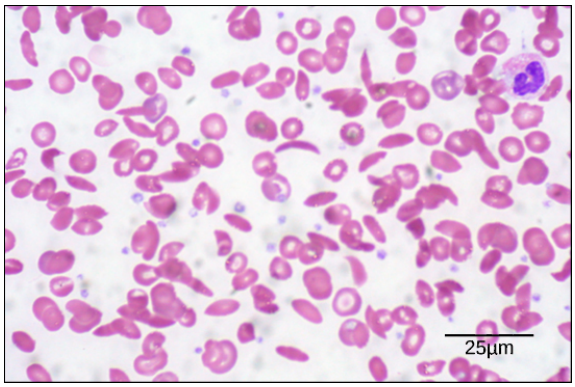


Figure **3.4.3.1**: Sickle cell disease: Sickle cells are crescent shaped, while normal cells are disc-shaped.

Secondary Structure

A protein's secondary structure is whatever regular structures arise from interactions between neighboring or near-by amino acids as the polypeptide starts to fold into its functional three-dimensional form. Secondary structures arise as H bonds form between local groups of amino acids in a region of the polypeptide chain. Rarely does a single secondary structure extend throughout the polypeptide chain. It is usually just in a section of the chain. The most common forms of secondary structure are the α-helix and β-pleated sheet structures and they play an important structural role in most globular and fibrous proteins.

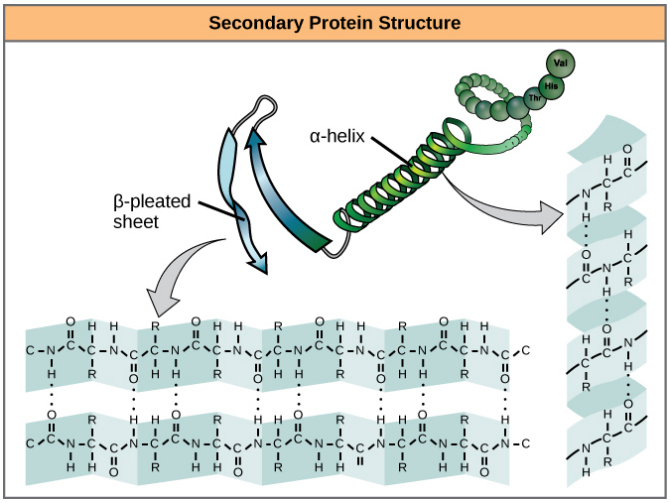


Figure **3.4.3.1**: Secondary structure: The α-helix and β-pleated sheet form because of hydrogen bonding between carbonyl and amino groups in the peptide backbone. Certain amino acids have a propensity to form an α-helix, while others have a propensity to form a β-pleated sheet.

In the α-helix chain, the hydrogen bond forms between the oxygen atom in the polypeptide backbone carbonyl group in one amino acid and the hydrogen atom in the polypeptide backbone amino group of another amino acid that is four amino acids farther along the chain. This holds the stretch of amino acids in a right-handed coil. Every helical turn in an alpha helix has 3.6 amino acid residues. The R groups (the side chains) of the polypeptide protrude out from the α-helix chain and are not involved in the H bonds that maintain the α-helix structure.

In β-pleated sheets, stretches of amino acids are held in an almost fully-extended conformation that "pleats" or zig-zags due to the non-linear nature of single C-C and C-N covalent bonds. β-pleated sheets never occur alone. They have to held in place by other β-pleated sheets. The stretches of amino acids in β-pleated sheets are held in their pleated sheet structure because hydrogen bonds form between the oxygen atom in a polypeptide backbone carbonyl group of one β-pleated sheet and the hydrogen atom in a polypeptide backbone amino group of another β-pleated sheet. The β-pleated sheets which hold each other together align parallel or antiparallel to each other. The R groups of the amino acids in a β-pleated sheet point out perpendicular to the hydrogen bonds holding the β-pleated sheets together, and are not involved in maintaining the β-pleated sheet structure.

Tertiary Structure

The tertiary structure of a polypeptide chain is its overall three-dimensional shape, once all the secondary structure elements have folded together among each other. Interactions between polar, nonpolar, acidic, and basic R group within the polypeptide chain create the complex three-dimensional tertiary structure of a protein. When protein folding takes place in the aqueous environment of the body, the hydrophobic R groups of nonpolar amino acids mostly lie in the interior of the protein, while the hydrophilic R groups lie mostly on the outside. Cysteine side chains form disulfide linkages in the presence of oxygen, the only covalent bond forming during protein folding. All of these interactions, weak and strong, determine the final three-dimensional shape of the protein. When a protein loses its three-dimensional shape, it will no longer be functional.

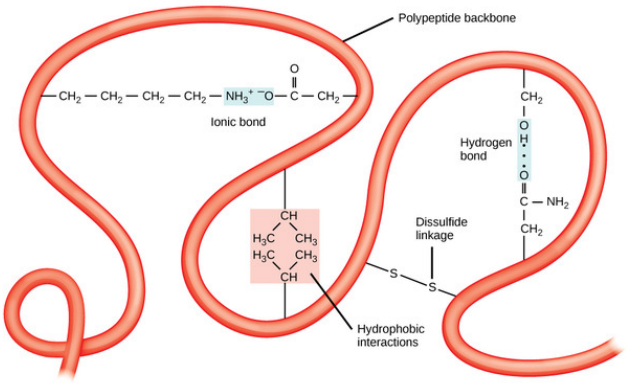


Figure **3.4.3.1**: Tertiary structure: The tertiary structure of proteins is determined by hydrophobic interactions, ionic bonding, hydrogen bonding, and disulfide linkages.

Quaternary Structure

The quaternary structure of a protein is how its subunits are oriented and arranged with respect to one another. As a result, quaternary structure only applies to multi-subunit proteins; that is, proteins made from more than one polypeptide chain. Proteins made from a single polypeptide will not have a quaternary structure.

In proteins with more than one subunit, weak interactions between the subunits help to stabilize the overall structure. Enzymes often play key roles in bonding subunits to form the final, functioning protein.

For example, insulin is a ball-shaped, globular protein that contains both hydrogen bonds and disulfide bonds that hold its two polypeptide chains together. Silk is a fibrous protein that results from hydrogen bonding between different β-pleated chains.

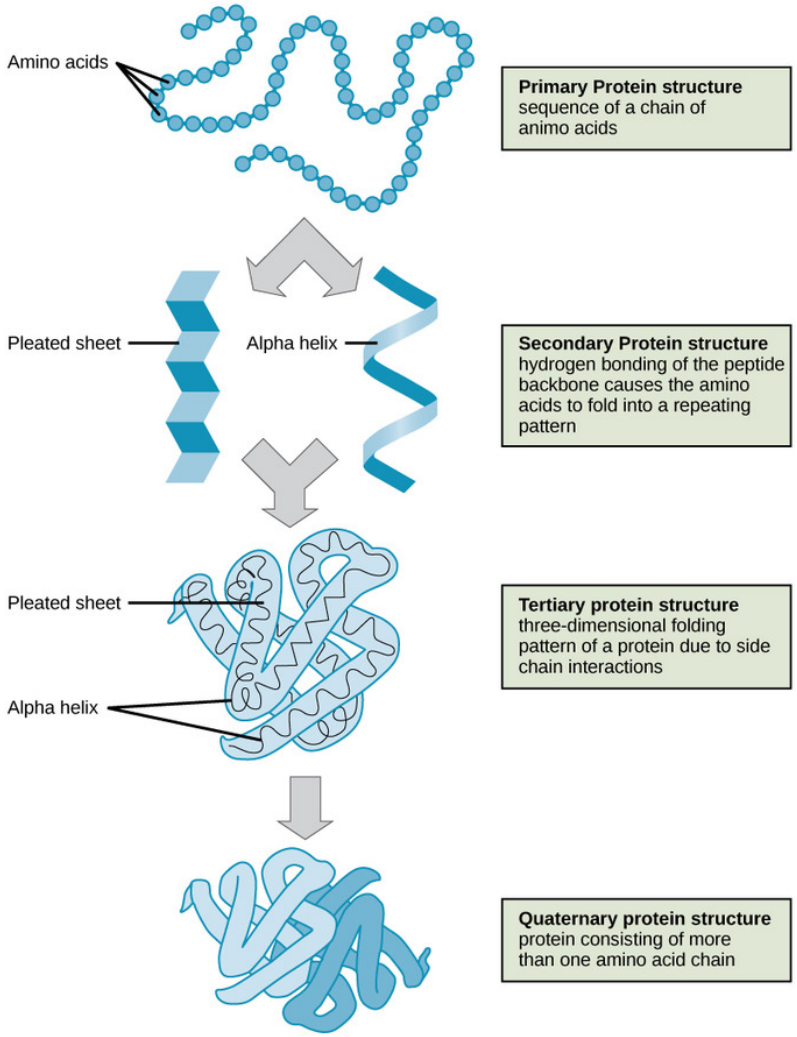


Figure **3.4.3.1**: Four levels of protein structure: The four levels of protein structure can be observed in these illustrations.

Key Points

- Protein structure depends on its amino acid sequence and local, low-energy chemical bonds between atoms in both the polypeptide backbone and in amino acid side chains.
- Protein structure plays a key role in its function; if a protein loses its shape at any structural level, it may no longer be functional.
- Primary structure is the amino acid sequence.
- Secondary structure is local interactions between stretches of a polypeptide chain and includes α-helix and β-pleated sheet structures.
- Tertiary structure is the overall the three-dimension folding driven largely by interactions between R groups.
- Quarternary structures is the orientation and arrangement of subunits in a multi-subunit protein.

Key Terms

- **antiparallel**: The nature of the opposite orientations of the two strands of DNA or two beta strands that comprise a protein's secondary structure
- **disulfide bond**: A bond, consisting of a covalent bond between two sulfur atoms, formed by the reaction of two thiol groups, especially between the thiol groups of two proteins
- **β-pleated sheet**: secondary structure of proteins where N-H groups in the backbone of one fully-extended strand establish hydrogen bonds with C=O groups in the backbone of an adjacent fully-extended strand

- **α-helix**: secondary structure of proteins where every backbone N-H creates a hydrogen bond with the C=O group of the amino acid four residues earlier in the same helix.

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3.4.4: Denaturation and Protein Folding

Learning Objectives

- Discuss the process of protein denaturation

Each protein has its own unique sequence of amino acids and the interactions between these amino acids create a specify shape. This shape determines the protein's function, from digesting protein in the stomach to carrying oxygen in the blood.

Changing the Shape of a Protein

If the protein is subject to changes in temperature, pH, or exposure to chemicals, the internal interactions between the protein's amino acids can be altered, which in turn may alter the shape of the protein. Although the amino acid sequence (also known as the protein's primary structure) does not change, the protein's shape may change so much that it becomes dysfunctional, in which case the protein is considered denatured. Pepsin, the enzyme that breaks down protein in the stomach, only operates at a very low pH. At higher pHs pepsin's conformation, the way its polypeptide chain is folded up in three dimensions, begins to change. The stomach maintains a very low pH to ensure that pepsin continues to digest protein and does not denature.

Because almost all biochemical reactions require enzymes, and because almost all enzymes only work optimally within relatively narrow temperature and pH ranges, many homeostatic mechanisms regulate appropriate temperatures and pH so that the enzymes can maintain the shape of their active site.

Reversing Denaturation

It is often possible to reverse denaturation because the primary structure of the polypeptide, the covalent bonds holding the amino acids in their correct sequence, is intact. Once the denaturing agent is removed, the original interactions between amino acids return the protein to its original conformation and it can resume its function. However, denaturation can be irreversible in extreme situations, like frying an egg. The heat from a pan denatures the albumin protein in the liquid egg white and it becomes insoluble. The protein in meat also denatures and becomes firm when cooked.

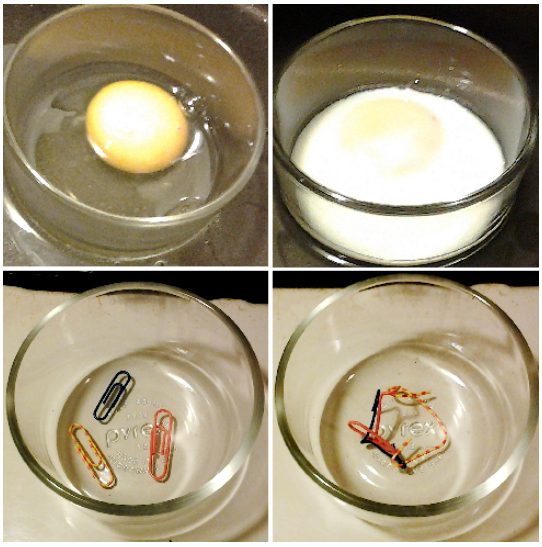


Figure **3.4.4.1**: Denaturing a protein is occasionally irreversible: (Top) The protein albumin in raw and cooked egg white. (Bottom) A paperclip analogy visualizes the process: when cross-linked, paperclips ('amino acids') no longer move freely; their structure is rearranged and 'denatured'.

Chaperone proteins (or chaperonins) are helper proteins that provide favorable conditions for protein folding to take place. The chaperonins clump around the forming protein and prevent other polypeptide chains from aggregating. Once the target protein folds, the chaperonins disassociate.

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Key Points

- Proteins change their shape when exposed to different pH or temperatures.
- The body strictly regulates pH and temperature to prevent proteins such as enzymes from denaturing.
- Some proteins can refold after denaturation while others cannot.
- Chaperone proteins help some proteins fold into the correct shape.

Key Terms

- **chaperonin**: proteins that provide favorable conditions for the correct folding of other proteins, thus preventing aggregation
- **denaturation**: the change of folding structure of a protein (and thus of physical properties) caused by heating, changes in pH, or exposure to certain chemicals

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SECTION OVERVIEW

3.5: Lipids- Hydrophobic Molecules

3.5.1: Lipid Molecules

3.5.2: Phospholipids

3.5.3: Steroids

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3.5.1: Lipid Molecules

Learning Objectives

- Differentiate between saturated and unsaturated fatty acids

Glycerol and Fatty Acids

A fat molecule consists of two main components: glycerol and fatty acids. Glycerol is an alcohol with three carbons, five hydrogens, and three hydroxyl (OH) groups. Fatty acids have a long chain of hydrocarbons with a carboxyl group attached and may have 4-36 carbons; however, most of them have 12-18. In a fat molecule, the fatty acids are attached to each of the three carbons of the glycerol molecule with an ester bond through the oxygen atom. During the ester bond formation, three molecules are released. Since fats consist of three fatty acids and a glycerol, they are also called triacylglycerols or triglycerides.

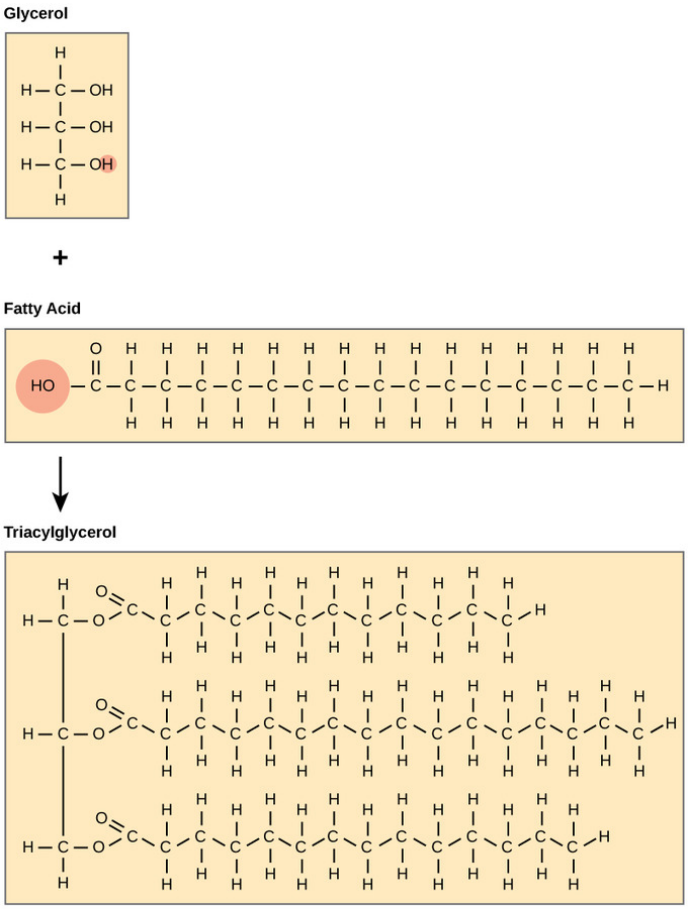


Figure **3.5.1.1**: Triacylglycerols: Triacylglycerol is formed by the joining of three fatty acids to a glycerol backbone in a dehydration reaction. Three molecules of water are released in the process.

Saturated vs. Unsaturated Fatty Acids

Fatty acids may be saturated or unsaturated. In a fatty acid chain, if there are only single bonds between neighboring carbons in the hydrocarbon chain, the fatty acid is said to be saturated. Saturated fatty acids are saturated with hydrogen since single bonds increase the number of hydrogens on each carbon. Stearic acid and palmitic acid, which are commonly found in meat, are examples of saturated fats.

When the hydrocarbon chain contains a double bond, the fatty acid is said to be unsaturated. Oleic acid is an example of an unsaturated fatty acid. Most unsaturated fats are liquid at room temperature and are called oils. If there is only one double bond in the molecule, then it is known as a monounsaturated fat; e.g. olive oil. If there is more than one double bond, then it is known as a

polyunsaturated fat; e.g. canola oil. Unsaturated fats help to lower blood cholesterol levels whereas saturated fats contribute to plaque formation in the arteries.

Unsaturated fats or oils are usually of plant origin and contain cis unsaturated fatty acids. Cis and trans indicate the configuration of the molecule around the double bond. If hydrogens are present in the same plane, it is referred to as a cis fat; if the hydrogen atoms are on two different planes, it is referred to as a trans fat. The cis double bond causes a bend or a “kink” that prevents the fatty acids from packing tightly, keeping them liquid at room temperature.

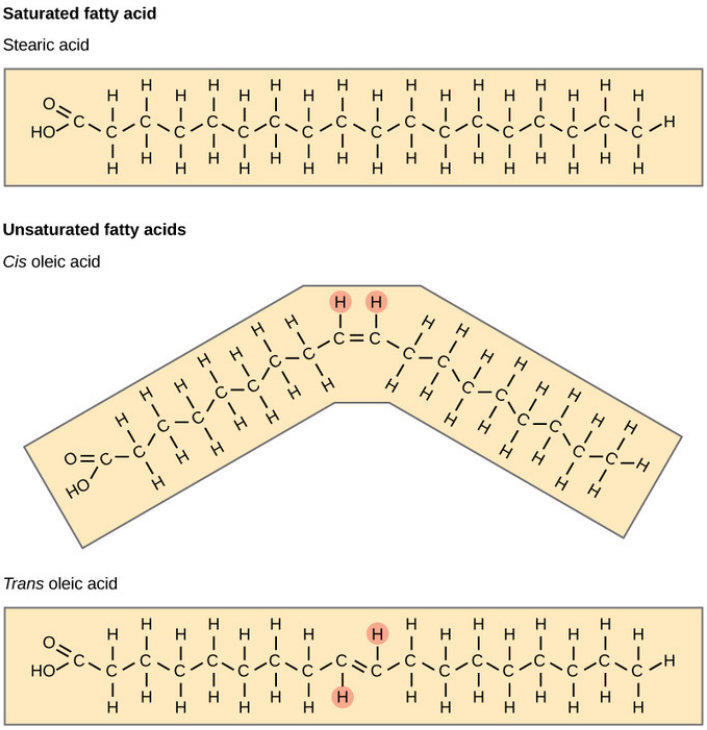


Figure 3.5.1.1: Fatty Acids: Saturated fatty acids have hydrocarbon chains connected by single bonds only. Unsaturated fatty acids have one or more double bonds. Each double bond may be in a cis or trans configuration. In the cis configuration, both hydrogens are on the same side of the hydrocarbon chain. In the trans configuration, the hydrogens are on opposite sides. A cis double bond causes a kink in the chain.

Trans Fats

In the food industry, oils are artificially hydrogenated to make them semi-solid and of a consistency desirable for many processed food products. During this hydrogenation process, gas is bubbled through oils to solidify them, and the double bonds of the cis-conformation in the hydrocarbon chain may be converted to double bonds in the trans-conformation.

Margarine, some types of peanut butter, and shortening are examples of artificially-hydrogenated trans fats. Recent studies have shown that an increase in trans fats in the human diet may lead to an increase in levels of low-density lipoproteins (LDL), or “bad” cholesterol, which in turn may lead to plaque deposition in the arteries, resulting in heart disease. Many fast food restaurants have recently banned the use of trans fats, and food labels are required to display the trans fat content.

Essential Fatty Acids

Essential fatty acids are fatty acids required for biological processes, but not synthesized by the human body. Consequently, they have to be supplemented through ingestion via the diet and are nutritionally very important. Omega-3 fatty acid, or alpha-linoleic acid (ALA), falls into this category and is one of only two fatty acids known to be essential for humans (the other being omega-6 fatty acid, or linoleic acid). These polyunsaturated fatty acids are called omega-3 because the third carbon from the end of the hydrocarbon chain is connected to its neighboring carbon by a double bond. Salmon, trout, and tuna are good sources of omega-3 fatty acids.

Research indicates that omega-3 fatty acids reduce the risk of sudden death from heart attacks, reduce triglycerides in the blood, lower blood pressure, and prevent thrombosis by inhibiting blood clotting. They also reduce inflammation and may help reduce the

risk of some cancers in animals.

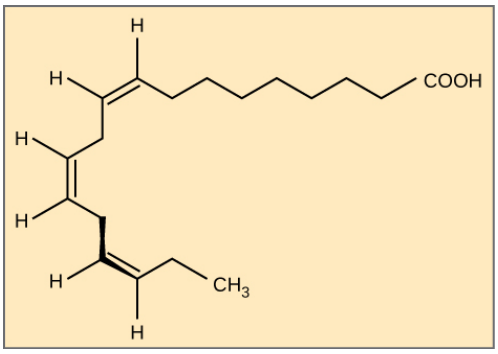


Figure **3.5.1.1**: Omega Fatty Acids: Alpha-linolenic acid is an example of an omega-3 fatty acid. It has three cis double bonds and, as a result, a curved shape. For clarity, the carbons are not shown. Each singly bonded carbon has two hydrogens associated with it, also not shown.

Fats have important functions, and many vitamins are fat soluble. Fats serve as a long-term storage form of fatty acids and act as a source of energy. They also provide insulation for the body.

Key Points

- Fats provide energy, insulation, and storage of fatty acids for many organisms.
- Fats may be saturated (having single bonds) or unsaturated (having double bonds).
- Unsaturated fats may be cis (hydrogens in same plane) or trans (hydrogens in two different planes).
- Olive oil, a monounsaturated fat, has a single double bond whereas canola oil, a polyunsaturated fat, has more than one double bond.
- Omega-3 fatty acid and omega-6 fatty acid are essential for human biological processes, but they must be ingested in the diet because they cannot be synthesized.

Key Terms

- **hydrogenation**: The chemical reaction of hydrogen with another substance, especially with an unsaturated organic compound, and usually under the influence of temperature, pressure and catalysts.
- **ester**: Compound most often formed by the condensation of an alcohol and an acid, by removing water. It contains the functional group carbon-oxygen double bond joined via carbon to another oxygen atom.
- **carboxyl**: A univalent functional group consisting of a carbonyl and a hydroxyl functional group (-CO.OH); characteristic of carboxylic acids.

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3.5.2: Phospholipids

Learning Objectives

- Describe phospholipids and their role in cells

Defining Characteristics of Phospholipids

Phospholipids are major components of the plasma membrane, the outermost layer of animal cells. Like fats, they are composed of fatty acid chains attached to a glycerol backbone. Unlike triglycerides, which have three fatty acids, phospholipids have two fatty acids that help form a diacylglycerol. The third carbon of the glycerol backbone is also occupied by a modified phosphate group. However, just a phosphate group attached to a diacylglycerol does not qualify as a phospholipid. This would be considered a phosphatidate (diacylglycerol 3-phosphate), the precursor to phospholipids. To qualify as a phospholipid, the phosphate group should be modified by an alcohol. Phosphatidylcholine and phosphatidylserine are examples of two important phospholipids that are found in plasma membranes.

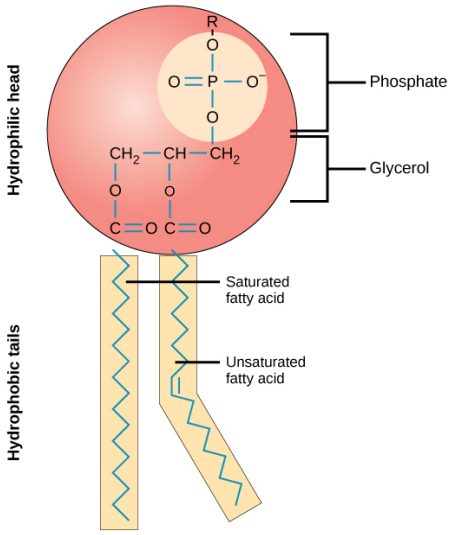


Figure **3.5.2.1**: Phospholipid Molecule: A phospholipid is a molecule with two fatty acids and a modified phosphate group attached to a glycerol backbone. The phosphate may be modified by the addition of charged or polar chemical groups. Two chemical groups that may modify the phosphate, choline and serine, are shown here. Both choline and serine attach to the phosphate group at the position labeled R via the hydroxyl group indicated in green.

Structure of a Phospholipid Molecule

A phospholipid is an amphipathic molecule which means it has both a hydrophobic and a hydrophilic component. A single phospholipid molecule has a phosphate group on one end, called the “head,” and two side-by-side chains of fatty acids that make up the lipid “tails. ” The phosphate group is negatively charged, making the head polar and hydrophilic, or “water loving.” The phosphate heads are thus attracted to the water molecules in their environment.

The lipid tails, on the other hand, are uncharged, nonpolar, and hydrophobic, or “water fearing.” A hydrophobic molecule repels and is repelled by water. Some lipid tails consist of saturated fatty acids and some contain unsaturated fatty acids. This combination adds to the fluidity of the tails that are constantly in motion.

Phospholipids and Biological Membranes

The cell membrane consists of two adjacent layers of phospholipids, which form a bilayer. The fatty acid tails of phospholipids face inside, away from water, whereas the phosphate heads face the outward aqueous side. Since the heads face outward, one layer is exposed to the interior of the cell and one layer is exposed to the exterior. As the phosphate groups are polar and hydrophilic, they are attracted to water in the intracellular fluid.

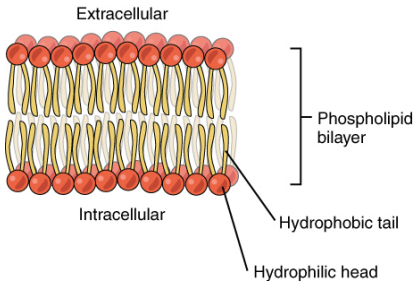


Figure 3.5.2.1: Phospholipid Bilayer: The phospholipid bilayer consists of two adjacent sheets of phospholipids, arranged tail to tail. The hydrophobic tails associate with one another, forming the interior of the membrane. The polar heads contact the fluid inside and outside of the cell.

Because of the phospholipds' chemical and physical characteristics, the lipid bilayer acts as a semipermeable membrane; only lipophilic solutes can easily pass the phospholipd bilayer. As a result, there are two distinct aqueous compartments on each side of the membrane. This separation is essential for many biological functions, including cell communication and metabolism.

Membrane Fluidity

A cell's plasma membrane contain proteins and other lipids (such as cholesterol) within the phospholipid bilayer. Biological membranes remain fluid because of the unsaturated hydrophobic tails, which prevent phospholipid molecules from packing together and forming a solid.

If a drop of phospholipids is placed in water, the phospholipids spontaneously form a structure known as a micelle, with their hydrophilic heads oriented toward the water. Micelles are lipid molecules that arrange themselves in a spherical form in aqueous solution. The formation of a micelle is a response to the amphipathic nature of fatty acids, meaning that they contain both hydrophilic and hydrophobic regions.

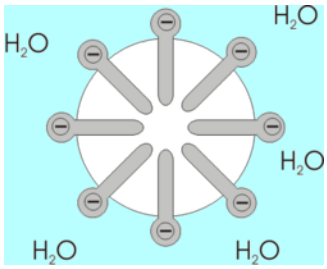


Figure 3.5.2.1: Micelles: An example of micelles in water.

Key Points

- Phospholipids consist of a glycerol molecule, two fatty acids, and a phosphate group that is modified by an alcohol.
- The phosphate group is the negatively-charged polar head, which is hydrophilic.
- The fatty acid chains are the uncharged, nonpolar tails, which are hydrophobic.
- Since the tails are hydrophobic, they face the inside, away from the water and meet in the inner region of the membrane.
- Since the heads are hydrophilic, they face outward and are attracted to the intracellular and extracellular fluid.
- If phospholipids are placed in water, they form into micelles, which are lipid molecules that arrange themselves in a spherical form in aqueous solutions.

Key Terms

- **micelle**: Lipid molecules that arrange themselves in a spherical form in aqueous solutions.
- **amphipathic**: Describing a molecule, such as a detergent, which has both hydrophobic and hydrophilic groups.

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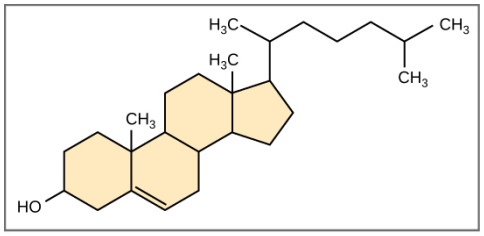
3.5.3: Steroids

Learning Objectives

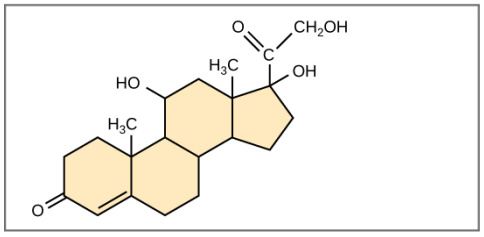
- Describe some functions of steroids

Structure of Steroid Molecules

Unlike phospholipids and fats, steroids have a fused ring structure. Although they do not resemble the other lipids, they are grouped with them because they are also hydrophobic and insoluble in water. All steroids have four linked carbon rings, and many of them, like cholesterol, have a short tail. Many steroids also have the –OH functional group, and these steroids are classified as alcohols called sterols.



Cholesterol



Cortisol

Figure **3.5.3.1**: Steroid Structures: Steroids, such as cholesterol and cortisol, are composed of four fused hydrocarbon rings.

Cholesterol

Cholesterol is the most common steroid and is mainly synthesized in the liver; it is the precursor to vitamin D. Cholesterol is also a precursor to many important steroid hormones like estrogen, testosterone, and progesterone, which are secreted by the gonads and endocrine glands. Therefore, steroids play very important roles in the body's reproductive system. Cholesterol also plays a role in synthesizing the steroid hormones aldosterone, which is used for osmoregulation, and cortisol, which plays a role in metabolism.

Cholesterol is also the precursor to bile salts, which help in the emulsification of fats and their absorption by cells. It is a component of the plasma membrane of animal cells and the phospholipid bilayer. Being the outermost structure in animal cells, the plasma membrane is responsible for the transport of materials and cellular recognition; and it is involved in cell-to-cell communication. Thus, steroids also play an important role in the structure and function of membranes.

It has also been discovered that steroids can be active in the brain where they affect the nervous system, These neurosteroids alter electrical activity in the brain. They can either activate or tone down receptors that communicate messages from neurotransmitters. Since these neurosteroids can tone down receptors and decrease brain activity, steroids are often used in anesthetic medicines.

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Key Points

- Steroids are lipids because they are hydrophobic and insoluble in water, but they do not resemble lipids since they have a structure composed of four fused rings.
- Cholesterol is the most common steroid and is the precursor to vitamin D, testosterone, estrogen, progesterone, aldosterone, cortisol, and bile salts.
- Cholesterol is a component of the phospholipid bilayer and plays a role in the structure and function of membranes.
- Steroids are found in the brain and alter electrical activity in the brain.
- Because they can tone down receptors that communicate messages from neurotransmitters, steroids are often used in anesthetic medicines.

Key Terms

- **neurotransmitter**: any substance, such as acetylcholine or dopamine, responsible for sending nerve signals across a synapse between two neurons
- **osmoregulation**: the homeostatic regulation of osmotic pressure in the body in order to maintain a constant water content
- **hormone**: any substance produced by one tissue and conveyed by the bloodstream to another to affect physiological activity

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CHAPTER OVERVIEW

4: Cell Structure

- 4.1: Cell Theory
  - 4.1.1: Cells as the Basic Unit of Life
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SECTION OVERVIEW

4.1: Cell Theory

4.1.1: Cells as the Basic Unit of Life

4.1.2: Microscopy

4.1.3: Cell Theory

4.1.4: Cell Size

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4.1.1: Cells as the Basic Unit of Life

Learning Objectives

- State the general characteristics of a cell

Close your eyes and picture a brick wall. What is the basic building block of that wall? A single brick, of course. Like a brick wall, your body is composed of basic building blocks, and the building blocks of your body are cells.

Cells as Building Blocks

A cell is the smallest unit of a living thing. A living thing, whether made of one cell (like bacteria) or many cells (like a human), is called an organism. Thus, cells are the basic building blocks of all organisms. Several cells of one kind that interconnect with each other and perform a shared function form tissues; several tissues combine to form an organ (your stomach, heart, or brain); and several organs make up an organ system (such as the digestive system, circulatory system, or nervous system). Several systems that function together form an organism (like a human being). There are many types of cells all grouped into one of two broad categories: prokaryotic and eukaryotic. For example, both animal and plant cells are classified as eukaryotic cells, whereas bacterial cells are classified as prokaryotic.

Types of Specialized Cells

Your body has many kinds of cells, each specialized for a specific purpose. Just as a home is made from a variety of building materials, the human body is constructed from many cell types. For example, epithelial cells protect the surface of the body and cover the organs and body cavities within. Bone cells help to support and protect the body. Cells of the immune system fight invading bacteria. Additionally, blood and blood cells carry nutrients and oxygen throughout the body while removing carbon dioxide. Each of these cell types plays a vital role during the growth, development, and day-to-day maintenance of the body. In spite of their enormous variety, however, cells from all organisms—even ones as diverse as bacteria, onion, and human—share certain fundamental characteristics.

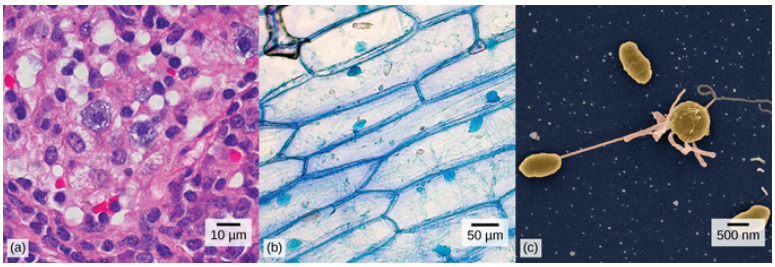


Figure **4.1.1.1**: Various Cell Types: (a) Nasal sinus cells (viewed with a light microscope), (b) onion cells (viewed with a light microscope), and (c) Vibrio tasmaniensis bacterial cells (seen through a scanning electron microscope) are from very different organisms, yet all share certain characteristics of basic cell structure.

Key Points

- A living thing can be composed of either one cell or many cells.
- There are two broad categories of cells: prokaryotic and eukaryotic cells.
- Cells can be highly specialized with specific functions and characteristics.

Key Terms

- **prokaryotic**: Small cells in the domains Bacteria and Archaea that do not contain a membrane-bound nucleus or other membrane-bound organelles.
- **eukaryotic**: Having complex cells in which the genetic material is contained within membrane-bound nuclei.
- **cell**: The basic unit of a living organism, consisting of a quantity of protoplasm surrounded by a cell membrane, which is able to synthesize proteins and replicate itself.

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4.1.2: Microscopy

Learning Objectives

- Compare and contrast light and electron microscopy.

Microscopy

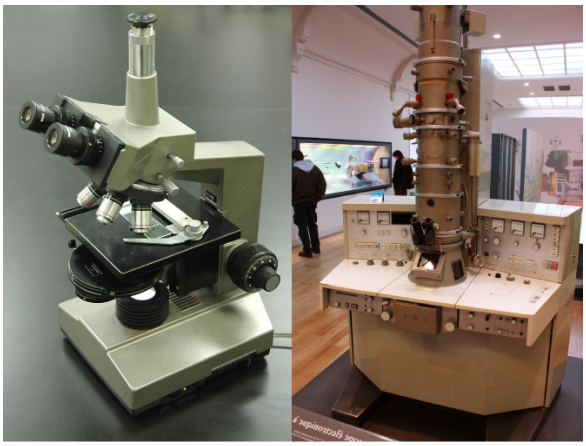
Cells vary in size. With few exceptions, individual cells cannot be seen with the naked eye, so scientists use microscopes (micro- = “small”; -scope = “to look at”) to study them. A microscope is an instrument that magnifies an object. Most photographs of cells are taken with a microscope; these images can also be called micrographs.

The optics of a microscope’s lenses change the orientation of the image that the user sees. A specimen that is right-side up and facing right on the microscope slide will appear upside-down and facing left when viewed through a microscope, and vice versa. Similarly, if the slide is moved left while looking through the microscope, it will appear to move right, and if moved down, it will seem to move up. This occurs because microscopes use two sets of lenses to magnify the image. Because of the manner by which light travels through the lenses, this system of two lenses produces an inverted image (binocular, or dissecting microscopes, work in a similar manner, but they include an additional magnification system that makes the final image appear to be upright).

Light Microscopes

To give you a sense of cell size, a typical human red blood cell is about eight millionths of a meter or eight micrometers (abbreviated as eight µm) in diameter; the head of a pin of is about two thousandths of a meter (two mm) in diameter. That means about 250 red blood cells could fit on the head of a pin.

Most student microscopes are classified as light microscopes. Visible light passes and is bent through the lens system to enable the user to see the specimen. Light microscopes are advantageous for viewing living organisms, but since individual cells are generally transparent, their components are not distinguishable unless they are colored with special stains. Staining, however, usually kills the cells.



(a) (b)

Figure **4.1.2.1**: Light and Electron Microscopes: (a) Most light microscopes used in a college biology lab can magnify cells up to approximately 400 times and have a resolution of about 200 nanometers. (b) Electron microscopes provide a much higher magnification, 100,000x, and a have a resolution of 50 picometers.

Light microscopes, commonly used in undergraduate college laboratories, magnify up to approximately 400 times. Two parameters that are important in microscopy are magnification and resolving power. Magnification is the process of enlarging an object in appearance. Resolving power is the ability of a microscope to distinguish two adjacent structures as separate: the higher the resolution, the better the clarity and detail of the image. When oil immersion lenses are used for the study of small objects, magnification is usually increased to 1,000 times. In order to gain a better understanding of cellular structure and function, scientists typically use electron microscopes.

Electron Microscopes

In contrast to light microscopes, electron microscopes use a beam of electrons instead of a beam of light. Not only does this allow for higher magnification and, thus, more detail, it also provides higher resolving power. The method used to prepare the specimen for viewing with an electron microscope kills the specimen. Electrons have short wavelengths (shorter than photons) that move best in a vacuum, so living cells cannot be viewed with an electron microscope.

In a scanning electron microscope, a beam of electrons moves back and forth across a cell's surface, creating details of cell surface characteristics. In a transmission electron microscope, the electron beam penetrates the cell and provides details of a cell's internal structures. As you might imagine, electron microscopes are significantly more bulky and expensive than light microscopes.

Key Points

- Light microscopes allow for magnification of an object approximately up to 400-1000 times depending on whether the high power or oil immersion objective is used.
- Light microscopes use visible light which passes and bends through the lens system.
- Electron microscopes use a beam of electrons, opposed to visible light, for magnification.
- Electron microscopes allow for higher magnification in comparison to a light microscope thus, allowing for visualization of cell internal structures.

Key Terms

- **resolution**: The degree of fineness with which an image can be recorded or produced, often expressed as the number of pixels per unit of length (typically an inch).
- **electron**: The subatomic particle having a negative charge and orbiting the nucleus; the flow of electrons in a conductor constitutes electricity.

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4.1.3: Cell Theory

Learning Objectives

- Identify the components of cell theory

Cell Theory

The microscopes we use today are far more complex than those used in the 1600s by Antony van Leeuwenhoek, a Dutch shopkeeper who had great skill in crafting lenses. Despite the limitations of his now-ancient lenses, van Leeuwenhoek observed the movements of protista (a type of single-celled organism) and sperm, which he collectively termed “animalcules. ”

In a 1665 publication called *Micrographia*, experimental scientist Robert Hooke coined the term “cell” for the box-like structures he observed when viewing cork tissue through a lens. In the 1670s, van Leeuwenhoek discovered bacteria and protozoa. Later advances in lenses, microscope construction, and staining techniques enabled other scientists to see some components inside cells.

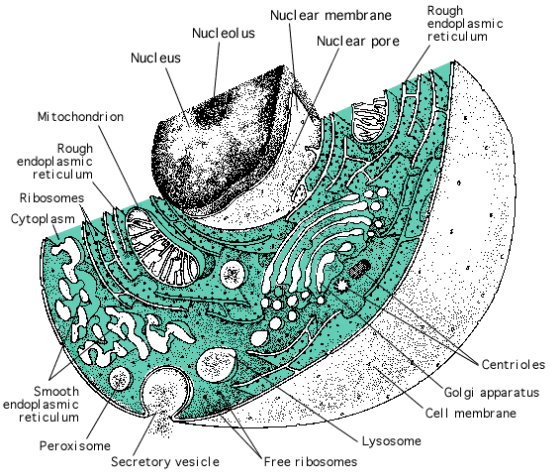


Figure 4.1.3.1: Structure of an Animal Cell: The cell is the basic unit of life and the study of the cell led to the development of the cell theory.

By the late 1830s, botanist Matthias Schleiden and zoologist Theodor Schwann were studying tissues and proposed the unified cell theory. The unified cell theory states that: all living things are composed of one or more cells; the cell is the basic unit of life; and new cells arise from existing cells. Rudolf Virchow later made important contributions to this theory.

Schleiden and Schwann proposed spontaneous generation as the method for cell origination, but spontaneous generation (also called abiogenesis) was later disproven. Rudolf Virchow famously stated “Omnis cellula e cellula”… “All cells only arise from pre-existing cells. “The parts of the theory that did not have to do with the origin of cells, however, held up to scientific scrutiny and are widely agreed upon by the scientific community today. The generally accepted portions of the modern Cell Theory are as follows:

1. The cell is the fundamental unit of structure and function in living things.
2. All organisms are made up of one or more cells.
3. Cells arise from other cells through cellular division.

The expanded version of the cell theory can also include:

- Cells carry genetic material passed to daughter cells during cellular division
- All cells are essentially the same in chemical composition
- Energy flow (metabolism and biochemistry) occurs within cells

Key Points

- The cell theory describes the basic properties of all cells.

- The three scientists that contributed to the development of cell theory are Matthias Schleiden, Theodor Schwann, and Rudolf Virchow.
- A component of the cell theory is that all living things are composed of one or more cells.
- A component of the cell theory is that the cell is the basic unit of life.
- A component of the cell theory is that all new cells arise from existing cells.

Key Terms

- **cell theory**: The scientific theory that all living organisms are made of cells as the smallest functional unit.

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4.1.4: Cell Size

Learning Objectives

- Describe the factors limiting cell size and the adaptations cells make to overcome the surface area to volume issue

At 0.1 to 5.0 μm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10 to 100 μm. The small size of prokaryotes allows ions and organic molecules that enter them to quickly diffuse to other parts of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly diffuse out. This is not the case in eukaryotic cells, which have developed different structural adaptations to enhance intracellular transport.

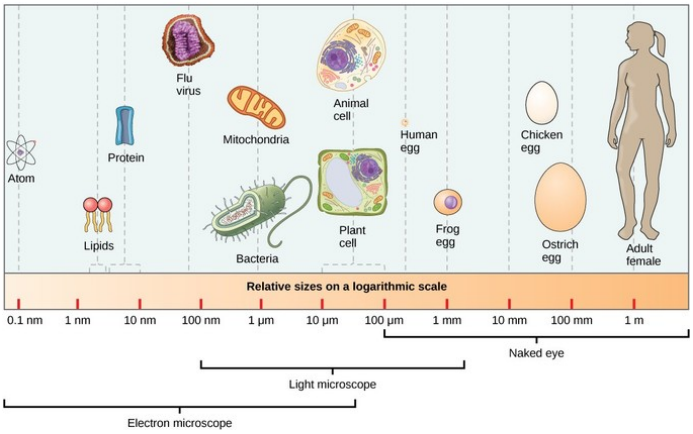


Figure 4.1.4.1: Relative Size of Atoms to Humans: This figure shows relative sizes on a logarithmic scale (recall that each unit of increase in a logarithmic scale represents a 10-fold increase in the quantity being measured).

In general, small size is necessary for all cells, whether prokaryotic or eukaryotic. Consider the area and volume of a typical cell. Not all cells are spherical in shape, but most tend to approximate a sphere. The formula for the surface area of a sphere is $4\pi r^2$, while the formula for its volume is $4\pi r^3/3$. As the radius of a cell increases, its surface area increases as the square of its radius, but its volume increases as the cube of its radius (much more rapidly).

Therefore, as a cell increases in size, its surface area-to-volume ratio decreases. This same principle would apply if the cell had the shape of a cube (below). If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume. In other words, as a cell grows, it becomes less efficient. One way to become more efficient is to divide; another way is to develop organelles that perform specific tasks. These adaptations lead to the development of more sophisticated cells called eukaryotic cells.

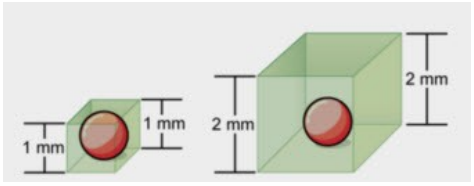


Figure 4.1.4.1: Surface Area to Volume Ratios: Notice that as a cell increases in size, its surface area-to-volume ratio decreases. When there is insufficient surface area to support a cell's increasing volume, a cell will either divide or die. The cell on the left has a volume of 1 mm3 and a surface area of 6 mm2, with a surface area-to-volume ratio of 6 to 1, whereas the cell on the right has a volume of 8 mm3 and a surface area of 24 mm2, with a surface area-to-volume ratio of 3 to 1.

Smaller single-celled organisms have a high surface area to volume ratio, which allows them to rely on oxygen and material diffusing into the cell (and wastes diffusing out) in order to survive. The higher the surface area to volume ratio they have, the more effective this process can be. Larger animals require specialized organs (lungs, kidneys, intestines, etc.) that effectively increase the surface area available for exchange processes, and a circulatory system to move material and heat energy between the surface and the core of the organism.

Increased volume can lead to biological problems. King Kong, the fictional giant gorilla, would have insufficient lung surface area to meet his oxygen needs, and could not survive. For small organisms with their high surface area to volume ratio, friction and fluid

dynamics (wind, water flow) are relatively much more important, and gravity much less important, than for large animals.

However, increased surface area can cause problems as well. More contact with the environment through the surface of a cell or an organ (relative to its volume) increases loss of water and dissolved substances. High surface area to volume ratios also present problems of temperature control in unfavorable environments.

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Key Points

- As a cell grows, its volume increases much more rapidly than its surface area. Since the surface of the cell is what allows the entry of oxygen, large cells cannot get as much oxygen as they would need to support themselves.
- As animals increase in size they require specialized organs that effectively increase the surface area available for exchange processes.

Key Terms

- **surface area**: The total area on the surface of an object.

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SECTION OVERVIEW

4.2: Prokaryotic Cells

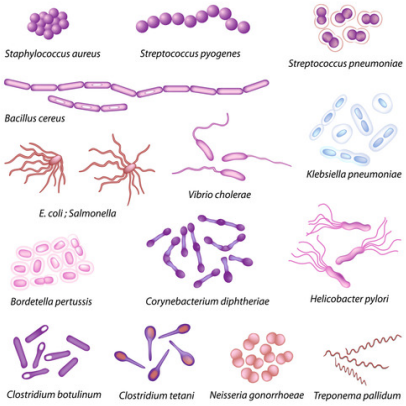
4.2.1: Prokaryotic Structure

4.2.2: Prokaryotic Classification

4.2.3: Prokaryotic Cells

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4.2.1: Prokaryotic Structure



Does the shape matter?

It does if you're a bacterium. Prokaryotic cells are distinguished by their shape. And as you can imagine, shape may have something to do with mobility.

Prokaryote Structure

Most prokaryotic cells are much smaller than eukaryotic cells. Although they are tiny, prokaryotic cells can be distinguished by their shapes. The most common shapes are helices, spheres, and rods (see **Figure** below).

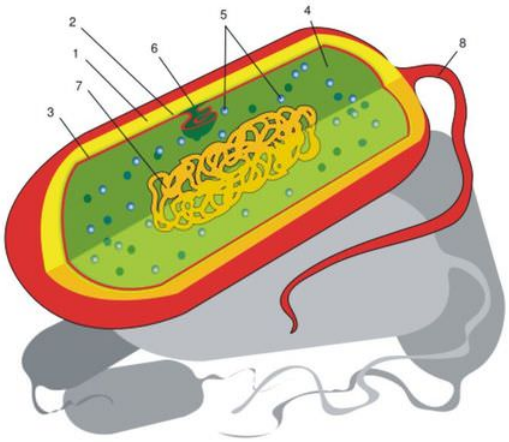


Prokaryotic Cell Shapes. The three most common prokaryotic cell shapes are shown here.

Plasma Membrane and Cell Wall

Like other cells, prokaryotic cells have a plasma membrane (see **Figure** below). It controls what enters and leaves the cell. It is also the site of many metabolic reactions. For example, cellular respiration and photosynthesis take place in the plasma membrane.

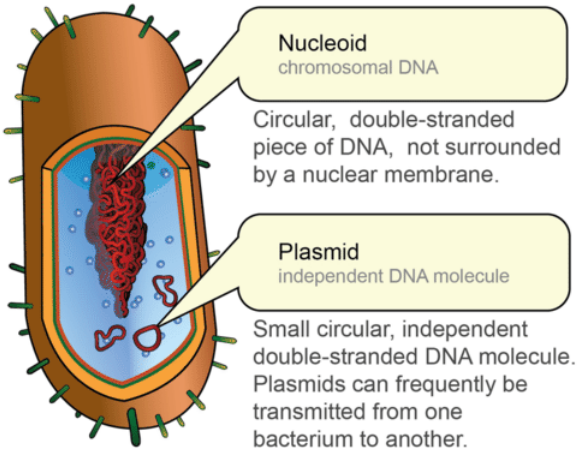
Most prokaryotes also have a cell wall. It lies just outside the plasma membrane. It gives strength and rigidity to the cell. Bacteria and Archaea differ in the makeup of their cell wall. The cell wall of Bacteria contains **peptidoglycan**, composed of sugars and amino acids. The cell wall of most Archaea lacks peptidoglycan.



Prokaryotic Cell. The main parts of a prokaryotic cell are shown in this diagram. The structure called a mesosome was once thought to be an organelle. More evidence has convinced most scientists that it is not a true cell structure at all. Instead, it seems to be an artifact of cell preparation. This is a good example of how scientific knowledge is revised as more evidence becomes available. Can you identify each of the labeled structures?

Cytoplasm and Cell Structures

Inside the plasma membrane of prokaryotic cells is the cytoplasm. It contains several structures, including ribosomes, a cytoskeleton, and genetic material. Ribosomes are sites where proteins are made. The cytoskeleton helps the cell keep its shape. The genetic material is usually a single loop of DNA. There may also be small, circular pieces of DNA, called **plasmids**. (see **Figure** below). The cytoplasm may contain microcompartments as well. These are tiny structures enclosed by proteins. They contain enzymes and are involved in metabolic processes.

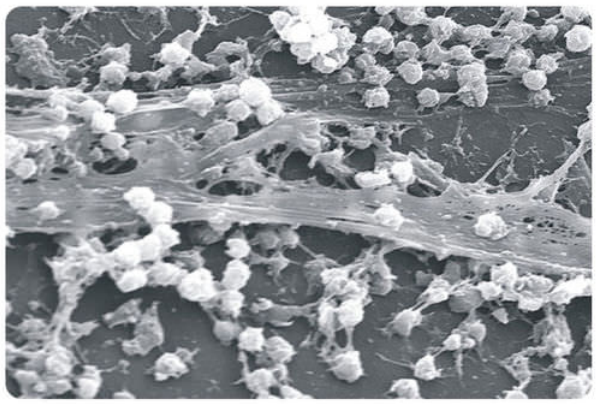


Prokaryotic DNA. The DNA of a prokaryotic cell is in the cytoplasm because the cell lacks a nucleus.

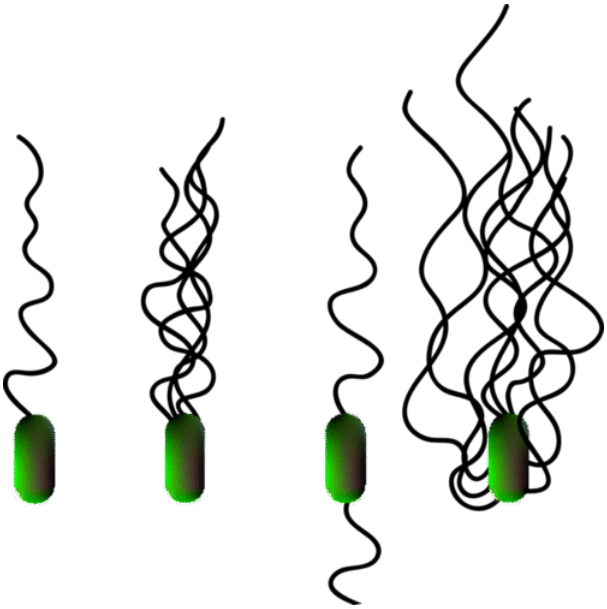
Extracellular Structures

Many prokaryotes have an extra layer, called a capsule, outside the cell wall. The **capsule**protects the cell from chemicals and from drying out. It also allows the cell to stick to surfaces and to other cells. Because of this, many prokaryotes can form biofilms, like the one shown in **Figure** below. A **biofilm** is a colony of prokaryotes that is stuck to a surface such as a rock or a host's tissues. The sticky plaque that collects on your teeth between brushings is a biofilm. It consists of millions of bacteria.

Most prokaryotes also have long, thin protein structures called **flagella** (singular, **flagellum**). They extend from the plasma membrane. Flagella help prokaryotes move. They spin around a fixed base, causing the cell to roll and tumble. As shown in **Figure** below, prokaryotes may have one or more flagella.



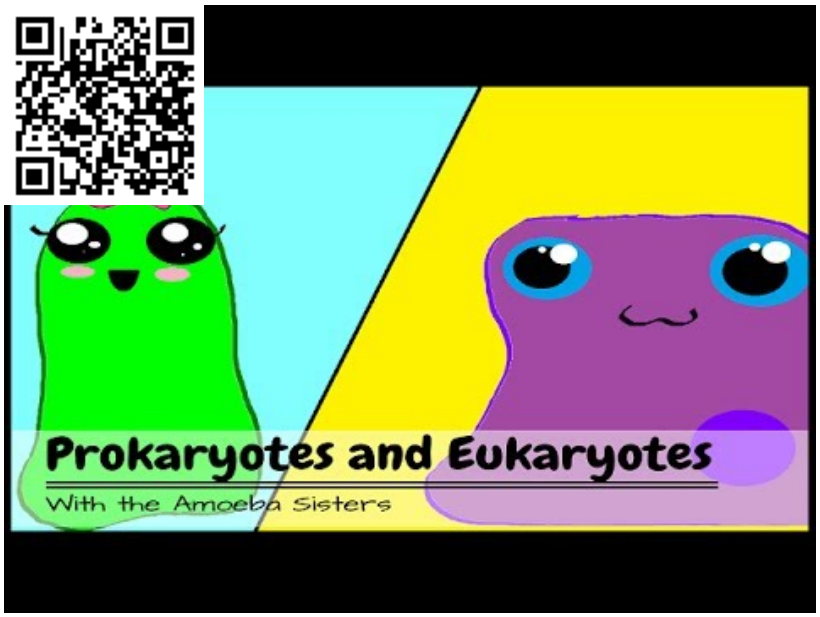
Bacterial Biofilm. The greatly magnified biofilm shown here was found on a medical catheter (tubing) removed from a patient's body.



Variations in the Flagella of Bacteria. Flagella in prokaryotes may be located at one or both ends of the cell or all around it. They help prokaryotes move toward food or away from toxins.

Endospores

Many organisms form spores for reproduction. Some prokaryotes form spores for survival. Called **endospores**, they form inside prokaryotic cells when they are under stress. The stress could be UV radiation, high temperatures, or harsh chemicals. Endospores enclose the DNA and help it survive under conditions that may kill the cell. Endospores are commonly found in soil and water. They may survive for long periods of time.



Summary

- Most prokaryotic cells are much smaller than eukaryotic cells.
- Prokaryotic cells have a cell wall outside their plasma membrane.
- Prokaryotic DNA consists of a single loop. Some prokaryotes also have small, circular pieces of DNA called plasmids.

Review

1. Identify the three most common shapes of prokaryotic cells.
2. Describe a typical prokaryotic cell.
3. What are the roles of flagella and endospores in prokaryotes?

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4.2.2: Prokaryotic Classification



With so many different bacteria, how are they all classified?

By shape? By size? By some other criteria? As you can imagine, classifying bacteria is probably not an easy task. Bacteria are classified by their traits, some of which have to do with their shape, others with the cell wall, and even additional traits.

The Prokaryotic Domains

Domain Bacteria

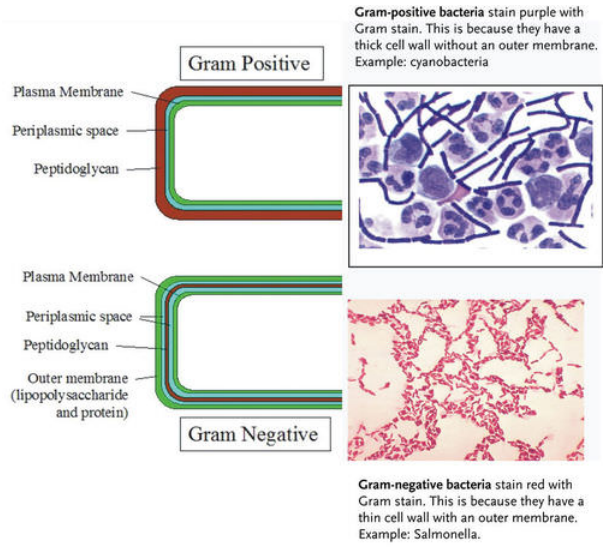
Bacteria are the most diverse and abundant group of organisms on Earth. They live in almost all environments. They are found in the ocean, the soil, and the intestines of animals. They are even found in rocks deep below Earth's surface. Any surface that has not been sterilized is likely to be covered with bacteria. The total number of bacteria in the world is amazing. It's estimated to be 5×10^{30}, or five million trillion. You have more bacteria in and on your body than you have body cells!

Bacteria called **cyanobacteria** are very important. They are bluish green in color (see **Figure** below) because they contain chlorophyll (but not chloroplasts, of course). They make food through photosynthesis and release oxygen into the air. These bacteria were probably responsible for adding oxygen to the air on early Earth. This changed the planet's atmosphere. It also changed the direction of evolution. Ancient cyanobacteria also may have evolved into the chloroplasts of plant cells.



Cyanobacteria Bloom. The green streaks in this lake consist of trillions of cyanobacteria. Excessive nutrients in the water led to overgrowth of the bacteria.

Thousands of species of bacteria have been discovered, and many more are thought to exist. The known species can be classified on the basis of various traits. One classification is based on differences in their cell walls and outer membranes. It groups bacteria into **Gram-positive**and **Gram-negative** bacteria, as described in **Figure** below.

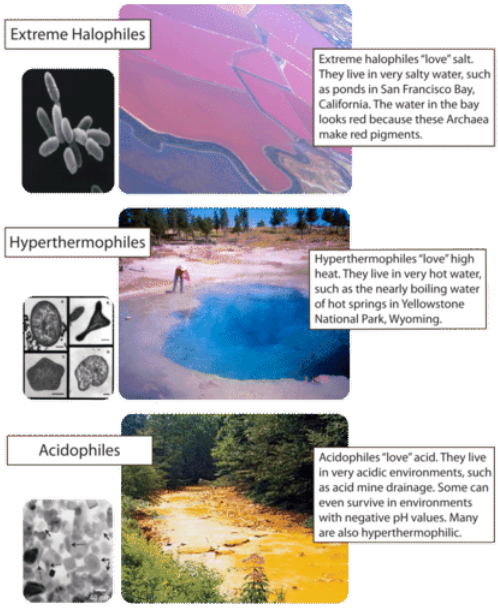


Classification of Bacteria. Different types of bacteria stain a different color when stained with Gram stain. This makes them easy to identify.

Domain Archaea

Scientists still know relatively little about Archaea. This is partly because they are hard to grow in the lab. Many live inside the bodies of animals, including humans. However, none are known for certain to cause disease.

Archaea were first discovered in extreme environments. For example, some were found in hot springs. Others were found around deep sea vents. Such Archaea are called **extremophiles**, or "lovers of extremes." **Figure** below describes three different types of Archaean extremophiles. The places where some of them live are thought to be similar to the environment on ancient Earth. This suggests that they may have evolved very early in Earth's history.



Extremophile Archaea. Many Archaea are specialized to live in extreme environments. Just three types are described here.

Archaea are now known to live just about everywhere on Earth. They are particularly numerous in the ocean. Archaea in plankton may be one of the most abundant types of organisms on the planet. Archaea are also thought to play important roles in the carbon and nitrogen cycles. For these reasons, Archaea are now recognized as a major aspect of life on Earth.



Summary

- Bacteria live in virtually all environments on Earth.
- Archaea live everywhere on Earth, including extreme environments.

Review

1. Distinguish between Gram-positive and Gram-negative bacteria, and give an example of each.
2. Summarize the evolutionary significance of cyanobacteria.
3. What are extremophiles? Name three types.
4. Describe the habitat of extreme halophiles.

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4.2.3: Prokaryotic Cells

Skills to Develop

- Name examples of prokaryotic and eukaryotic organisms
- Compare and contrast prokaryotic cells and eukaryotic cells
- Describe the relative sizes of different kinds of cells
- Explain why cells must be small

Cells fall into one of two broad categories: prokaryotic and eukaryotic. Only the predominantly single-celled organisms of the domains Bacteria and Archaea are classified as prokaryotes (pro- = “before”; -kary- = “nucleus”). Cells of animals, plants, fungi, and protists are all eukaryotes (eu- = “true”) and are made up of eukaryotic cells.

Components of Prokaryotic Cells

All cells share four common components: 1) a plasma membrane, an outer covering that separates the cell’s interior from its surrounding environment; 2) cytoplasm, consisting of a jelly-like cytosol within the cell in which other cellular components are found; 3) DNA, the genetic material of the cell; and 4) ribosomes, which synthesize proteins. However, prokaryotes differ from eukaryotic cells in several ways.

A prokaryote is a simple, mostly single-celled (unicellular) organism that lacks a nucleus, or any other membrane-bound organelle. We will shortly come to see that this is significantly different in eukaryotes. Prokaryotic DNA is found in a central part of the cell: the nucleoid (Figure **4.2.3.1**).

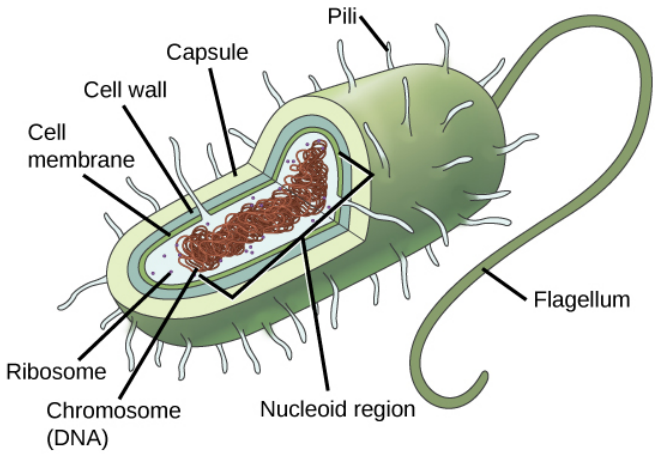


Figure **4.2.3.1**: This figure shows the generalized structure of a prokaryotic cell. All prokaryotes have chromosomal DNA localized in a nucleoid, ribosomes, a cell membrane, and a cell wall. The other structures shown are present in some, but not all, bacteria.

Most prokaryotes have a peptidoglycan cell wall and many have a polysaccharide capsule (Figure **4.2.3.1**). The cell wall acts as an extra layer of protection, helps the cell maintain its shape, and prevents dehydration. The capsule enables the cell to attach to surfaces in its environment. Some prokaryotes have flagella, pili, or fimbriae. Flagella are used for locomotion. Pili are used to exchange genetic material during a type of reproduction called conjugation. Fimbriae are used by bacteria to attach to a host cell.

Career Connection: Microbiologist

The most effective action anyone can take to prevent the spread of contagious illnesses is to wash his or her hands. Why? Because microbes (organisms so tiny that they can only be seen with microscopes) are ubiquitous. They live on doorknobs, money, your hands, and many other surfaces. If someone sneezes into his hand and touches a doorknob, and afterwards you touch that same doorknob, the microbes from the sneezer’s mucus are now on your hands. If you touch your hands to your mouth, nose, or eyes, those microbes can enter your body and could make you sick.

However, not all microbes (also called microorganisms) cause disease; most are actually beneficial. You have microbes in your gut that make vitamin K. Other microorganisms are used to ferment beer and wine.

Microbiologists are scientists who study microbes. Microbiologists can pursue a number of careers. Not only do they work in the food industry, they are also employed in the veterinary and medical fields. They can work in the pharmaceutical sector, serving key roles in research and development by identifying new sources of antibiotics that could be used to treat bacterial infections.

Environmental microbiologists may look for new ways to use specially selected or genetically engineered microbes for the removal of pollutants from soil or groundwater, as well as hazardous elements from contaminated sites. These uses of microbes are called bioremediation technologies. Microbiologists can also work in the field of bioinformatics, providing specialized knowledge and insight for the design, development, and specificity of computer models of, for example, bacterial epidemics.

Cell Size

At 0.1 to 5.0 μm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10 to 100 μm (Figure **4.2.3.2**). The small size of prokaryotes allows ions and organic molecules that enter them to quickly diffuse to other parts of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly diffuse out. This is not the case in eukaryotic cells, which have developed different structural adaptations to enhance intracellular transport.

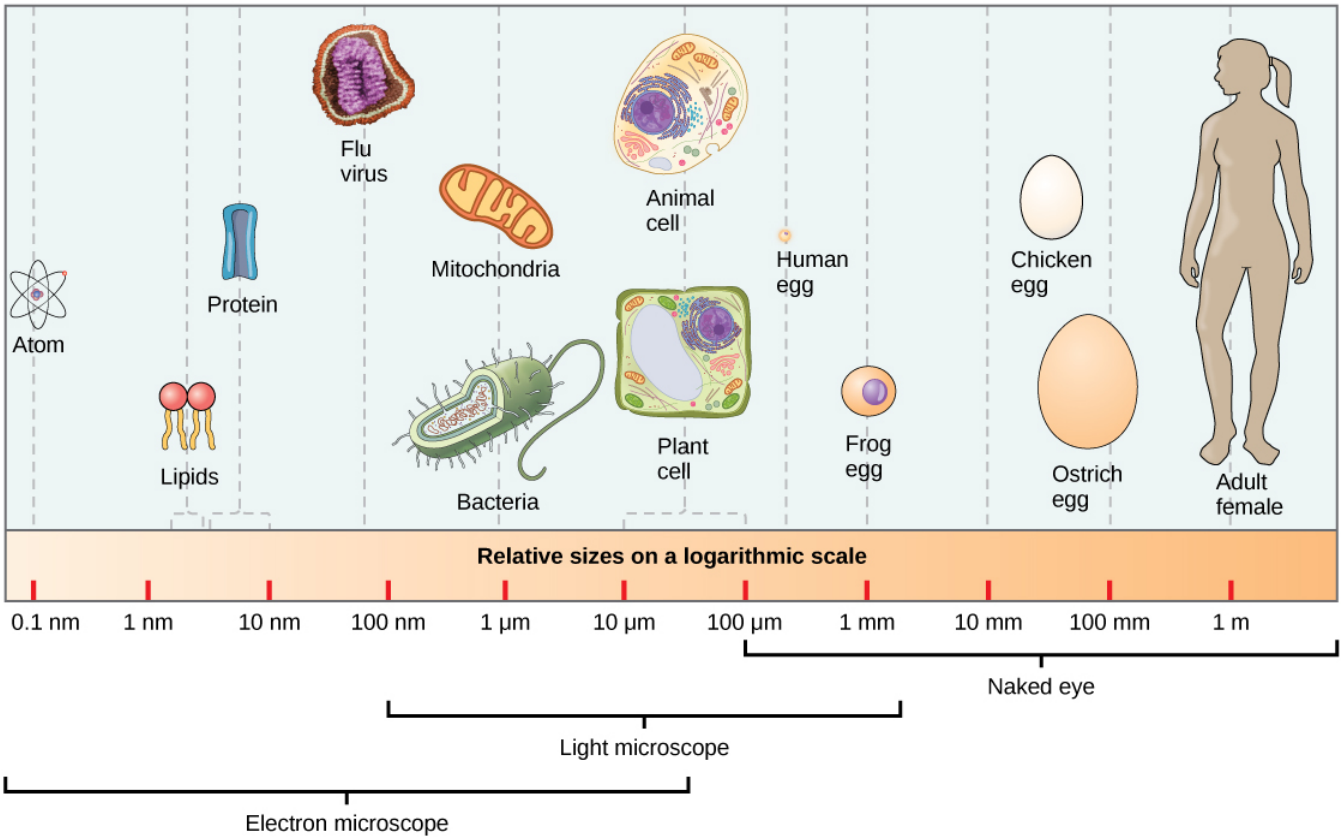


Figure **4.2.3.2**: This figure shows relative sizes of microbes on a logarithmic scale (recall that each unit of increase in a logarithmic scale represents a 10-fold increase in the quantity being measured).

Small size, in general, is necessary for all cells, whether prokaryotic or eukaryotic. Let's examine why that is so. First, we'll consider the area and volume of a typical cell. Not all cells are spherical in shape, but most tend to approximate a sphere. You may remember from your high school geometry course that the formula for the surface area of a sphere is $4\pi r^2$, while the formula for its volume is $4\pi r^2/3$. Thus, as the radius of a cell increases, its surface area increases as the square of its radius, but its volume increases as the cube of its radius (much more rapidly). Therefore, as a cell increases in size, its surface area-to-volume ratio decreases. This same principle would apply if the cell had the shape of a cube (Figure **4.2.3.3**). If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume. In other words, as a cell grows, it becomes less efficient. One way to become more efficient is to divide; another way is to develop

organelles that perform specific tasks. These adaptations lead to the development of more sophisticated cells called eukaryotic cells.

Art Connection

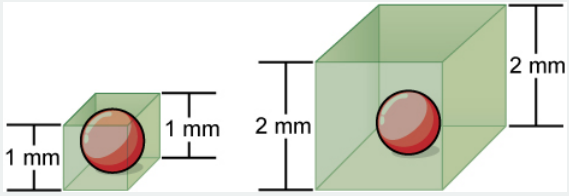


Figure **4.2.3.3**: Notice that as a cell increases in size, its surface area-to-volume ratio decreases. When there is insufficient surface area to support a cell's increasing volume, a cell will either divide or die. The cell on the left has a volume of $1\ mm^3$ and a surface area of $6\ mm^2$, with a surface area-to-volume ratio of **6** to **1**, whereas the cell on the right has a volume of $8\ mm^3$ and a surface area of $24\ mm^2$, with a surface area-to-volume ratio of **3** to **1**.

Prokaryotic cells are much smaller than eukaryotic cells. What advantages might small cell size confer on a cell? What advantages might large cell size have?

Summary

Prokaryotes are predominantly single-celled organisms of the domains Bacteria and Archaea. All prokaryotes have plasma membranes, cytoplasm, ribosomes, and DNA that is not membrane-bound. Most have peptidoglycan cell walls and many have polysaccharide capsules. Prokaryotic cells range in diameter from 0.1 to 5.0 µm.

As a cell increases in size, its surface area-to-volume ratio decreases. If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume.

Art Connections

Figure **4.2.3.3**: Prokaryotic cells are much smaller than eukaryotic cells. What advantages might small cell size confer on a cell? What advantages might large cell size have?

Answer

Substances can diffuse more quickly through small cells. Small cells have no need for organelles and therefore do not need to expend energy getting substances across organelle membranes. Large cells have organelles that can separate cellular processes, enabling them to build molecules that are more complex.

Glossary

nucleoid

central part of a prokaryotic cell in which the chromosome is found

prokaryote

unicellular organism that lacks a nucleus or any other membrane-bound organelle

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4.3: Eukaryotic Cells

At this point, it should be clear that eukaryotic cells have a more complex structure than do prokaryotic cells. Organelles allow for various functions to occur in the cell at the same time. Before discussing the functions of organelles within a eukaryotic cell, let us first examine two important components of the cell: the plasma membrane and the cytoplasm.

ART CONNECTION

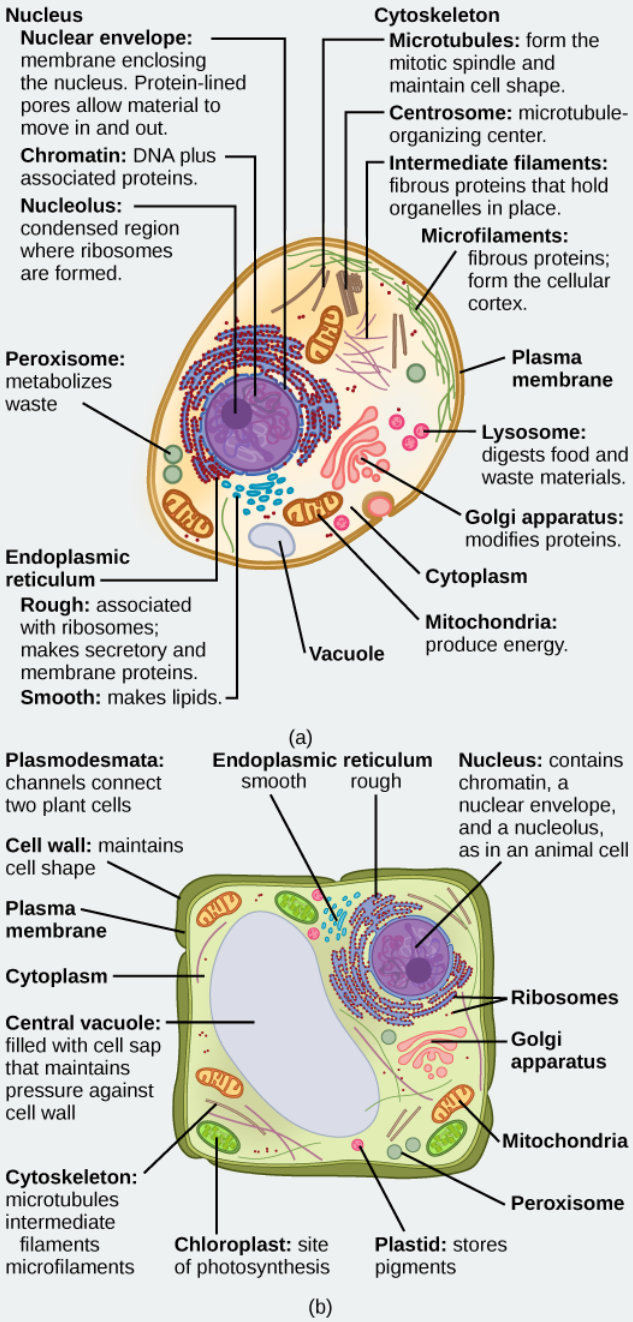


Figure 4.3.1: This figure shows (a) a typical animal cell and (b) a typical plant cell.

What structures does a plant cell have that an animal cell does not have? What structures does an animal cell have that a plant cell does not have?

The Plasma Membrane

Like prokaryotes, eukaryotic cells have a plasma membrane (Figure **4.3.2**) made up of a phospholipid bilayer with embedded proteins that separates the internal contents of the cell from its surrounding environment. A phospholipid is a lipid molecule composed of two fatty acid chains, a glycerol backbone, and a phosphate group. The plasma membrane regulates the passage of some substances, such as organic molecules, ions, and water, preventing the passage of some to maintain internal conditions, while actively bringing in or removing others. Other compounds move passively across the membrane.

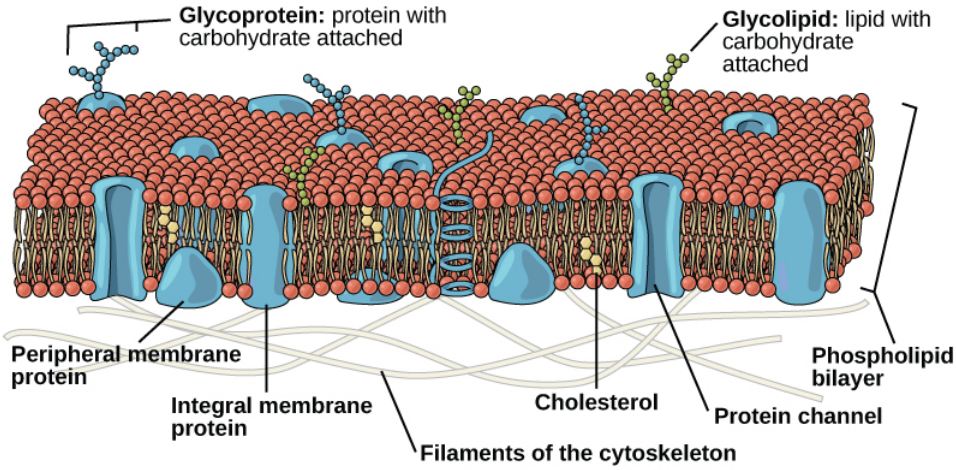


Figure 4.3.2: The plasma membrane is a phospholipid bilayer with embedded proteins. There are other components, such as cholesterol and carbohydrates, which can be found in the membrane in addition to phospholipids and protein.

The plasma membranes of cells that specialize in absorption are folded into fingerlike projections called microvilli (singular = microvillus). This folding increases the surface area of the plasma membrane. Such cells are typically found lining the small intestine, the organ that absorbs nutrients from digested food. This is an excellent example of form matching the function of a structure.

People with celiac disease have an immune response to gluten, which is a protein found in wheat, barley, and rye. The immune response damages microvilli, and thus, afflicted individuals cannot absorb nutrients. This leads to malnutrition, cramping, and diarrhea. Patients suffering from celiac disease must follow a gluten-free diet.

The Cytoplasm

The cytoplasm comprises the contents of a cell between the plasma membrane and the nuclear envelope (a structure to be discussed shortly). It is made up of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals (Figure **4.3.1**). Even though the cytoplasm consists of 70 to 80 percent water, it has a semi-solid consistency, which comes from the proteins within it. However, proteins are not the only organic molecules found in the cytoplasm. Glucose and other simple sugars, polysaccharides, amino acids, nucleic acids, fatty acids, and derivatives of glycerol are found there too. Ions of sodium, potassium, calcium, and many other elements are also dissolved in the cytoplasm. Many metabolic reactions, including protein synthesis, take place in the cytoplasm.

The Cytoskeleton

If you were to remove all the organelles from a cell, would the plasma membrane and the cytoplasm be the only components left? No. Within the cytoplasm, there would still be ions and organic molecules, plus a network of protein fibers that helps to maintain the shape of the cell, secures certain organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move independently. Collectively, this network of protein fibers is known as the cytoskeleton. There are three types of fibers within the cytoskeleton: microfilaments, also known as actin filaments, intermediate filaments, and microtubules (Figure **4.3.3**).

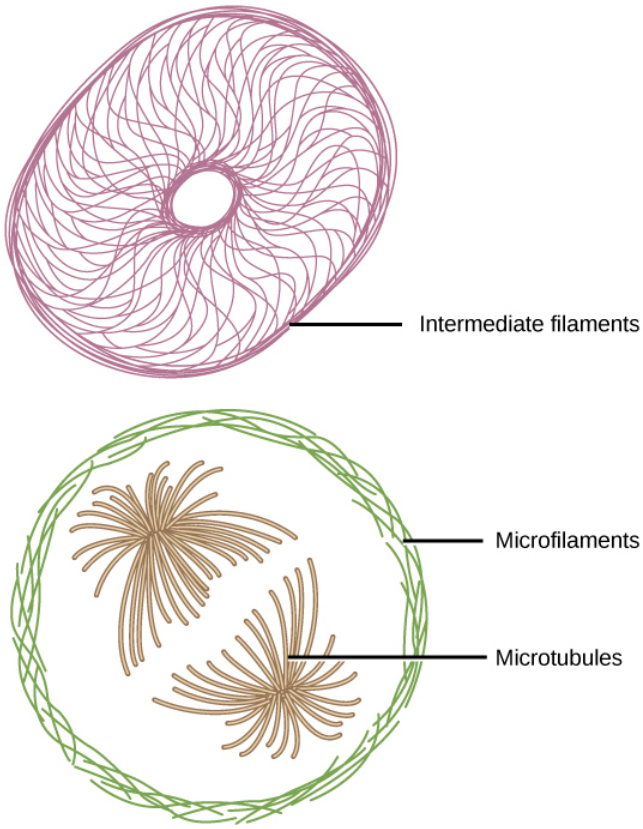


Figure 4.3.3: Microfilaments, intermediate filaments, and microtubules compose a cell's cytoskeleton.

Microfilaments are the thinnest of the cytoskeletal fibers and function in moving cellular components, for example, during cell division. They also maintain the structure of microvilli, the extensive folding of the plasma membrane found in cells dedicated to absorption. These components are also common in muscle cells and are responsible for muscle cell contraction. Intermediate filaments are of intermediate diameter and have structural functions, such as maintaining the shape of the cell and anchoring organelles. Keratin, the compound that strengthens hair and nails, forms one type of intermediate filament. Microtubules are the thickest of the cytoskeletal fibers. These are hollow tubes that can dissolve and reform quickly. Microtubules guide organelle movement and are the structures that pull chromosomes to their poles during cell division. They are also the structural components of flagella and cilia. In cilia and flagella, the microtubules are organized as a circle of nine double microtubules on the outside and two microtubules in the center.

The centrosome is a region near the nucleus of animal cells that functions as a microtubule-organizing center. It contains a pair of centrioles, two structures that lie perpendicular to each other. Each centriole is a cylinder of nine triplets of microtubules.

The centrosome replicates itself before a cell divides, and the centrioles play a role in pulling the duplicated chromosomes to opposite ends of the dividing cell. However, the exact function of the centrioles in cell division is not clear, since cells that have the centrioles removed can still divide, and plant cells, which lack centrioles, are capable of cell division.

Flagella and Cilia

Flagella (singular = flagellum) are long, hair-like structures that extend from the plasma membrane and are used to move an entire cell, (for example, sperm, *Euglena*). When present, the cell has just one flagellum or a few flagella. When cilia (singular = cilium) are present, however, they are many in number and extend along the entire surface of the plasma membrane. They are short, hair-like structures that are used to move entire cells (such as paramecium) or move substances along the outer surface of the cell (for example, the cilia of cells lining the fallopian tubes that move the ovum toward the uterus, or cilia lining the cells of the respiratory tract that move particulate matter toward the throat that mucus has trapped).

The Endomembrane System

The endomembrane system (*endo* = within) is a group of membranes and organelles (Figure **4.3.3**) in eukaryotic cells that work together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, the endoplasmic reticulum and Golgi apparatus, which we will cover shortly. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles.

The Nucleus

Typically, the nucleus is the most prominent organelle in a cell (Figure **4.3.1**). The nucleus (plural = nuclei) houses the cell's DNA in the form of chromatin and directs the synthesis of ribosomes and proteins. Let us look at it in more detail (Figure **4.3.4**).

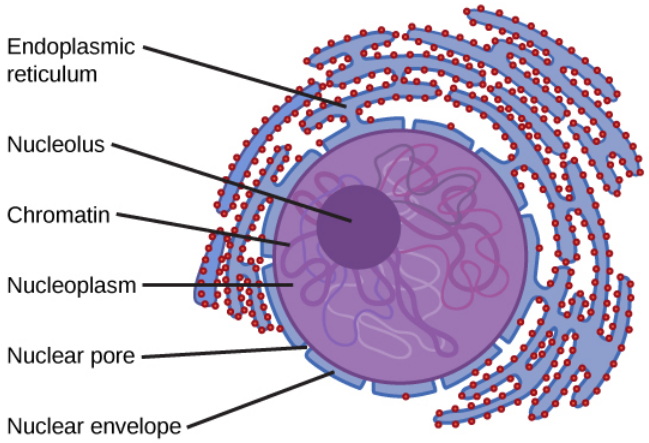


Figure 4.3.4: The outermost boundary of the nucleus is the nuclear envelope. Notice that the nuclear envelope consists of two phospholipid bilayers (membranes)—an outer membrane and an inner membrane—in contrast to the plasma membrane (Figure **4.3.2**), which consists of only one phospholipid bilayer. (credit: modification of work by NIGMS, NIH)

The nuclear envelope is a double-membrane structure that constitutes the outermost portion of the nucleus (Figure **4.3.4**). Both the inner and outer membranes of the nuclear envelope are phospholipid bilayers.

The nuclear envelope is punctuated with pores that control the passage of ions, molecules, and RNA between the nucleoplasm and the cytoplasm.

To understand chromatin, it is helpful to first consider chromosomes. Chromosomes are structures within the nucleus that are made up of DNA, the hereditary material, and proteins. This combination of DNA and proteins is called chromatin. In eukaryotes, chromosomes are linear structures. Every species has a specific number of chromosomes in the nucleus of its body cells. For example, in humans, the chromosome number is 46, whereas in fruit flies, the chromosome number is eight.

Chromosomes are only visible and distinguishable from one another when the cell is getting ready to divide. When the cell is in the growth and maintenance phases of its life cycle, the chromosomes resemble an unwound, jumbled bunch of threads.

We already know that the nucleus directs the synthesis of ribosomes, but how does it do this? Some chromosomes have sections of DNA that encode ribosomal RNA. A darkly staining area within the nucleus, called the nucleolus (plural = nucleoli), aggregates the ribosomal RNA with associated proteins to assemble the ribosomal subunits that are then transported through the nuclear pores into the cytoplasm.

The Endoplasmic Reticulum

The endoplasmic reticulum (ER) (Figure **4.3.7**) is a series of interconnected membranous tubules that collectively modify proteins and synthesize lipids. However, these two functions are performed in separate areas of the endoplasmic reticulum: the rough endoplasmic reticulum and the smooth endoplasmic reticulum, respectively.

The hollow portion of the ER tubules is called the lumen or cisternal space. The membrane of the ER, which is a phospholipid bilayer embedded with proteins, is continuous with the nuclear envelope.

The rough endoplasmic reticulum (RER) is so named because the ribosomes attached to its cytoplasmic surface give it a studded appearance when viewed through an electron microscope.

The ribosomes synthesize proteins while attached to the ER, resulting in transfer of their newly synthesized proteins into the lumen of the RER where they undergo modifications such as folding or addition of sugars. The RER also makes phospholipids for cell membranes.

If the phospholipids or modified proteins are not destined to stay in the RER, they will be packaged within vesicles and transported from the RER by budding from the membrane (Figure **4.3.7**). Since the RER is engaged in modifying proteins that will be secreted from the cell, it is abundant in cells that secrete proteins, such as the liver.

The smooth endoplasmic reticulum (SER) is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (see Figure **4.3.1**). The SER's functions include synthesis of carbohydrates, lipids (including phospholipids), and steroid hormones; detoxification of medications and poisons; alcohol metabolism; and storage of calcium ions.

The Golgi Apparatus

We have already mentioned that vesicles can bud from the ER, but where do the vesicles go? Before reaching their final destination, the lipids or proteins within the transport vesicles need to be sorted, packaged, and tagged so that they wind up in the right place. The sorting, tagging, packaging, and distribution of lipids and proteins take place in the Golgi apparatus (also called the Golgi body), a series of flattened membranous sacs (Figure **4.3.5**).

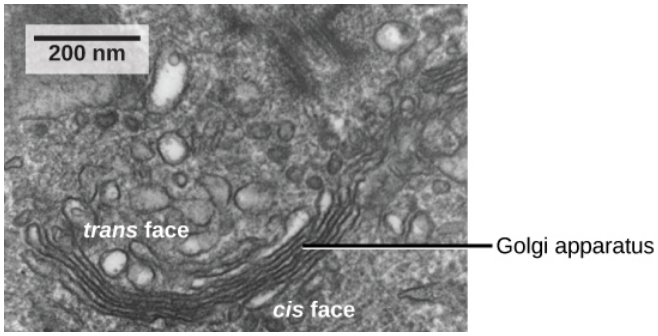


Figure 4.3.5: The Golgi apparatus in this transmission electron micrograph of a white blood cell is visible as a stack of semicircular flattened rings in the lower portion of this image. Several vesicles can be seen near the Golgi apparatus. (credit: modification of work by Louisa Howard; scale-bar data from Matt Russell)

The Golgi apparatus has a receiving face near the endoplasmic reticulum and a releasing face on the side away from the ER, toward the cell membrane. The transport vesicles that form from the ER travel to the receiving face, fuse with it, and empty their contents into the lumen of the Golgi apparatus. As the proteins and lipids travel through the Golgi, they undergo further modifications. The most frequent modification is the addition of short chains of sugar molecules. The newly modified proteins and lipids are then tagged with small molecular groups to enable them to be routed to their proper destinations.

Finally, the modified and tagged proteins are packaged into vesicles that bud from the opposite face of the Golgi. While some of these vesicles, transport vesicles, deposit their contents into other parts of the cell where they will be used, others, secretory vesicles, fuse with the plasma membrane and release their contents outside the cell.

The amount of Golgi in different cell types again illustrates that form follows function within cells. Cells that engage in a great deal of secretory activity (such as cells of the salivary glands that secrete digestive enzymes or cells of the immune system that secrete antibodies) have an abundant number of Golgi.

In plant cells, the Golgi has an additional role of synthesizing polysaccharides, some of which are incorporated into the cell wall and some of which are used in other parts of the cell.

Lysosomes

In animal cells, the lysosomes are the cell's "garbage disposal." Digestive enzymes within the lysosomes aid the breakdown of proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles. In single-celled eukaryotes, lysosomes are important for digestion of the food they ingest and the recycling of organelles. These enzymes are active at a much lower pH (more acidic)

than those located in the cytoplasm. Many reactions that take place in the cytoplasm could not occur at a low pH, thus the advantage of compartmentalizing the eukaryotic cell into organelles is apparent.

Lysosomes also use their hydrolytic enzymes to destroy disease-causing organisms that might enter the cell. A good example of this occurs in a group of white blood cells called macrophages, which are part of your body's immune system. In a process known as phagocytosis, a section of the plasma membrane of the macrophage invaginates (folds in) and engulfs a pathogen. The invaginated section, with the pathogen inside, then pinches itself off from the plasma membrane and becomes a vesicle. The vesicle fuses with a lysosome. The lysosome's hydrolytic enzymes then destroy the pathogen (Figure **4.3.6**).

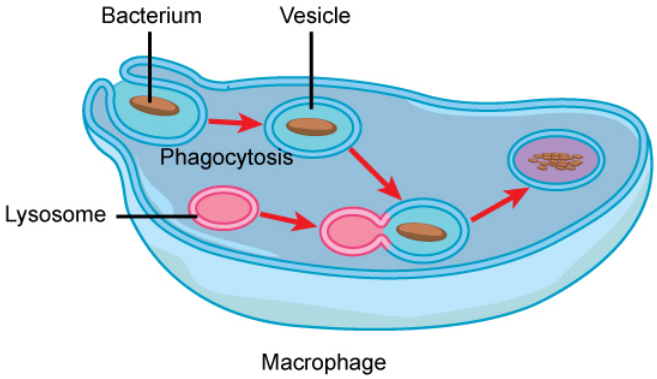


Figure 4.3.6: A macrophage has phagocytized a potentially pathogenic bacterium into a vesicle, which then fuses with a lysosome within the cell so that the pathogen can be destroyed. Other organelles are present in the cell, but for simplicity, are not shown.

Vesicles and Vacuoles

Vesicles and vacuoles are membrane-bound sacs that function in storage and transport. Vacuoles are somewhat larger than vesicles, and the membrane of a vacuole does not fuse with the membranes of other cellular components. Vesicles can fuse with other membranes within the cell system. Additionally, enzymes within plant vacuoles can break down macromolecules.

ART CONNECTION

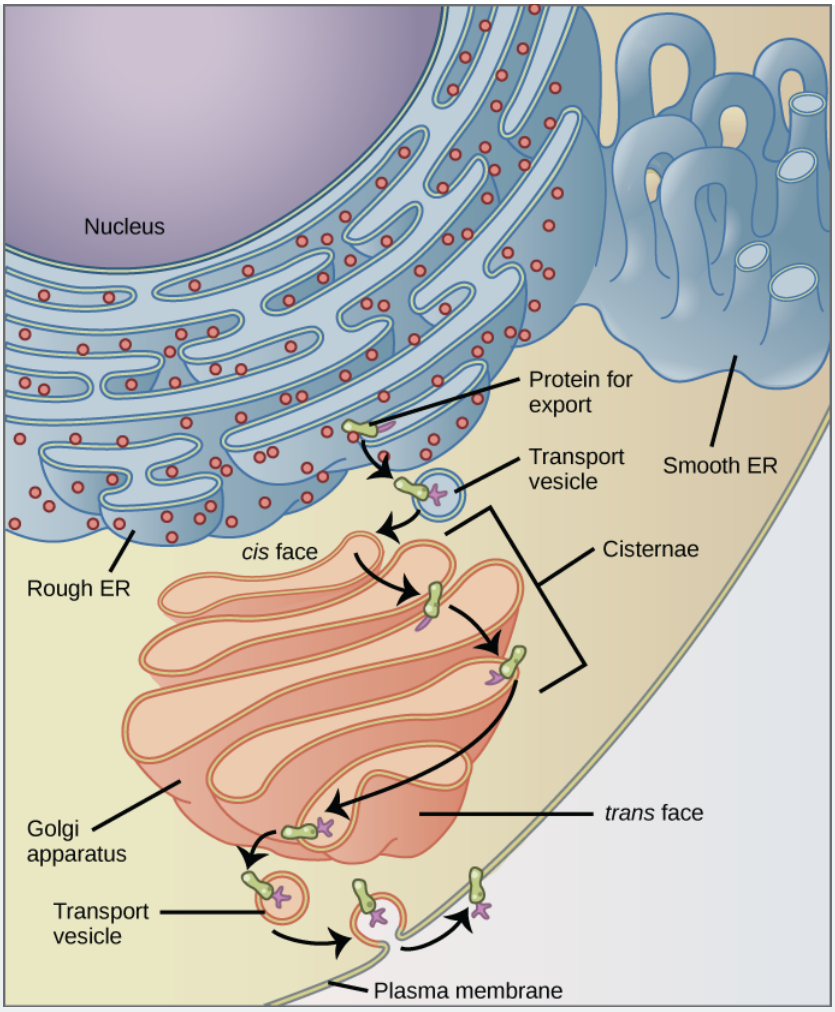


Figure 4.3.7: The endomembrane system works to modify, package, and transport lipids and proteins. (credit: modification of work by Magnus Manske)

Why does the *cis* face of the Golgi not face the plasma membrane?

Ribosomes

Ribosomes are the cellular structures responsible for protein synthesis. When viewed through an electron microscope, free ribosomes appear as either clusters or single tiny dots floating freely in the cytoplasm. Ribosomes may be attached to either the cytoplasmic side of the plasma membrane or the cytoplasmic side of the endoplasmic reticulum (Figure **4.3.7**). Electron microscopy has shown that ribosomes consist of large and small subunits. Ribosomes are enzyme complexes that are responsible for protein synthesis.

Because protein synthesis is essential for all cells, ribosomes are found in practically every cell, although they are smaller in prokaryotic cells. They are particularly abundant in immature red blood cells for the synthesis of hemoglobin, which functions in the transport of oxygen throughout the body.

Mitochondria

Mitochondria (singular = mitochondrion) are often called the “powerhouses” or “energy factories” of a cell because they are responsible for making adenosine triphosphate (ATP), the cell’s main energy-carrying molecule. The formation of ATP from the breakdown of glucose is known as cellular respiration. Mitochondria are oval-shaped, double-membrane organelles (Figure **4.3.8**) that have their own ribosomes and DNA. Each membrane is a phospholipid bilayer embedded with proteins. The inner layer has folds called cristae, which increase the surface area of the inner membrane. The area surrounded by the folds is called the mitochondrial matrix. The cristae and the matrix have different roles in cellular respiration.

In keeping with our theme of form following function, it is important to point out that muscle cells have a very high concentration of mitochondria because muscle cells need a lot of energy to contract.

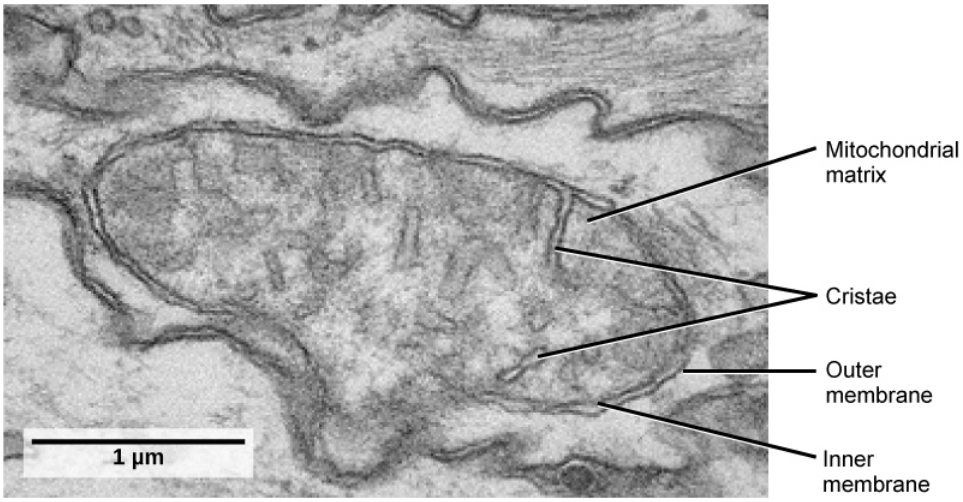


Figure 4.3.8: This transmission electron micrograph shows a mitochondrion as viewed with an electron microscope. Notice the inner and outer membranes, the cristae, and the mitochondrial matrix. (credit: modification of work by Matthew Britton; scale-bar data from Matt Russell)

Peroxisomes

Peroxisomes are small, round organelles enclosed by single membranes. They carry out oxidation reactions that break down fatty acids and amino acids. They also detoxify many poisons that may enter the body. Alcohol is detoxified by peroxisomes in liver cells. A byproduct of these oxidation reactions is hydrogen peroxide, H_2O_2, which is contained within the peroxisomes to prevent the chemical from causing damage to cellular components outside of the organelle. Hydrogen peroxide is safely broken down by peroxisomal enzymes into water and oxygen.

Animal Cells versus Plant Cells

Despite their fundamental similarities, there are some striking differences between animal and plant cells (see Table **4.3.1**). Animal cells have centrioles, centrosomes (discussed under the cytoskeleton), and lysosomes, whereas plant cells do not. Plant cells have a cell wall, chloroplasts, plasmodesmata, and plastids used for storage, and a large central vacuole, whereas animal cells do not.

The Cell Wall

In Figure **4.3.1b**, the diagram of a plant cell, you see a structure external to the plasma membrane called the cell wall. The cell wall is a rigid covering that protects the cell, provides structural support, and gives shape to the cell. Fungal and protist cells also have cell walls.

While the chief component of prokaryotic cell walls is peptidoglycan, the major organic molecule in the plant cell wall is cellulose, a polysaccharide made up of long, straight chains of glucose units. When nutritional information refers to dietary fiber, it is referring to the cellulose content of food.

Chloroplasts

Like mitochondria, chloroplasts also have their own DNA and ribosomes. Chloroplasts function in photosynthesis and can be found in eukaryotic cells such as plants and algae. In photosynthesis, carbon dioxide, water, and light energy are used to make glucose and oxygen. This is the major difference between plants and animals: Plants (autotrophs) are able to make their own food, like glucose, whereas animals (heterotrophs) must rely on other organisms for their organic compounds or food source.

Like mitochondria, chloroplasts have outer and inner membranes, but within the space enclosed by a chloroplast's inner membrane is a set of interconnected and stacked, fluid-filled membrane sacs called thylakoids (Figure **4.3.9**). Each stack of thylakoids is called a granum (plural = grana). The fluid enclosed by the inner membrane and surrounding the grana is called the stroma.

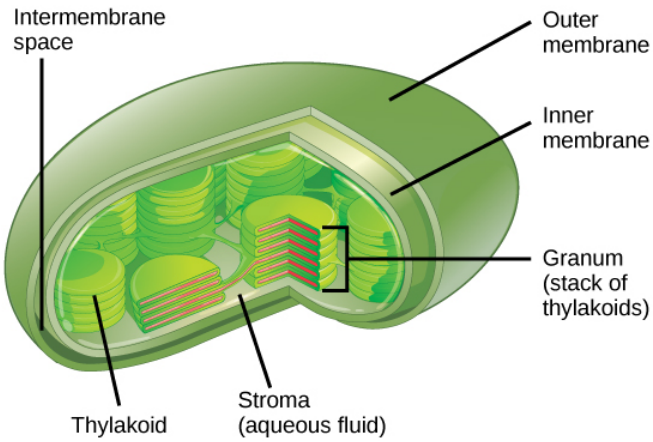


Figure 4.3.9: This simplified diagram of a chloroplast shows the outer membrane, inner membrane, thylakoids, grana, and stroma.

The chloroplasts contain a green pigment called chlorophyll, which captures the energy of sunlight for photosynthesis. Like plant cells, photosynthetic protists also have chloroplasts. Some bacteria also perform photosynthesis, but they do not have chloroplasts. Their photosynthetic pigments are located in the thylakoid membrane within the cell itself.

EVOLUTION IN ACTION: Endosymbiosis

We have mentioned that both mitochondria and chloroplasts contain DNA and ribosomes. Have you wondered why? Strong evidence points to endosymbiosis as the explanation.

Symbiosis is a relationship in which organisms from two separate species live in close association and typically exhibit specific adaptations to each other. Endosymbiosis (*endo*-= within) is a relationship in which one organism lives inside the other. Endosymbiotic relationships abound in nature. Microbes that produce vitamin K live inside the human gut. This relationship is beneficial for us because we are unable to synthesize vitamin K. It is also beneficial for the microbes because they are protected from other organisms and are provided a stable habitat and abundant food by living within the large intestine.

Scientists have long noticed that bacteria, mitochondria, and chloroplasts are similar in size. We also know that mitochondria and chloroplasts have DNA and ribosomes, just as bacteria do. Scientists believe that host cells and bacteria formed a mutually beneficial endosymbiotic relationship when the host cells ingested aerobic bacteria and cyanobacteria but did not destroy them. Through evolution, these ingested bacteria became more specialized in their functions, with the aerobic bacteria becoming mitochondria and the photosynthetic bacteria becoming chloroplasts.

The Central Vacuole

Previously, we mentioned vacuoles as essential components of plant cells. If you look at Figure **4.3.1**, you will see that plant cells each have a large, central vacuole that occupies most of the cell. The central vacuole plays a key role in regulating the cell's concentration of water in changing environmental conditions. In plant cells, the liquid inside the central vacuole provides turgor pressure, which is the outward pressure caused by the fluid inside the cell. Have you ever noticed that if you forget to water a plant for a few days, it wilts? That is because as the water concentration in the soil becomes lower than the water concentration in the plant, water moves out of the central vacuoles and cytoplasm and into the soil. As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the cell walls of a plant results in the wilted appearance. Additionally, this fluid has a very bitter taste, which discourages consumption by insects and animals. The central vacuole also functions to store proteins in developing seed cells.

Extracellular Matrix of Animal Cells

Most animal cells release materials into the extracellular space. The primary components of these materials are glycoproteins and the protein collagen. Collectively, these materials are called the extracellular matrix (Figure **4.3.10**). Not only does the extracellular matrix hold the cells together to form a tissue, but it also allows the cells within the tissue to communicate with each other.

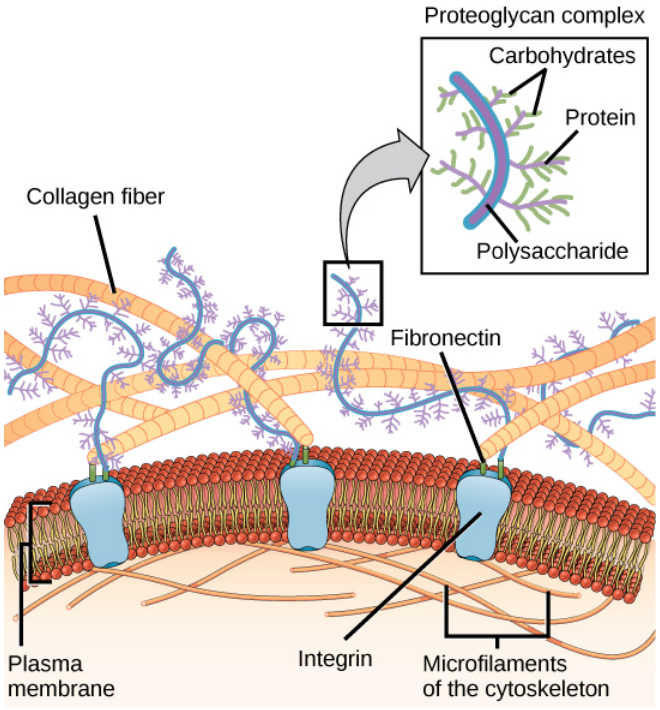


Figure 4.3.10: The extracellular matrix consists of a network of substances secreted by cells.

Blood clotting provides an example of the role of the extracellular matrix in cell communication. When the cells lining a blood vessel are damaged, they display a protein receptor called tissue factor. When tissue factor binds with another factor in the extracellular matrix, it causes platelets to adhere to the wall of the damaged blood vessel, stimulates adjacent smooth muscle cells in the blood vessel to contract (thus constricting the blood vessel), and initiates a series of steps that stimulate the platelets to produce clotting factors.

Intercellular Junctions

Cells can also communicate with each other by direct contact, referred to as intercellular junctions. There are some differences in the ways that plant and animal cells do this. Plasmodesmata (singular = plasmodesma) are junctions between plant cells, whereas animal cell contacts include tight and gap junctions, and desmosomes.

In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell walls surrounding each cell. Plasmodesmata are numerous channels that pass between the cell walls of adjacent plant cells, connecting their cytoplasm and enabling signal molecules and nutrients to be transported from cell to cell (Figure **4.3.11a**).

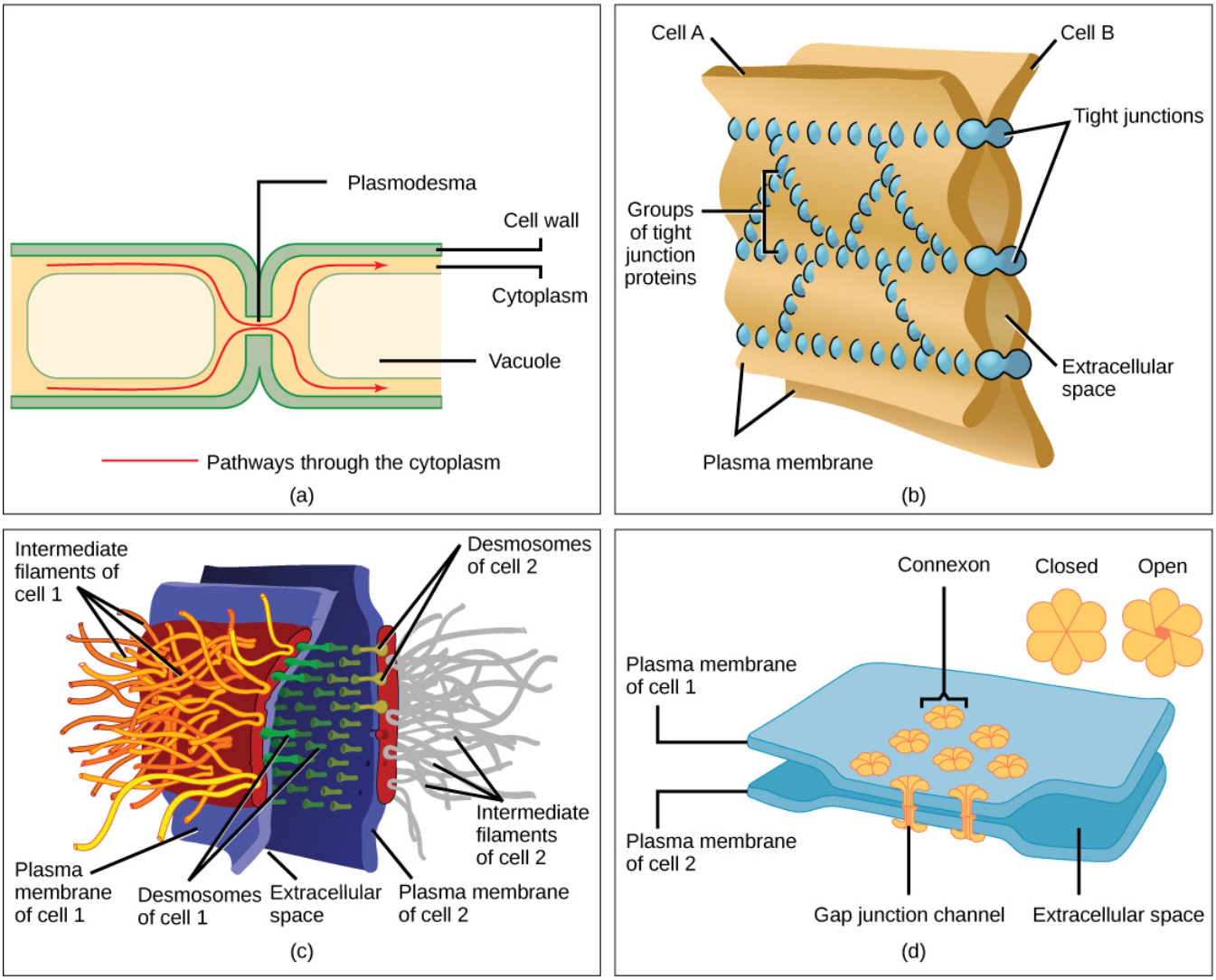


Figure 4.3.11: There are four kinds of connections between cells. (a) A plasmodesma is a channel between the cell walls of two adjacent plant cells. (b) Tight junctions join adjacent animal cells. (c) Desmosomes join two animal cells together. (d) Gap junctions act as channels between animal cells. (credit b, c, d: modification of work by Mariana Ruiz Villareal)

A tight junction is a watertight seal between two adjacent animal cells (Figure **4.3.11b**). Proteins hold the cells tightly against each other. This tight adhesion prevents materials from leaking between the cells. Tight junctions are typically found in the epithelial tissue that lines internal organs and cavities, and composes most of the skin. For example, the tight junctions of the epithelial cells lining the urinary bladder prevent urine from leaking into the extracellular space.

Also found only in animal cells are desmosomes, which act like spot welds between adjacent epithelial cells (Figure **4.3.11c**). They keep cells together in a sheet-like formation in organs and tissues that stretch, like the skin, heart, and muscles.

Gap junctions in animal cells are like plasmodesmata in plant cells in that they are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate (Figure **4.3.11d**). Structurally, however, gap junctions and plasmodesmata differ.

Table 4.3.1: This table provides the components of prokaryotic and eukaryotic cells and their respective functions.

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Plasma membrane	Separates cell from external environment; controls passage of organic molecules, ions, water, oxygen, and wastes into and out of the cell	Yes	Yes	Yes
Cytoplasm	Provides structure to cell; site of many metabolic reactions; medium in which organelles are found	Yes	Yes	Yes
Nucleoid	Location of DNA	Yes	No	No
Nucleus	Cell organelle that houses DNA and directs synthesis of ribosomes and proteins	No	Yes	Yes
Ribosomes	Protein synthesis	Yes	Yes	Yes
Mitochondria	ATP production/cellular respiration	No	Yes	Yes
Peroxisomes	Oxidizes and breaks down fatty acids and amino acids, and detoxifies poisons	No	Yes	Yes
Vesicles and vacuoles	Storage and transport; digestive function in plant cells	No	Yes	Yes
Centrosome	Unspecified role in cell division in animal cells; organizing center of microtubules in animal cells	No	Yes	No
Lysosomes	Digestion of macromolecules; recycling of worn-out organelles	No	Yes	No
Cell wall	Protection, structural support and maintenance of cell shape	Yes, primarily peptidoglycan in bacteria but not Archaea	No	Yes, primarily cellulose
Chloroplasts	Photosynthesis	No	No	Yes
Endoplasmic reticulum	Modifies proteins and synthesizes lipids	No	Yes	Yes
Golgi apparatus	Modifies, sorts, tags,	No	Yes	Yes

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
	packages, and distributes lipids and proteins			
Cytoskeleton	Maintains cell's shape, secures organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move independently	Yes	Yes	Yes
Flagella	Cellular locomotion	Some	Some	No, except for some plant sperm
Cilia	Cellular locomotion, movement of particles along extracellular surface of plasma membrane, and filtration	No	Some	No

Summary

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes, but a eukaryotic cell is typically larger than a prokaryotic cell, has a true nucleus (meaning its DNA is surrounded by a membrane), and has other membrane-bound organelles that allow for compartmentalization of functions. The plasma membrane is a phospholipid bilayer embedded with proteins. The nucleolus within the nucleus is the site for ribosome assembly. Ribosomes are found in the cytoplasm or are attached to the cytoplasmic side of the plasma membrane or endoplasmic reticulum. They perform protein synthesis. Mitochondria perform cellular respiration and produce ATP. Peroxisomes break down fatty acids, amino acids, and some toxins. Vesicles and vacuoles are storage and transport compartments. In plant cells, vacuoles also help break down macromolecules.

Animal cells also have a centrosome and lysosomes. The centrosome has two bodies, the centrioles, with an unknown role in cell division. Lysosomes are the digestive organelles of animal cells.

Plant cells have a cell wall, chloroplasts, and a central vacuole. The plant cell wall, whose primary component is cellulose, protects the cell, provides structural support, and gives shape to the cell. Photosynthesis takes place in chloroplasts. The central vacuole expands, enlarging the cell without the need to produce more cytoplasm.

The endomembrane system includes the nuclear envelope, the endoplasmic reticulum, Golgi apparatus, lysosomes, vesicles, as well as the plasma membrane. These cellular components work together to modify, package, tag, and transport membrane lipids and proteins.

The cytoskeleton has three different types of protein elements. Microfilaments provide rigidity and shape to the cell, and facilitate cellular movements. Intermediate filaments bear tension and anchor the nucleus and other organelles in place. Microtubules help the cell resist compression, serve as tracks for motor proteins that move vesicles through the cell, and pull replicated chromosomes to opposite ends of a dividing cell. They are also the structural elements of centrioles, flagella, and cilia.

Animal cells communicate through their extracellular matrices and are connected to each other by tight junctions, desmosomes, and gap junctions. Plant cells are connected and communicate with each other by plasmodesmata.

Art Connections

Figure **4.3.1**: What structures does a plant cell have that an animal cell does not have? What structures does an animal cell have that a plant cell does not have?

Answer

Plant cells have plasmodesmata, a cell wall, a large central vacuole, chloroplasts, and plastids. Animal cells have lysosomes and centrosomes.

Figure **4.3.7**: Why does the *cis* face of the Golgi not face the plasma membrane?

Answer

Because that face receives chemicals from the ER, which is toward the center of the cell.

Glossary

cell wall
a rigid cell covering made of cellulose in plants, peptidoglycan in bacteria, non-peptidoglycan compounds in Archaea, and chitin in fungi that protects the cell, provides structural support, and gives shape to the cell

central vacuole
a large plant cell organelle that acts as a storage compartment, water reservoir, and site of macromolecule degradation

chloroplast
a plant cell organelle that carries out photosynthesis

cilium
(plural: cilia) a short, hair-like structure that extends from the plasma membrane in large numbers and is used to move an entire cell or move substances along the outer surface of the cell

cytoplasm
the entire region between the plasma membrane and the nuclear envelope, consisting of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals

cytoskeleton
the network of protein fibers that collectively maintains the shape of the cell, secures some organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move

cytosol
the gel-like material of the cytoplasm in which cell structures are suspended

desmosome
a linkage between adjacent epithelial cells that forms when cadherins in the plasma membrane attach to intermediate filaments

endomembrane system
the group of organelles and membranes in eukaryotic cells that work together to modify, package, and transport lipids and proteins

endoplasmic reticulum (ER)
a series of interconnected membranous structures within eukaryotic cells that collectively modify proteins and synthesize lipids

extracellular matrix
the material, primarily collagen, glycoproteins, and proteoglycans, secreted from animal cells that holds cells together as a tissue, allows cells to communicate with each other, and provides mechanical protection and anchoring for cells in the tissue

flagellum
(plural: flagella) the long, hair-like structure that extends from the plasma membrane and is used to move the cell

gap junction

a channel between two adjacent animal cells that allows ions, nutrients, and other low-molecular weight substances to pass between the cells, enabling the cells to communicate

Golgi apparatus
a eukaryotic organelle made up of a series of stacked membranes that sorts, tags, and packages lipids and proteins for distribution

lysosome
an organelle in an animal cell that functions as the cell's digestive component; it breaks down proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles

mitochondria
(singular: mitochondrion) the cellular organelles responsible for carrying out cellular respiration, resulting in the production of ATP, the cell's main energy-carrying molecule

nuclear envelope
the double-membrane structure that constitutes the outermost portion of the nucleus

nucleolus
the darkly staining body within the nucleus that is responsible for assembling ribosomal subunits

nucleus
the cell organelle that houses the cell's DNA and directs the synthesis of ribosomes and proteins

peroxisome
a small, round organelle that contains hydrogen peroxide, oxidizes fatty acids and amino acids, and detoxifies many poisons

plasma membrane
a phospholipid bilayer with embedded (integral) or attached (peripheral) proteins that separates the internal contents of the cell from its surrounding environment

plasmodesma
(plural: plasmodesmata) a channel that passes between the cell walls of adjacent plant cells, connects their cytoplasm, and allows materials to be transported from cell to cell

ribosome
a cellular structure that carries out protein synthesis

rough endoplasmic reticulum (RER)
the region of the endoplasmic reticulum that is studded with ribosomes and engages in protein modification

smooth endoplasmic reticulum (SER)
the region of the endoplasmic reticulum that has few or no ribosomes on its cytoplasmic surface and synthesizes carbohydrates, lipids, and steroid hormones; detoxifies chemicals like pesticides, preservatives, medications, and environmental pollutants, and stores calcium ions

tight junction
a firm seal between two adjacent animal cells created by protein adherence

vacuole
a membrane-bound sac, somewhat larger than a vesicle, that functions in cellular storage and transport

vesicle

a small, membrane-bound sac that functions in cellular storage and transport; its membrane is capable of fusing with the plasma membrane and the membranes of the endoplasmic reticulum and Golgi apparatus

Contributors and Attributions

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4.4: The Endomembrane System

Skills to Develop

- List the components of the endomembrane system
- Recognize the relationship between the endomembrane system and its functions

The endomembrane system (endo = “within”) is a group of membranes and organelles (Figure **4.4.1**) in eukaryotic cells that works together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, which we’ve already mentioned, and the endoplasmic reticulum and Golgi apparatus, which we will cover shortly. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles. The endomembrane system does not include the membranes of either mitochondria or chloroplasts.

Art Connection

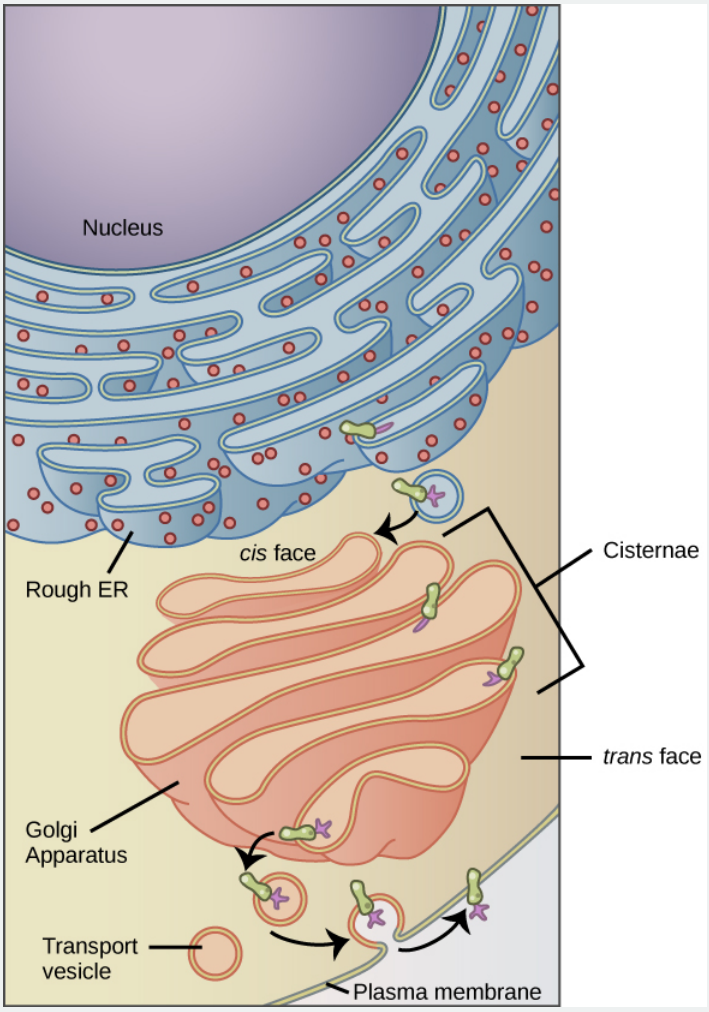


Figure **4.4.1**: Membrane and secretory proteins are synthesized in the rough endoplasmic reticulum (RER). The RER also sometimes modifies proteins. In this illustration, a (green) integral membrane protein in the ER is modified by attachment of a (purple) carbohydrate. Vesicles with the integral protein bud from the ER and fuse with the cis face of the Golgi apparatus. As the protein passes along the Golgi’s cisternae, it is further modified by the addition of more carbohydrates. After its synthesis is complete, it exits as integral membrane protein of the vesicle that bud from the Golgi’s trans face and when the vesicle fuses with the cell membrane the protein becomes integral portion of that cell membrane. (credit: modification of work by Magnus Manske)

If a peripheral membrane protein were synthesized in the lumen (inside) of the ER, would it end up on the inside or outside of the plasma membrane?

The Endoplasmic Reticulum

The endoplasmic reticulum (ER) (Figure **4.4.1**) is a series of interconnected membranous sacs and tubules that collectively modifies proteins and synthesizes lipids. However, these two functions are performed in separate areas of the ER: the rough ER and the smooth ER, respectively.

The hollow portion of the ER tubules is called the lumen or cisternal space. The membrane of the ER, which is a phospholipid bilayer embedded with proteins, is continuous with the nuclear envelope.

Rough ER

The rough endoplasmic reticulum (RER) is so named because the ribosomes attached to its cytoplasmic surface give it a studded appearance when viewed through an electron microscope (Figure **4.4.2**).

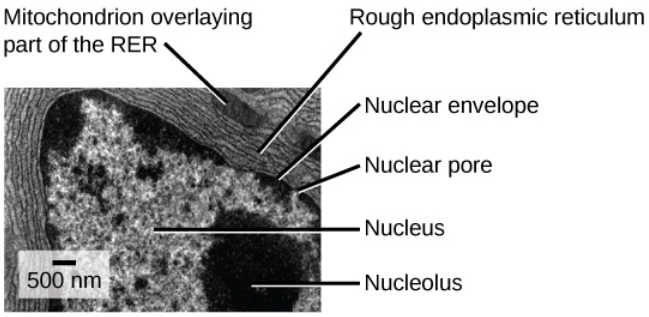


Figure **4.4.2**: This transmission electron micrograph shows the rough endoplasmic reticulum and other organelles in a pancreatic cell. (credit: modification of work by Louisa Howard)

Ribosomes transfer their newly synthesized proteins into the lumen of the RER where they undergo structural modifications, such as folding or the acquisition of side chains. These modified proteins will be incorporated into cellular membranes—the membrane of the ER or those of other organelles—or secreted from the cell (such as protein hormones, enzymes). The RER also makes phospholipids for cellular membranes.

If the phospholipids or modified proteins are not destined to stay in the RER, they will reach their destinations via transport vesicles that bud from the RER's membrane (Figure **4.4.1**).

Since the RER is engaged in modifying proteins (such as enzymes, for example) that will be secreted from the cell, you would be correct in assuming that the RER is abundant in cells that secrete proteins. This is the case with cells of the liver, for example.

Smooth ER

The smooth endoplasmic reticulum (SER) is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (Figure **4.4.1**). Functions of the SER include synthesis of carbohydrates, lipids, and steroid hormones; detoxification of medications and poisons; and storage of calcium ions.

In muscle cells, a specialized SER called the sarcoplasmic reticulum is responsible for storage of the calcium ions that are needed to trigger the coordinated contractions of the muscle cells.

Link to Learning



Video 4.4.1: You can watch an excellent animation of the endomembrane system here.

Career Connection: Cardiologist

Heart disease is the leading cause of death in the United States. This is primarily due to our sedentary lifestyle and our high trans-fat diets.

Heart failure is just one of many disabling heart conditions. Heart failure does not mean that the heart has stopped working. Rather, it means that the heart can't pump with sufficient force to transport oxygenated blood to all the vital organs. Left untreated, heart failure can lead to kidney failure and failure of other organs.

The wall of the heart is composed of cardiac muscle tissue. Heart failure occurs when the endoplasmic reticula of cardiac muscle cells do not function properly. As a result, an insufficient number of calcium ions are available to trigger a sufficient contractile force.

Cardiologists (cardi- = "heart"; -ologist = "one who studies") are doctors who specialize in treating heart diseases, including heart failure. Cardiologists can make a diagnosis of heart failure via physical examination, results from an electrocardiogram (ECG, a test that measures the electrical activity of the heart), a chest X-ray to see whether the heart is enlarged, and other tests. If heart failure is diagnosed, the cardiologist will typically prescribe appropriate medications and recommend a reduction in table salt intake and a supervised exercise program.

The Golgi Apparatus

We have already mentioned that vesicles can bud from the ER and transport their contents elsewhere, but where do the vesicles go? Before reaching their final destination, the lipids or proteins within the transport vesicles still need to be sorted, packaged, and tagged so that they wind up in the right place. Sorting, tagging, packaging, and distribution of lipids and proteins takes place in the Golgi apparatus (also called the Golgi body), a series of flattened membranes (Figure 4.4.3).

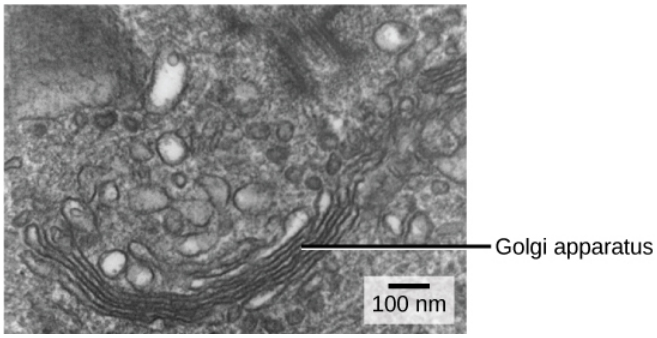


Figure 4.4.3: The Golgi apparatus in this white blood cell is visible as a stack of semicircular, flattened rings in the lower portion of the image. Several vesicles can be seen near the Golgi apparatus. (credit: modification of work by Louisa Howard)

The receiving side of the Golgi apparatus is called the *cis* face. The opposite side is called the *trans* face. The transport vesicles that formed from the ER travel to the *cis* face, fuse with it, and empty their contents into the lumen of the Golgi apparatus. As the proteins and lipids travel through the Golgi, they undergo further modifications that allow them to be sorted. The most frequent modification is the addition of short chains of sugar molecules. These newly modified proteins and lipids are then tagged with phosphate groups or other small molecules so that they can be routed to their proper destinations.

Finally, the modified and tagged proteins are packaged into secretory vesicles that bud from the *trans* face of the Golgi. While some of these vesicles deposit their contents into other parts of the cell where they will be used, other secretory vesicles fuse with the plasma membrane and release their contents outside the cell.

In another example of form following function, cells that engage in a great deal of secretory activity (such as cells of the salivary glands that secrete digestive enzymes or cells of the immune system that secrete antibodies) have an abundance of Golgi.

In plant cells, the Golgi apparatus has the additional role of synthesizing polysaccharides, some of which are incorporated into the cell wall and some of which are used in other parts of the cell.

Career Connection: Geneticist

Many diseases arise from genetic mutations that prevent the synthesis of critical proteins. One such disease is Lowe disease (also called oculocerebrorenal syndrome, because it affects the eyes, brain, and kidneys). In Lowe disease, there is a deficiency in an enzyme localized to the Golgi apparatus. Children with Lowe disease are born with cataracts, typically develop kidney disease after the first year of life, and may have impaired mental abilities.

Lowe disease is a genetic disease caused by a mutation on the X chromosome. The X chromosome is one of the two human sex chromosome, as these chromosomes determine a person's sex. Females possess two X chromosomes while males possess one X and one Y chromosome. In females, the genes on only one of the two X chromosomes are expressed. Therefore, females who carry the Lowe disease gene on one of their X chromosomes have a 50/50 chance of having the disease. However, males only have one X chromosome and the genes on this chromosome are always expressed. Therefore, males will always have Lowe disease if their X chromosome carries the Lowe disease gene. The location of the mutated gene, as well as the locations of many other mutations that cause genetic diseases, has now been identified. Through prenatal testing, a woman can find out if the fetus she is carrying may be afflicted with one of several genetic diseases.

Geneticists analyze the results of prenatal genetic tests and may counsel pregnant women on available options. They may also conduct genetic research that leads to new drugs or foods, or perform DNA analyses that are used in forensic investigations.

Lysosomes

In addition to their role as the digestive component and organelle-recycling facility of animal cells, lysosomes are considered to be parts of the endomembrane system. Lysosomes also use their hydrolytic enzymes to destroy pathogens (disease-causing organisms) that might enter the cell. A good example of this occurs in a group of white blood cells called macrophages, which are part of your body’s immune system. In a process known as phagocytosis or endocytosis, a section of the plasma membrane of the macrophage invaginates (folds in) and engulfs a pathogen. The invaginated section, with the pathogen inside, then pinches itself off from the plasma membrane and becomes a vesicle. The vesicle fuses with a lysosome. The lysosome’s hydrolytic enzymes then destroy the pathogen (Figure **4.4.4**).

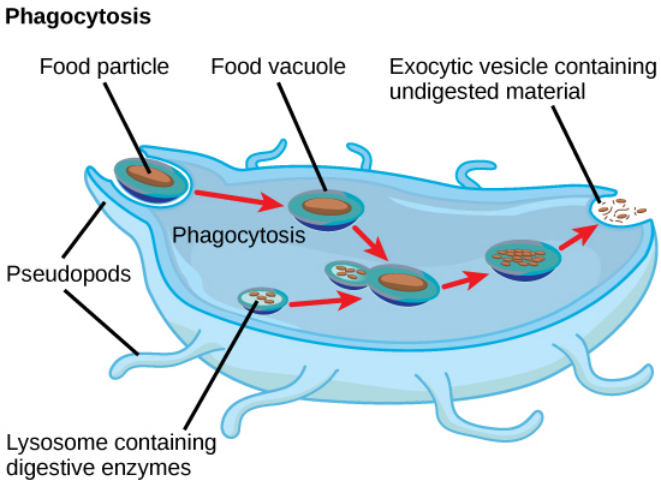


Figure **4.4.4**: A macrophage has engulfed (phagocytized) a potentially pathogenic bacterium and then fuses with a lysosomes within the cell to destroy the pathogen. Other organelles are present in the cell but for simplicity are not shown.

Summary

The endomembrane system includes the nuclear envelope, lysosomes, vesicles, the ER, and Golgi apparatus, as well as the plasma membrane. These cellular components work together to modify, package, tag, and transport proteins and lipids that form the membranes.

The RER modifies proteins and synthesizes phospholipids used in cell membranes. The SER synthesizes carbohydrates, lipids, and steroid hormones; engages in the detoxification of medications and poisons; and stores calcium ions. Sorting, tagging, packaging, and distribution of lipids and proteins take place in the Golgi apparatus. Lysosomes are created by the budding of the membranes of the RER and Golgi. Lysosomes digest macromolecules, recycle worn-out organelles, and destroy pathogens.

Art Connections

Figure **4.4.1**: If a peripheral membrane protein were synthesized in the lumen (inside) of the ER, would it end up on the inside or outside of the plasma membrane?

Answer

It would end up on the outside. After the vesicle passes through the Golgi apparatus and fuses with the plasma membrane, it turns inside out.

Glossary

endomembrane system

group of organelles and membranes in eukaryotic cells that work together modifying, packaging, and transporting lipids and proteins

endoplasmic reticulum (ER)

series of interconnected membranous structures within eukaryotic cells that collectively modify proteins and synthesize lipids

Golgi apparatus

eukaryotic organelle made up of a series of stacked membranes that sorts, tags, and packages lipids and proteins for distribution

rough endoplasmic reticulum (RER)

region of the endoplasmic reticulum that is studded with ribosomes and engages in protein modification and phospholipid synthesis

smooth endoplasmic reticulum (SER)

region of the endoplasmic reticulum that has few or no ribosomes on its cytoplasmic surface and synthesizes carbohydrates, lipids, and steroid hormones; detoxifies certain chemicals (like pesticides, preservatives, medications, and environmental pollutants), and stores calcium ions

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SECTION OVERVIEW

4.5: Mitochondria and Chloroplasts- Cellular Generators

4.5.1: Mitochondria

4.5.2: Chloroplasts

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4.5.1: Mitochondria



Sperm cells and muscle cells need lots of energy. What do they have in common?

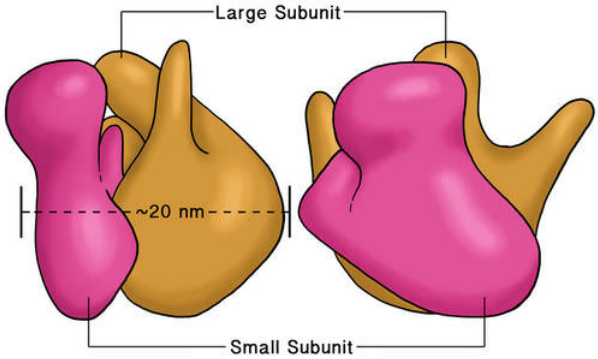
They have lots of mitochondria. Mitochondria are called the power plants of the cell, as these organelles are where most of the cell's energy is produced. Cells that need lots of energy have lots of mitochondria.

Other Organelles

In addition to the nucleus, eukaryotic cells have many other organelles, including ribosomes and mitochondria. Ribosomes are present in all cells.

Ribosomes

Ribosomes are small organelles and are the sites of protein synthesis (or assembly). They are made of ribosomal protein and ribosomal RNA, and are found in both eukaryotic and prokaryotic cells. Unlike other organelles, ribosomes are not surrounded by a membrane. Each ribosome has two parts, a large and a small subunit, as shown in **Figure** below. The subunits are attached to one another. Ribosomes can be found alone or in groups within the cytoplasm. Some ribosomes are attached to the endoplasmic reticulum (ER) (as shown in **Figure** below), and others are attached to the nuclear envelope.



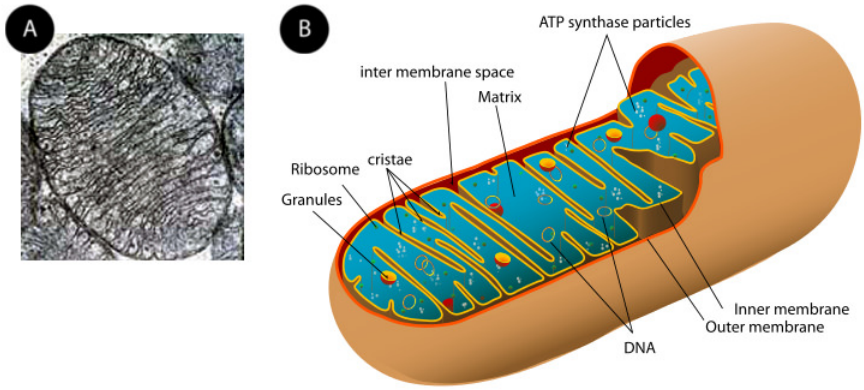
The two subunits that make up a ribosome, small organelles that are intercellular protein factories.

Ribozymes are RNA molecules that catalyze chemical reactions, such as translation.**Translation** is the process of ordering the amino acids in the assembly of a protein, and translation will be discussed more in another concept. Briefly, the ribosomes interact with other RNA molecules to make chains of amino acids called polypeptide chains, due to the peptide bond that forms between individual amino acids. Polypeptide chains are built from the genetic instructions held within a messenger RNA (mRNA) molecule. Polypeptide chains that are made on the rough ER (discussed below) are inserted directly into the ER and then are transported to their various cellular destinations. Ribosomes on the rough ER usually produce proteins that are destined for the cell membrane.

Ribosomes are found in both eukaryotic and prokaryotic cells. Ribosomes are not surrounded by a membrane. The other organelles found in eukaryotic cells are surrounded by a membrane.

Mitochondria

A mitochondrion (**mitochondria**, plural), is a membrane-enclosed organelle that is found in most eukaryotic cells. Mitochondria are called the "power plants" of the cell because they are the sites of cellular respiration, where they use energy from organic compounds to make ATP (adenosine triphosphate). **ATP** is the cell's energy source that is used for such things such as movement and cell division. Some ATP is made in the cytosol of the cell, but most of it is made inside mitochondria. The number of mitochondria in a cell depends on the cell's energy needs. For example, active human muscle cells may have thousands of mitochondria, while less active red blood cells do not have any.



(a): Electron micrograph of a single mitochondrion, within which you can see many cristae. Mitochondria range from 1 to 10 µm in size. **(b):** This model of a mitochondrion shows the organized arrangement of the inner and outer membranes, the protein matrix, and the folded inner mitochondrial membranes.

As **Figure** above **(a)** and **(b)** show, a mitochondrion has two phospholipid membranes. The smooth outer membrane separates the mitochondrion from the cytosol. The inner membrane has many folds, called **cristae**. The fluid-filled inside of the mitochondrion, called **matrix**, is where most of the cell's ATP is made.

Although most of a cell's DNA is contained in the cell nucleus, mitochondria have their own DNA. Mitochondria are able to reproduce asexually, and scientists think that they are descended from prokaryotes. According to the endosymbiotic theory, mitochondria were once free-living prokaryotes that infected or were engulfed by ancient eukaryotic cells. The invading prokaryotes were protected inside the eukaryotic host cell, and in turn the prokaryote supplied extra ATP to its host.

Summary

- Ribosomes are small organelles and are the site of protein synthesis. Ribosomes are found in all cells.
- Mitochondria are where energy from organic compounds is used to make ATP.

Explore More

Use this resource to answer the following questions.

- **Mitochondria** at http://www.nature.com/scitable/topicpage/mitochondria-14053590.

1. List three characteristics of mitochondria.
2. Describe how mitochondria originated?
3. What is the general function of proteins embedded within the mitochondria inner membrane?
4. What occurs in the mitochondrial matrix?
5. How do mitochondria divide?

Review

1. What is the function of a ribosome?
2. What is a significant difference between the structure of a ribosome and other organelles?
3. Identify the reason why mitochondria are called "power plants" of the cell.
4. Describe the structure of a mitochondrion.

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4.5.2: Chloroplasts



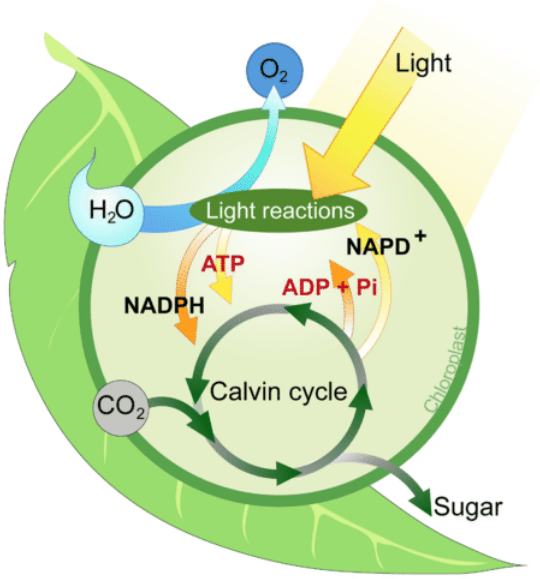
What do pancakes and chloroplasts have in common?

The chloroplast is the site of photosynthesis. Part of the photosynthesis reactions occur in an internal membrane within the organelle. The chloroplast contains many of these internal membranes, making photosynthesis very efficient. These internal membranes stack on top of each other, just like a stack of pancakes.

Stages of Photosynthesis

Photosynthesis occurs in two stages, which are shown in **Figure** below.

1. Stage I is called the **light reactions**. This stage uses water and changes light energy from the sun into chemical energy stored in ATP and NADPH (another energy-carrying molecule). This stage also releases oxygen as a waste product.
2. Stage II is called the **Calvin cycle**. This stage combines carbon from carbon dioxide in the air and uses the chemical energy in ATP and NADPH to make glucose.



The two stages of photosynthesis are the light reactions and the Calvin cycle. Do you see how the two stages are related?

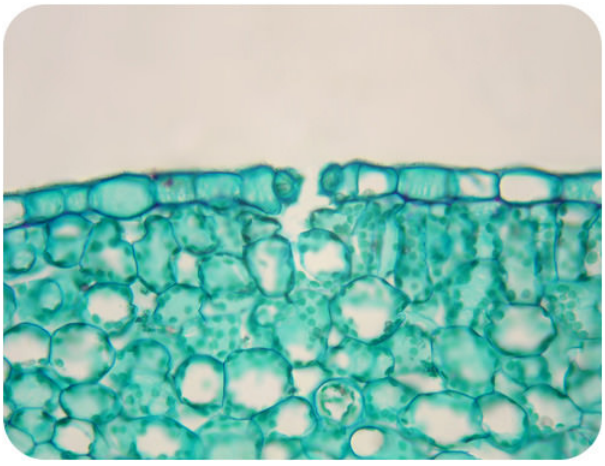
Before you read about these two stages of photosynthesis in greater detail, you need to know more about the chloroplast, where the two stages take place.

The Chloroplast

Chloroplasts: Theaters for Photosynthesis

Photosynthesis, the process of turning the energy of sunlight into ‘‘food,’’ is divided into two basic sets of reactions, known as the light reactions and the Calvin cycle, which uses carbon dioxide. As you study the details in other concepts, refer frequently to the chemical equation of photosynthesis: $6CO_2 + 6H_2O + \text{Light Energy} \rightarrow C_6H_{12}O_6 + 6O_2$. Photosynthesis occurs in the chloroplast, an organelle specific to plant cells.

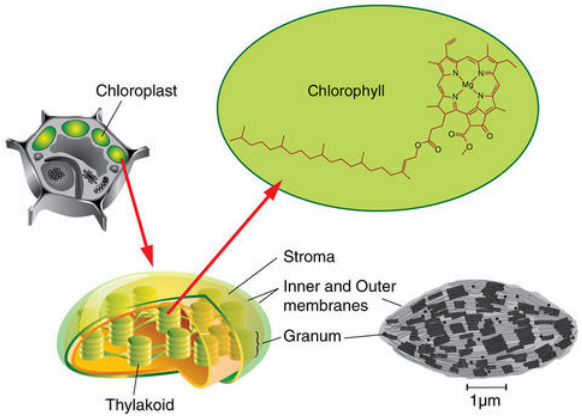
If you examine a single leaf of a Winter Jasmine leaf, shown in **Figure** below, under a microscope, you will see within each cell dozens of small green ovals. These are **chloroplasts**, the organelles which conduct photosynthesis in plants and algae. Chloroplasts closely resemble some types of bacteria and even contain their own circular DNA and ribosomes. In fact, the **endosymbiotic theory** holds that chloroplasts were once independently living bacteria (prokaryotes). So when we say that photosynthesis occurs within chloroplasts, we speak not only of the organelles within plants and algae, but also of some bacteria – in other words, virtually all photosynthetic autotrophs.



High power microscopic photo of the upper part of a Winter Jasmine leaf. Viewed under a microscope, many green chloroplasts are visible.

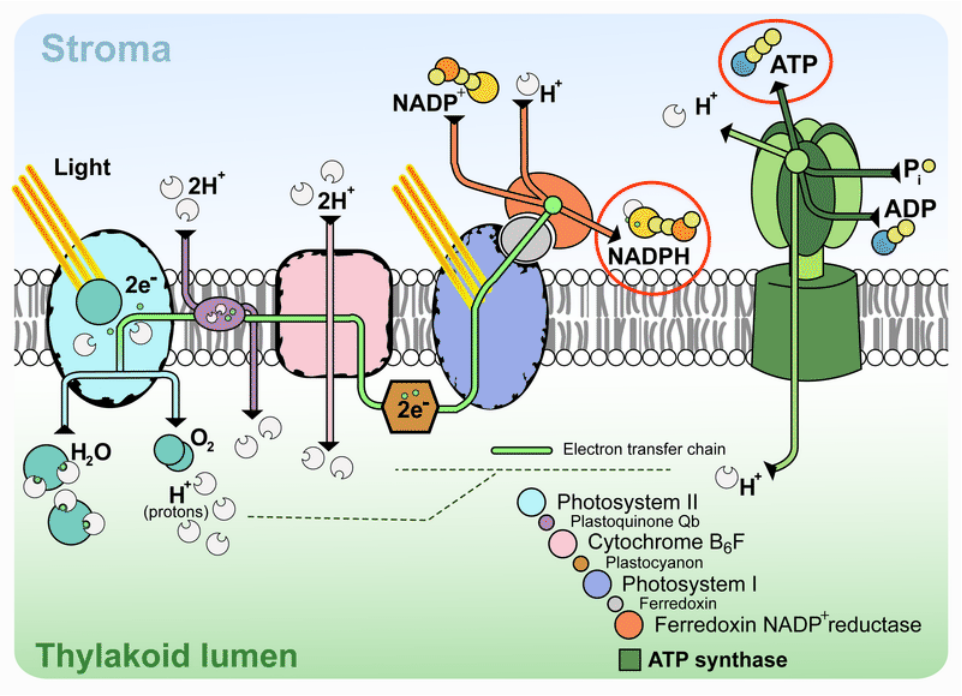
Each chloroplast contains neat stacks called **grana** (singular, granum). The grana consist of sac-like membranes, known as **thylakoid** membranes. These membranes contain **photosystems**, which are groups of molecules that include **chlorophyll**, a green pigment. The light reactions of photosynthesis occur in the thylakoid membranes. The **stroma** is the space outside the thylakoid membranes, as shown in **Figure** below. This is where the reactions of the Calvin cycle take place. In addition to enzymes, two basic types of molecules - pigments and **electron carriers** – are key players in this process and are also found in the thylakoid membranes.

You can take a video tour of a chloroplast at *Encyclopedia Britannica: Chloroplast*:www.britannica.com/EBchecked/...in-plant-cells.



A chloroplast consists of thylakoid membranes surrounded by stroma. The thylakoid membranes contain molecules of the green pigment chlorophyll.

Electron carrier molecules are usually arranged in **electron transport chains** (ETCs). These accept and pass along energy-carrying electrons in small steps (**Figure** below). In this way, they produce ATP and NADPH, which temporarily store chemical energy. Electrons in transport chains behave much like a ball bouncing down a set of stairs – a little energy is lost with each bounce. However, the energy "lost" at each step in an electron transport chain accomplishes a little bit of work, which eventually results in the synthesis of ATP.



This figure shows the light reactions of photosynthesis. This stage of photosynthesis begins with photosystem II (so named because it was discovered after photosystem I). Find the two electrons (2 e^-) in photosystem II, and then follow them through the electron transport chain (also called the electron transfer chain) to the formation of NADPH. Where do the hydrogen ions (H^+) come from that help make ATP?

Summary

- Photosynthesis occurs in the chloroplast, an organelle specific to plant cells.
- The light reactions of photosynthesis occur in the thylakoid membranes of the chloroplast.
- Electron carrier molecules are arranged in electron transport chains that produce ATP and NADPH, which temporarily store chemical energy.

Explore More

Use this resource to answer the questions that follow.

- http://www.hippocampus.org/Biology → Non-Majors Biology → Search: **Photosynthetic Structures**

1. What are the functions of a plant's leaves?
2. Where do the photosynthetic reactions occur?
3. What is a stomata? What is their role?
4. Describe the internal structure of a chloroplast.
5. What reactions occur in the thylakoid membranes?

Review

1. Describe the chloroplast's role in photosynthesis.
2. Explain how the structure of a chloroplast (its membranes and thylakoids) makes its function (the chemical reactions of photosynthesis) more efficient.

3. Describe electron carriers and the electron transport chain.

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SECTION OVERVIEW

4.6: The Cytoskeleton

4.6.1: Cytoplasm and Cytoskeletons

4.6.2: The Cytoskeleton

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4.6.1: Cytoplasm and Cytoskeletons



Does a cell have, or even need, a "skeleton"?

What do you get if you take some tubing, and make the tubes smaller and smaller and smaller? You get very small tubes, or microtubes. Very small tubes, or microtubules, together with microfilaments, form the basis of the "skeleton" inside the cell.

The Cytoplasm and Cytoskeleton

The **cytoplasm** consists of everything inside the plasma membrane of the cell, excluding the nucleus in a eukaryotic cell. It includes the watery, gel-like material called **cytosol**, as well as various structures. The water in the cytoplasm makes up about two thirds of the cell's weight and gives the cell many of its properties.

Functions of the Cytoplasm

The cytoplasm has several important functions, including:

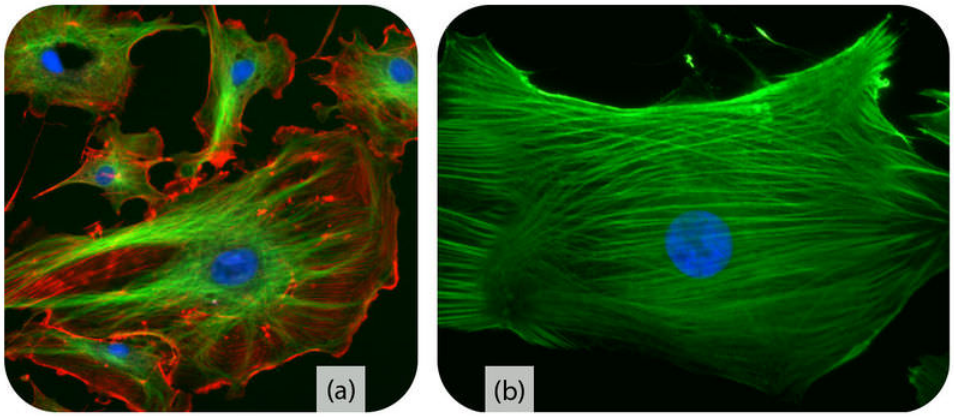
1. suspending cell organelles.
2. pushing against the plasma membrane to help the cell keep its shape.
3. providing a site for many of the biochemical reactions of the cell.

The Cytoskeleton

The **cytoskeleton** is a cellular "scaffolding" or "skeleton" that crisscrosses the cytoplasm. All eukaryotic cells have a cytoskeleton, and recent research has shown that prokaryotic cells also have a cytoskeleton. The eukaryotic cytoskeleton is made up of a network of long, thin protein fibers and has many functions. It helps to maintain cell shape. It holds organelles in place, and for some cells, it enables cell movement. The cytoskeleton also plays important roles in both the intracellular movement of substances and in cell division. Certain proteins act like a path that vesicles and organelles move along within the cell. The threadlike proteins that make up the cytoskeleton continually rebuild to adapt to the cell's constantly changing needs. Three main kinds of cytoskeleton fibers are microtubules, intermediate filaments, and microfilaments.

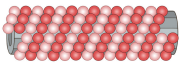
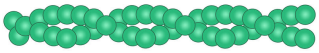
- **Microtubules**, shown in **Figure** below **(a)**, are hollow cylinders and are the thickest of the cytoskeleton structures. They are most commonly made of filaments which are polymers of alpha and beta tubulin, and radiate outwards from an area near the nucleus called the centrosome. **Tubulin** is the protein that forms microtubules. Two forms of tubulin, alpha and beta, form dimers (pairs) which come together to form the hollow cylinders. The cylinders are twisted around each other to form the microtubules. Microtubules help the cell keep its shape. They hold organelles in place and allow them to move around the cell, and they form the mitotic spindle during cell division. Microtubules also make up parts of cilia and flagella, the organelles that help a cell move.
- **Microfilaments**, shown in **Figure** below **(b)**, are made of two thin **actin** chains that are twisted around one another. Microfilaments are mostly concentrated just beneath the cell membrane, where they support the cell and help the cell keep its shape. Microfilaments form cytoplasmatic extensions, such as pseudopodia and microvilli, which allow certain cells to move. The actin of the microfilaments interacts with the protein myosin to cause contraction in muscle cells. Microfilaments are found in almost every cell, and are numerous in muscle cells and in cells that move by changing shape, such as phagocytes (white blood cells that search the body for bacteria and other invaders).

- **Intermediate filaments** differ in make-up from one cell type to another. Intermediate filaments organize the inside structure of the cell by holding organelles and providing strength. They are also structural components of the nuclear envelope. Intermediate filaments made of the protein keratin are found in skin, hair, and nails cells.

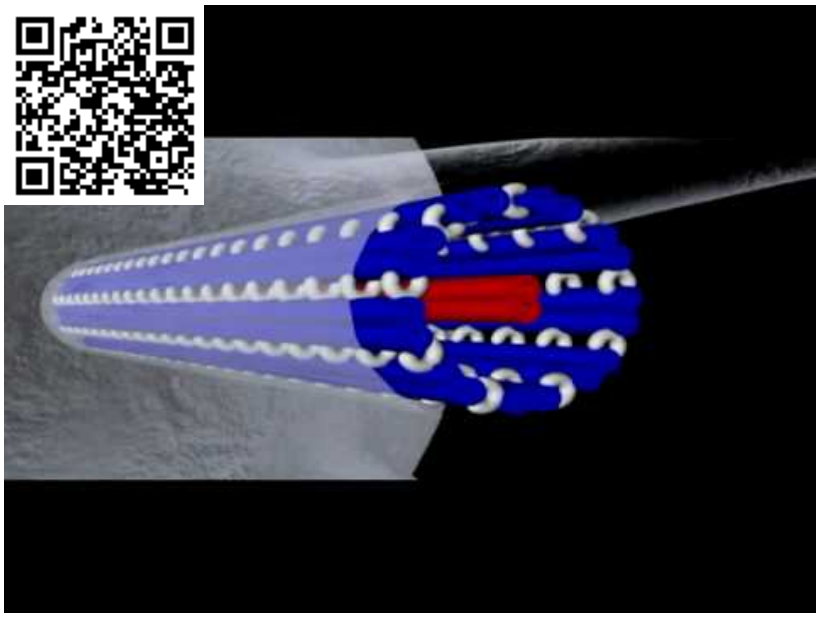


(a) The eukaryotic cytoskeleton. Microfilaments are shown in red, microtubules in green, and the nuclei are in blue. By linking regions of the cell together, the cytoskeleton helps support the shape of the cell. **(b)** Microscopy of microfilaments (actin filaments), shown in green, inside cells. The nucleus is shown in blue.

Cytoskeleton Structure

	Microtubules	Intermediate Filaments	Microfilaments
Fiber Diameter	About 25 nm	8 to 11 nm	Around 7 nm
Protein Composition	Tubulin, with two subunits, alpha and beta tubulin	One of different types of proteins such as lamin, vimentin, and keratin	Actin
Shape	Hollow cylinders made of two protein chains twisted around each other	Protein fiber coils twisted into each other	Two actin chains twisted around one another
Main Functions	Organelle and vesicle movement; form mitotic spindles during cell reproduction; cell motility (in cilia and flagella)	Organize cell shape; positions organelles in cytoplasm structural support of the nuclear envelope and sarcomeres; involved in cell-to-cell and cell-to-matrix junctions	Keep cellular shape; allows movement of certain cells by forming cytoplasmatic extensions or contraction of actin fibers; involved in some cell-to-cell or cell-to-matrix junctions
Representation			

The cytoskeleton is discussed in the following video: http://www.youtube.com/watch?v=5rqbmLiSkpk (4:50).



Summary

- The cytoplasm consists of everything inside the plasma membrane of the cell.
- The cytoskeleton is a cellular "skeleton" that crisscrosses the cytoplasm. Three main cytoskeleton fibers are microtubules, intermediate filaments, and microfilaments.
- Microtubules are the thickest of the cytoskeleton structures and are most commonly made of filaments which are polymers of alpha and beta tubulin.
- Microfilament are the thinnest of the cytoskeleton structures and are made of two thin actin chains that are twisted around one another.

Explore More

Use this resource to answer the following questions.

- **Cytoskeleton Tutorial** athttp://www.biology.arizona.edu/cell_bio/tutorials/cytoskeleton/main.html.

1. What is the role of the cytoskeleton?
2. What is the subunit of microfilaments and microtubules?
3. Describe the main function of microtubules.
4. What is the role of microtubules during mitosis?
5. How are microtubules associated with locomotion?
6. Describe the roles of microfilaments.

Review

1. What is the difference between cytoplasm and cytosol?
2. List two roles of the cytoplasm.
3. Name the three main types of cytoskeleton fibers.
4. List two functions of the eukaryotic cytoskeleton.

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4.6.2: The Cytoskeleton

Skills to Develop

- Describe the cytoskeleton
- Compare the roles of microfilaments, intermediate filaments, and microtubules
- Compare and contrast cilia and flagella
- Summarize the differences among the components of prokaryotic cells, animal cells, and plant cells

If you were to remove all the organelles from a cell, would the plasma membrane and the cytoplasm be the only components left? No. Within the cytoplasm, there would still be ions and organic molecules, plus a network of protein fibers that help maintain the shape of the cell, secure some organelles in specific positions, allow cytoplasm and vesicles to move within the cell, and enable cells within multicellular organisms to move. Collectively, this network of protein fibers is known as the cytoskeleton. There are three types of fibers within the cytoskeleton: microfilaments, intermediate filaments, and microtubules (Figure 4.6.2.1). Here, we will examine each.

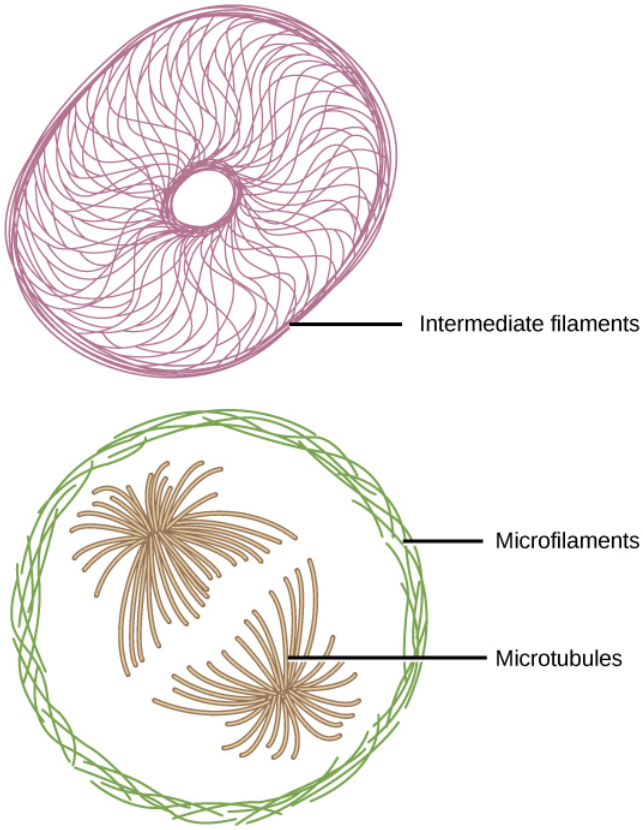


Figure 4.6.2.1: Microfilaments thicken the cortex around the inner edge of a cell; like rubber bands, they resist tension. Microtubules are found in the interior of the cell where they maintain cell shape by resisting compressive forces. Intermediate filaments are found throughout the cell and hold organelles in place.

Microfilaments

Of the three types of protein fibers in the cytoskeleton, microfilaments are the narrowest. They function in cellular movement, have a diameter of about 7 nm, and are made of two intertwined strands of a globular protein called actin (Figure 4.6.2.2). For this reason, microfilaments are also known as actin filaments.

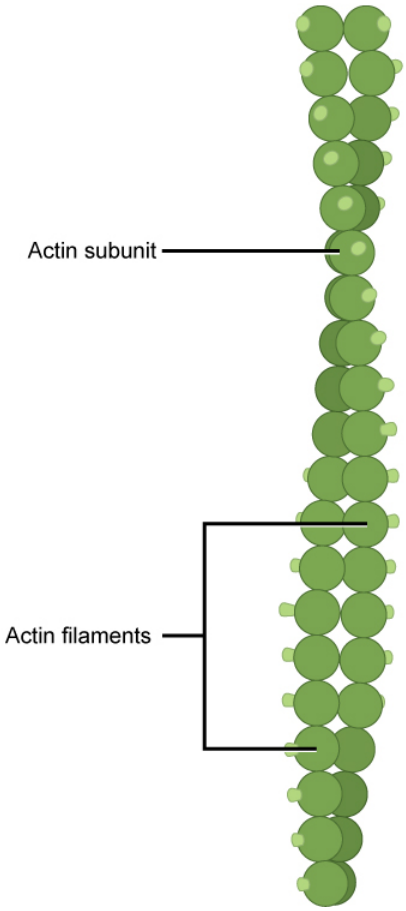


Figure **4.6.2.2**: Microfilaments are made of two intertwined strands of actin.

Actin is powered by ATP to assemble its filamentous form, which serves as a track for the movement of a motor protein called myosin. This enables actin to engage in cellular events requiring motion, such as cell division in animal cells and cytoplasmic streaming, which is the circular movement of the cell cytoplasm in plant cells. Actin and myosin are plentiful in muscle cells. When your actin and myosin filaments slide past each other, your muscles contract.

Microfilaments also provide some rigidity and shape to the cell. They can depolymerize (disassemble) and reform quickly, thus enabling a cell to change its shape and move. White blood cells (your body's infection-fighting cells) make good use of this ability. They can move to the site of an infection and phagocytize the pathogen.

Link to Learning



Video 4.6.2.1: To see an example of a white blood cell in action, watch a short time-lapse video of the cell capturing two bacteria. It engulfs one and then moves on to the other.

Intermediate Filaments

Intermediate filaments are made of several strands of fibrous proteins that are wound together (Figure 4.6.2.3). These elements of the cytoskeleton get their name from the fact that their diameter, 8 to 10 nm, is between those of microfilaments and microtubules.



Figure 4.6.2.3: Intermediate filaments consist of several intertwined strands of fibrous proteins.

Intermediate filaments have no role in cell movement. Their function is purely structural. They bear tension, thus maintaining the shape of the cell, and anchor the nucleus and other organelles in place. Figure 4.6.2.1 shows how intermediate filaments create a supportive scaffolding inside the cell.

The intermediate filaments are the most diverse group of cytoskeletal elements. Several types of fibrous proteins are found in the intermediate filaments. You are probably most familiar with keratin, the fibrous protein that strengthens your hair, nails, and the epidermis of the skin.

Microtubules

As their name implies, microtubules are small hollow tubes. The walls of the microtubule are made of polymerized dimers of α-tubulin and β-tubulin, two globular proteins (Figure 4.6.2.4). With a diameter of about 25 nm, microtubules are the widest components of the cytoskeleton. They help the cell resist compression, provide a track along which vesicles move through the cell, and pull replicated chromosomes to opposite ends of a dividing cell. Like microfilaments, microtubules can dissolve and reform quickly.

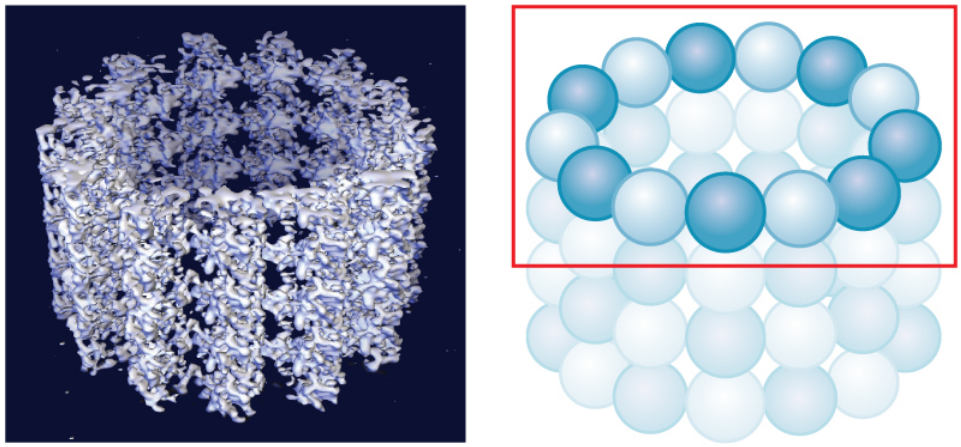


Figure 4.6.2.4: Microtubules are hollow. Their walls consist of 13 polymerized dimers of α-tubulin and β-tubulin (right image). The left image shows the molecular structure of the tube.

Microtubules are also the structural elements of flagella, cilia, and centrioles (the latter are the two perpendicular bodies of the centrosome). In fact, in animal cells, the centrosome is the microtubule-organizing center. In eukaryotic cells, flagella and cilia are quite different structurally from their counterparts in prokaryotes, as discussed below.

Flagella and Cilia

To refresh your memory, flagella (singular = flagellum) are long, hair-like structures that extend from the plasma membrane and are used to move an entire cell (for example, sperm, *Euglena*). When present, the cell has just one flagellum or a few flagella. When cilia (singular = cilium) are present, however, many of them extend along the entire surface of the plasma membrane. They are

short, hair-like structures that are used to move entire cells (such as paramecia) or substances along the outer surface of the cell (for example, the cilia of cells lining the Fallopian tubes that move the ovum toward the uterus, or cilia lining the cells of the respiratory tract that trap particulate matter and move it toward your nostrils.)

Despite their differences in length and number, flagella and cilia share a common structural arrangement of microtubules called a "9 + 2 array." This is an appropriate name because a single flagellum or cilium is made of a ring of nine microtubule doublets, surrounding a single microtubule doublet in the center (Figure **4.6.2.5**).

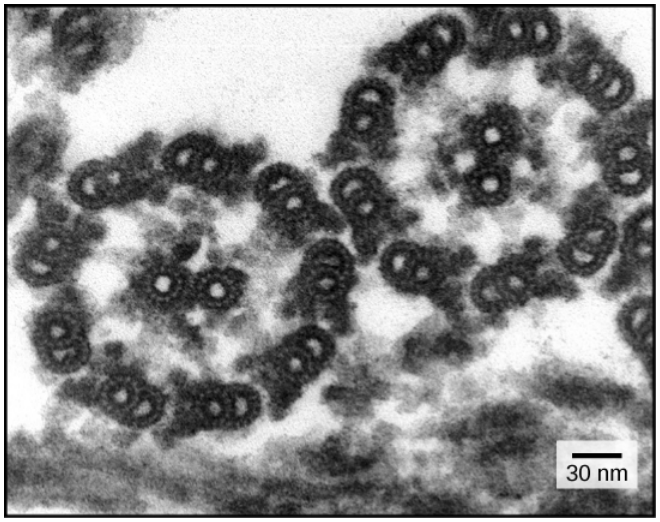


Figure **4.6.2.5**: This transmission electron micrograph of two flagella shows the 9 + 2 array of microtubules: nine microtubule doublets surround a single microtubule doublet. (credit: modification of work by Dartmouth Electron Microscope Facility, Dartmouth College; scale-bar data from Matt Russell)

You have now completed a broad survey of the components of prokaryotic and eukaryotic cells. For a summary of cellular components in prokaryotic and eukaryotic cells, see Table **4.6.2.1**.

Table **4.6.2.1**: Cellular components in prokaryotic and eukaryotic cells.

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Plasma membrane	Separates cell from external environment; controls passage of organic molecules, ions, water, oxygen, and wastes into and out of cell	Yes	Yes	Yes
Cytoplasm	Provides turgor pressure to plant cells as fluid inside the central vacuole; site of many metabolic reactions; medium in which organelles are found	Yes	Yes	Yes
Nucleolus	Darkened area within the nucleus where ribosomal subunits are synthesized.	No	Yes	Yes
Nucleus	Cell organelle that houses DNA and directs synthesis of ribosomes and proteins	No	Yes	Yes
Ribosomes	Protein synthesis	Yes	Yes	Yes
Mitochondria	ATP production/cellular respiration	No	Yes	Yes
Peroxisomes	Oxidizes and thus breaks down fatty acids and amino acids, and detoxifies poisons	No	Yes	Yes
Vesicles and vacuoles	Storage and transport; digestive function in plant cells	No	Yes	Yes
Centrosome	Unspecified role in cell division in animal cells; source of microtubules in animal cells	No	Yes	No
Lysosomes	Digestion of macromolecules; recycling of worn-out organelles	No	Yes	No
Cell wall	Protection, structural support and maintenance of cell shape	Yes, primarily peptidoglycan	No	Yes, primarily cellulose
Chloroplasts	Photosynthesis	No	No	Yes
Endoplasmic reticulum	Modifies proteins and	No	Yes	Yes

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
	synthesizes lipids			
Golgi apparatus	Modifies, sorts, tags, packages, and distributes lipids and proteins	No	Yes	Yes
Cytoskeleton	Maintains cell's shape, secures organelles in specific positions, allows cytoplasm and vesicles to move within cell, and enables unicellular organisms to move independently	Yes	Yes	Yes
Flagella	Cellular locomotion	Some	Some	No, except for some plant sperm cells.
Cilia	Cellular locomotion, movement of particles along extracellular surface of plasma membrane, and filtration	Some	Some	No

Summary

The cytoskeleton has three different types of protein elements. From narrowest to widest, they are the microfilaments (actin filaments), intermediate filaments, and microtubules. Microfilaments are often associated with myosin. They provide rigidity and shape to the cell and facilitate cellular movements. Intermediate filaments bear tension and anchor the nucleus and other organelles in place. Microtubules help the cell resist compression, serve as tracks for motor proteins that move vesicles through the cell, and pull replicated chromosomes to opposite ends of a dividing cell. They are also the structural element of centrioles, flagella, and cilia.

Glossary

cilium

(plural = cilia) short, hair-like structure that extends from the plasma membrane in large numbers and is used to move an entire cell or move substances along the outer surface of the cell

cytoskeleton

network of protein fibers that collectively maintain the shape of the cell, secure some organelles in specific positions, allow cytoplasm and vesicles to move within the cell, and enable unicellular organisms to move independently

flagellum

(plural = flagella) long, hair-like structure that extends from the plasma membrane and is used to move the cell

intermediate filament

cytoskeletal component, composed of several intertwined strands of fibrous protein, that bears tension, supports cell-cell junctions, and anchors cells to extracellular structures

microfilament

narrowest element of the cytoskeleton system; it provides rigidity and shape to the cell and enables cellular movements

microtubule

widest element of the cytoskeleton system; it helps the cell resist compression, provides a track along which vesicles move through the cell, pulls replicated chromosomes to opposite ends of a dividing cell, and is the structural element of centrioles, flagella, and cilia

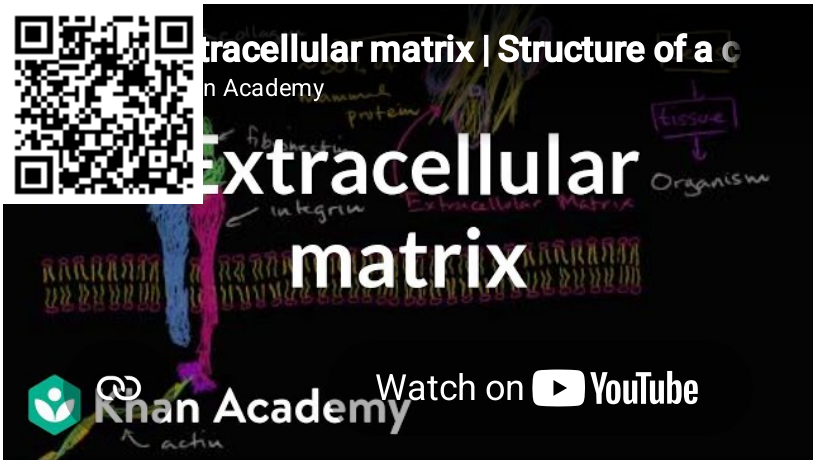
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SECTION OVERVIEW

4.7: Extracellular Structures and Cell Movement



4.7.1: Extracellular Matrix of Animal Cells

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4.7.1: Extracellular Matrix of Animal Cells

Learning Objectives

- Explain the role of the extracellular matrix in animal cells

Extracellular Matrix of Animal Cells

Most animal cells release materials into the extracellular space. The primary components of these materials are proteins. Collagen is the most abundant of the proteins. Its fibers are interwoven with carbohydrate-containing protein molecules called proteoglycans. Collectively, these materials are called the extracellular matrix. Not only does the extracellular matrix hold the cells together to form a tissue, but it also allows the cells within the tissue to communicate with each other.

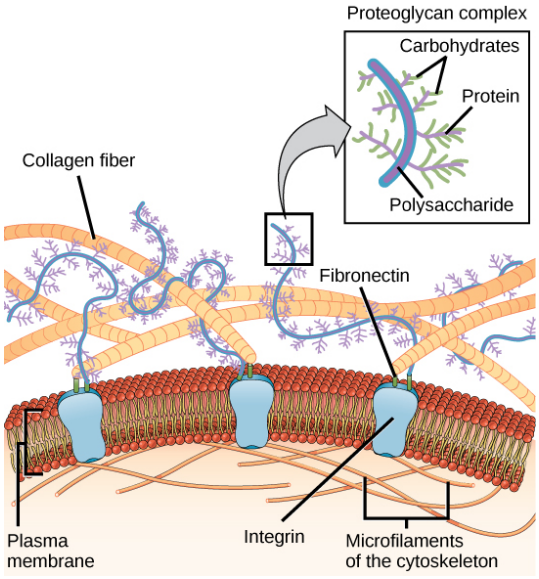


Figure 4.7.1.1: The Extracellular Matrix: The extracellular matrix consists of a network of proteins and carbohydrates.

How does this cell communication occur? Cells have protein receptors on the extracellular surfaces of their plasma membranes. When a molecule within the matrix binds to the receptor, it changes the molecular structure of the receptor. The receptor, in turn, changes the conformation of the microfilaments positioned just inside the plasma membrane. These conformational changes induce chemical signals inside the cell that reach the nucleus and turn “on” or “off” the transcription of specific sections of DNA. This affects the production of associated proteins, thus changing the activities within the cell.

An example of the role of the extracellular matrix in cell communication can be seen in blood clotting. When the cells lining a blood vessel are damaged, they display a protein receptor called tissue factor. When a tissue factor binds with another factor in the extracellular matrix, it causes platelets to adhere to the wall of the damaged blood vessel and stimulates the adjacent smooth muscle cells in the blood vessel to contract (thus constricting the blood vessel). Subsequently, a series of steps are initiated which then prompt the platelets to produce clotting factors.

Key Points

- The extracellular matrix of animal cells is made up of proteins and carbohydrates.
- Cell communication within tissue and tissue formation are main functions of the extracellular matrix of animal cells.
- Tissue communication is kick-started when a molecule within the matrix binds a receptor; the end results are conformational changes that induce chemical signals that ultimately change activities within the cell.

Key Terms

- **collagen**: Any of more than 28 types of glycoprotein that forms elongated fibers, usually found in the extracellular matrix of connective tissue.

- **proteoglycan**: Any of many glycoproteins that have heteropolysaccharide side chains
- **extracellular matrix**: All the connective tissues and fibres that are not part of a cell, but rather provide support.

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SECTION OVERVIEW

4.8: Cell-to-Cell Interactions

Cell–cell interaction refers to the direct interactions between cell surfaces that play a crucial role in the development and function of multicellular organisms. These interactions allow cells to communicate with each other in response to changes in their microenvironment. This ability to send and receive signals is essential for the survival of the cell. Interactions between cells can be stable such as those made through cell junctions. These junctions are involved in the communication and organization of cells within a particular tissue. Others are transient or temporary such as those between cells of the immune system or the interactions involved in tissue inflammation. These types of intercellular interactions are distinguished from other types such as those between cells and the extracellular matrix. The loss of communication between cells can result in uncontrollable cell growth and cancer.

4.8.1: Intercellular Junctions

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4.8.1: Intercellular Junctions

Learning Objectives

- Describe the purpose of intercellular junctions in the structure of cells

Intercellular Junctions

The extracellular matrix allows cellular communication within tissues through conformational changes that induce chemical signals, which ultimately transform activities within the cell. However, cells are also capable of communicating with each other via direct contact through intercellular junctions.

There are some differences in the ways that plant and animal cells communicate directly. Plasmodesmata are junctions between plant cells, whereas animal cell contacts are carried out through tight junctions, gap junctions, and desmosomes.

Junctions in Plant Cells

In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell wall that surrounds each cell. How then can a plant transfer water and other soil nutrients from its roots, through its stems, and to its leaves? This transport primarily uses the vascular tissues (xylem and phloem); however, there are also structural modifications called plasmodesmata (singular: plasmodesma) that facilitate direct communication in plant cells. Plasmodesmata are numerous channels that pass between cell walls of adjacent plant cells and connect their cytoplasm; thereby, enabling materials to be transported from cell to cell, and thus throughout the plant.

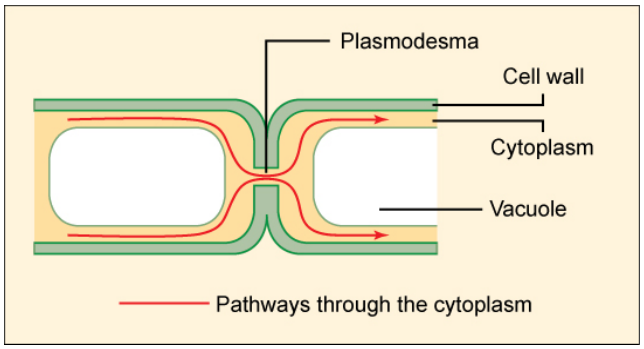


Figure 4.8.1.1: Plasmodesmata: A plasmodesma is a channel between the cell walls of two adjacent plant cells. Plasmodesmata allow materials to pass from the cytoplasm of one plant cell to the cytoplasm of an adjacent cell.

Junctions in Animal Cells

Communication between animal cells can be carried out through three types of junctions. The first, a tight junction, is a watertight seal between two adjacent animal cells. The cells are held tightly against each other by proteins (predominantly two proteins called claudins and occludins). This tight adherence prevents materials from leaking between the cells. These junctions are typically found in epithelial tissues that line internal organs and cavities and comprise most of the skin. For example, the tight junctions of the epithelial cells lining your urinary bladder prevent urine from leaking out into the extracellular space.

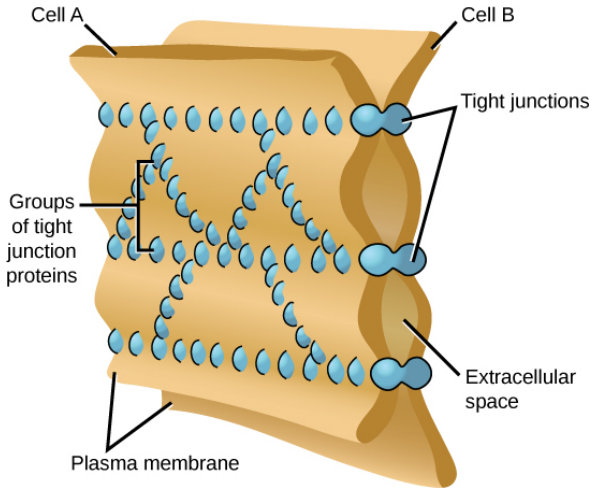


Figure **4.8.1.1**: Tight Junctions: Tight junctions form watertight connections between adjacent animal cells. Proteins create tight junction adherence.

Also found only in animal cells are desmosomes, the second type of intercellular junctions in these cell types. Desmosomes act like spot welds between adjacent epithelial cells, connecting them. Short proteins called cadherins in the plasma membrane connect to intermediate filaments to create desmosomes. The cadherins join two adjacent cells together and maintain the cells in a sheet-like formation in organs and tissues that stretch, such as the skin, heart, and muscles.

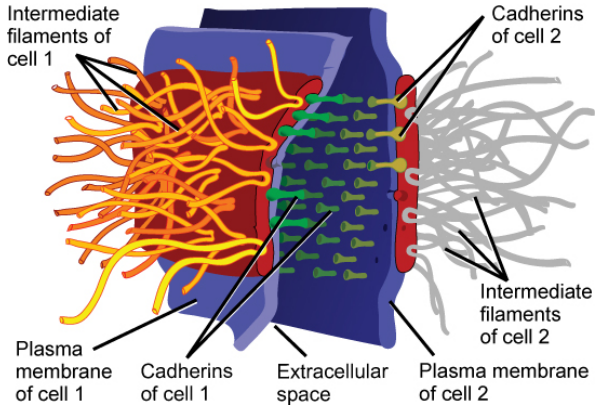


Figure **4.8.1.1**: Desmosomes: A desmosome forms a very strong spot weld between cells. It is created by the linkage of cadherins and intermediate filaments.

Lastly, similar to plasmodesmata in plant cells, gap junctions are the third type of direct junction found within animal cells. These junctions are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate. Structurally, however, gap junctions and plasmodesmata differ. Gap junctions develop when a set of six proteins (called connexins) in the plasma membrane arrange themselves in an elongated doughnut-like configuration called a connexon. When the pores ("doughnut holes") of connexons in adjacent animal cells align, a channel between the two cells forms. Gap junctions are particularly important in cardiac muscle. The electrical signal for the muscle to contract is passed efficiently through gap junctions, which allows the heart muscle cells to contract in tandem.

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Key Points

- Plasmodesmata are intercellular junctions between plant cells that enable the transportation of materials between cells.
- A tight junction is a watertight seal between two adjacent animal cells, which prevents materials from leaking out of cells.
- Desmosomes connect adjacent cells when cadherins in the plasma membrane connect to intermediate filaments.
- Similar to plasmodesmata, gap junctions are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances.

Key Terms

- **plasmodesma**: A microscopic channel traversing the cell walls of plant cells and some algal cells, enabling transport and communication between them.
- **connexon**: An assembly of six connexins forming a bridge called a gap junction between the cytoplasms of two adjacent cells.
- **occludin**: Together with the claudin group of proteins, it is the main component of the tight junctions.

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CHAPTER OVERVIEW

5: Membranes

5.1: The Structure of Membranes

5.2: Phospholipids- The Membrane's Foundation

5.3: Proteins- Multifunctional Components

5.4: Passive Transport Across Membranes

5.5: Active Transport Across Membranes

5.5.1: Active Transport I

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5.6: Bulk Transport by Endocytosis and Exocytosis

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5.1: The Structure of Membranes

Skills to Develop

- Understand the fluid mosaic model of cell membranes
- Describe the functions of phospholipids, proteins, and carbohydrates in membranes
- Discuss membrane fluidity

A cell's plasma membrane defines the cell, outlines its borders, and determines the nature of its interaction with its environment (see Table **5.1.1** for a summary). Cells exclude some substances, take in others, and excrete still others, all in controlled quantities. The plasma membrane must be very flexible to allow certain cells, such as red blood cells and white blood cells, to change shape as they pass through narrow capillaries. These are the more obvious functions of a plasma membrane. In addition, the surface of the plasma membrane carries markers that allow cells to recognize one another, which is vital for tissue and organ formation during early development, and which later plays a role in the "self" versus "non-self" distinction of the immune response.

Among the most sophisticated functions of the plasma membrane is the ability to transmit signals by means of complex, integral proteins known as receptors. These proteins act both as receivers of extracellular inputs and as activators of intracellular processes. These membrane receptors provide extracellular attachment sites for effectors like hormones and growth factors, and they activate intracellular response cascades when their effectors are bound. Occasionally, receptors are hijacked by viruses (HIV, human immunodeficiency virus, is one example) that use them to gain entry into cells, and at times, the genes encoding receptors become mutated, causing the process of signal transduction to malfunction with disastrous consequences.

Fluid Mosaic Model

The existence of the plasma membrane was identified in the 1890s, and its chemical components were identified in 1915. The principal components identified at that time were lipids and proteins. The first widely accepted model of the plasma membrane's structure was proposed in 1935 by Hugh Davson and James Danielli; it was based on the "railroad track" appearance of the plasma membrane in early electron micrographs. They theorized that the structure of the plasma membrane resembles a sandwich, with protein being analogous to the bread, and lipids being analogous to the filling. In the 1950s, advances in microscopy, notably transmission electron microscopy (TEM), allowed researchers to see that the core of the plasma membrane consisted of a double, rather than a single, layer. A new model that better explains both the microscopic observations and the function of that plasma membrane was proposed by S.J. Singer and Garth L. Nicolson in 1972.

The explanation proposed by Singer and Nicolson is called the fluid mosaic model. The model has evolved somewhat over time, but it still best accounts for the structure and functions of the plasma membrane as we now understand them. The fluid mosaic model describes the structure of the plasma membrane as a mosaic of components—including phospholipids, cholesterol, proteins, and carbohydrates—that gives the membrane a fluid character. Plasma membranes range from 5 to 10 nm in thickness. For comparison, human red blood cells, visible via light microscopy, are approximately 8 µm wide, or approximately 1,000 times wider than a plasma membrane. The membrane does look a bit like a sandwich (Figure **5.1.1**).

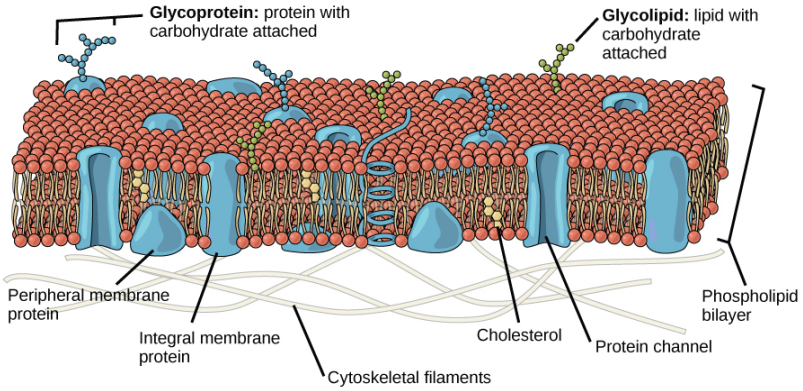


Figure 5.1.1: The fluid mosaic model of the plasma membrane describes the plasma membrane as a fluid combination of phospholipids, cholesterol, and proteins. Carbohydrates attached to lipids (glycolipids) and to proteins (glycoproteins) extend from the outward-facing surface of the membrane.

The principal components of a plasma membrane are lipids (phospholipids and cholesterol), proteins, and carbohydrates attached to some of the lipids and some of the proteins. A phospholipid is a molecule consisting of glycerol, two fatty acids, and a phosphate-linked head group. Cholesterol, another lipid composed of four fused carbon rings, is found alongside the phospholipids in the core of the membrane. The proportions of proteins, lipids, and carbohydrates in the plasma membrane vary with cell type, but for a typical human cell, protein accounts for about 50 percent of the composition by mass, lipids (of all types) account for about 40 percent of the composition by mass, with the remaining 10 percent of the composition by mass being carbohydrates. However, the concentration of proteins and lipids varies with different cell membranes. For example, myelin, an outgrowth of the membrane of specialized cells that insulates the axons of the peripheral nerves, contains only 18 percent protein and 76 percent lipid. The mitochondrial inner membrane contains 76 percent protein and only 24 percent lipid. The plasma membrane of human red blood cells is 30 percent lipid. Carbohydrates are present only on the exterior surface of the plasma membrane and are attached to proteins, forming glycoproteins, or attached to lipids, forming glycolipids.

Phospholipids

The main fabric of the membrane is composed of amphiphilic, phospholipid molecules. The hydrophilic or “water-loving” areas of these molecules (which look like a collection of balls in an artist’s rendition of the model) (Figure 5.1.1) are in contact with the aqueous fluid both inside and outside the cell. Hydrophobic, or water-hating molecules, tend to be non-polar. They interact with other non-polar molecules in chemical reactions, but generally do not interact with polar molecules. When placed in water, hydrophobic molecules tend to form a ball or cluster. The hydrophilic regions of the phospholipids tend to form hydrogen bonds with water and other polar molecules on both the exterior and interior of the cell. Thus, the membrane surfaces that face the interior and exterior of the cell are hydrophilic. In contrast, the interior of the cell membrane is hydrophobic and will not interact with water. Therefore, phospholipids form an excellent two-layer cell membrane that separates fluid within the cell from the fluid outside of the cell.

A phospholipid molecule (Figure 5.1.2) consists of a three-carbon glycerol backbone with two fatty acid molecules attached to carbons 1 and 2, and a phosphate-containing group attached to the third carbon. This arrangement gives the overall molecule an area described as its head (the phosphate-containing group), which has a polar character or negative charge, and an area called the tail (the fatty acids), which has no charge. The head can form hydrogen bonds, but the tail cannot. A molecule with this arrangement of a positively or negatively charged area and an uncharged, or non-polar, area is referred to as amphiphilic or “dual-loving.”

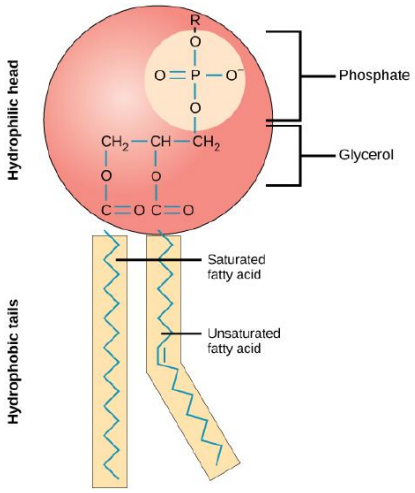


Figure **5.1.2**: This phospholipid molecule is composed of a hydrophilic head and two hydrophobic tails. The hydrophilic head group consists of a phosphate-containing group attached to a glycerol molecule. The hydrophobic tails, each containing either a saturated or an unsaturated fatty acid, are long hydrocarbon chains.

This characteristic is vital to the structure of a plasma membrane because, in water, phospholipids tend to become arranged with their hydrophobic tails facing each other and their hydrophilic heads facing out. In this way, they form a lipid bilayer—a barrier composed of a double layer of phospholipids that separates the water and other materials on one side of the barrier from the water and other materials on the other side. In fact, phospholipids heated in an aqueous solution tend to spontaneously form small spheres or droplets (called micelles or liposomes), with their hydrophilic heads forming the exterior and their hydrophobic tails on the inside (Figure **5.1.3**).

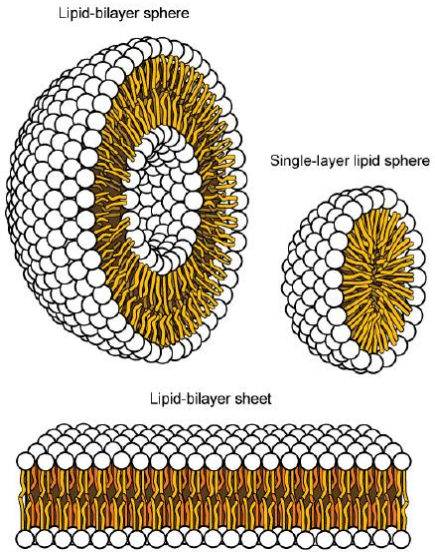


Figure **5.1.3**: In an aqueous solution, phospholipids tend to arrange themselves with their polar heads facing outward and their hydrophobic tails facing inward. (credit: modification of work by Mariana Ruiz Villareal)

Proteins

Proteins make up the second major component of plasma membranes. Integral proteins (some specialized types are called integrins) are, as their name suggests, integrated completely into the membrane structure, and their hydrophobic membrane-spanning regions interact with the hydrophobic region of the the phospholipid bilayer (Figure **5.1.1**). Single-pass integral membrane proteins usually have a hydrophobic transmembrane segment that consists of 20–25 amino acids. Some span only part of the membrane—associating with a single layer—while others stretch from one side of the membrane to the other, and are exposed on either side. Some complex proteins are composed of up to 12 segments of a single protein, which are extensively folded and embedded in the membrane (Figure **5.1.4**). This type of protein has a hydrophilic region or regions, and one or several mildly hydrophobic regions. This arrangement of regions of the protein tends to orient the protein alongside the phospholipids, with the hydrophobic region of

the protein adjacent to the tails of the phospholipids and the hydrophilic region or regions of the protein protruding from the membrane and in contact with the cytosol or extracellular fluid.

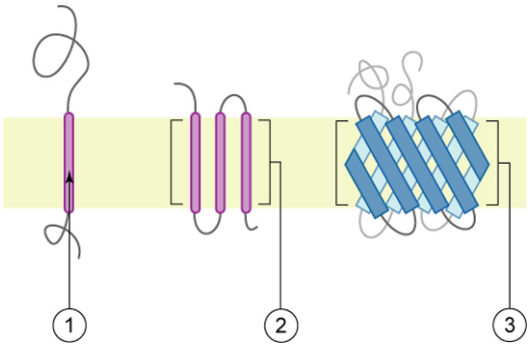


Figure **5.1.4**: Integral membranes proteins may have one or more alpha-helices that span the membrane (examples 1 and 2), or they may have beta-sheets that span the membrane (example 3). (credit: "Foobar"/Wikimedia Commons)

Peripheral proteins are found on the exterior and interior surfaces of membranes, attached either to integral proteins or to phospholipids. Peripheral proteins, along with integral proteins, may serve as enzymes, as structural attachments for the fibers of the cytoskeleton, or as part of the cell's recognition sites. These are sometimes referred to as "cell-specific" proteins. The body recognizes its own proteins and attacks foreign proteins associated with invasive pathogens.

Carbohydrates

Carbohydrates are the third major component of plasma membranes. They are always found on the exterior surface of cells and are bound either to proteins (forming glycoproteins) or to lipids (forming glycolipids) (Figure **5.1.1**). These carbohydrate chains may consist of 2–60 monosaccharide units and can be either straight or branched. Along with peripheral proteins, carbohydrates form specialized sites on the cell surface that allow cells to recognize each other. These sites have unique patterns that allow the cell to be recognized, much the way that the facial features unique to each person allow him or her to be recognized. This recognition function is very important to cells, as it allows the immune system to differentiate between body cells (called "self") and foreign cells or tissues (called "non-self"). Similar types of glycoproteins and glycolipids are found on the surfaces of viruses and may change frequently, preventing immune cells from recognizing and attacking them.

These carbohydrates on the exterior surface of the cell—the carbohydrate components of both glycoproteins and glycolipids—are collectively referred to as the glycocalyx (meaning "sugar coating"). The glycocalyx is highly hydrophilic and attracts large amounts of water to the surface of the cell. This aids in the interaction of the cell with its watery environment and in the cell's ability to obtain substances dissolved in the water. As discussed above, the glycocalyx is also important for cell identification, self/non-self determination, and embryonic development, and is used in cell-cell attachments to form tissues.

Evolution Connection: How Viruses Infect Specific Organs

Glycoprotein and glycolipid patterns on the surfaces of cells give many viruses an opportunity for infection. HIV and hepatitis viruses infect only specific organs or cells in the human body. HIV is able to penetrate the plasma membranes of a subtype of lymphocytes called T-helper cells, as well as some monocytes and central nervous system cells. The hepatitis virus attacks liver cells.

These viruses are able to invade these cells, because the cells have binding sites on their surfaces that are specific to and compatible with certain viruses (Figure **5.1.5**). Other recognition sites on the virus's surface interact with the human immune system, prompting the body to produce antibodies. Antibodies are made in response to the antigens or proteins associated with invasive pathogens, or in response to foreign cells, such as might occur with an organ transplant. These same sites serve as places for antibodies to attach and either destroy or inhibit the activity of the virus. Unfortunately, these recognition sites on HIV change at a rapid rate because of mutations, making the production of an effective vaccine against the virus very difficult, as the virus evolves and adapts. A person infected with HIV will quickly develop different populations, or variants, of the virus that are distinguished by differences in these recognition sites. This rapid change of surface markers decreases the effectiveness of the person's immune system in attacking the virus, because the antibodies will not recognize the new variations of the

surface patterns. In the case of HIV, the problem is compounded by the fact that the virus specifically infects and destroys cells involved in the immune response, further incapacitating the host.

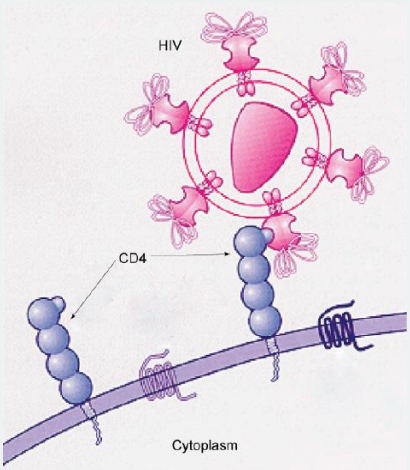


Figure 5.1.5: HIV binds to the CD4 receptor, a glycoprotein on the surfaces of T cells. (credit: modification of work by NIH, NIAID)

Membrane Fluidity

The mosaic characteristic of the membrane, described in the fluid mosaic model, helps to illustrate its nature. The integral proteins and lipids exist in the membrane as separate but loosely attached molecules. These resemble the separate, multicolored tiles of a mosaic picture, and they float, moving somewhat with respect to one another. The membrane is not like a balloon, however, that can expand and contract; rather, it is fairly rigid and can burst if penetrated or if a cell takes in too much water. However, because of its mosaic nature, a very fine needle can easily penetrate a plasma membrane without causing it to burst, and the membrane will flow and self-seal when the needle is extracted.

The mosaic characteristics of the membrane explain some but not all of its fluidity. There are two other factors that help maintain this fluid characteristic. One factor is the nature of the phospholipids themselves. In their saturated form, the fatty acids in phospholipid tails are saturated with bound hydrogen atoms. There are no double bonds between adjacent carbon atoms. This results in tails that are relatively straight. In contrast, unsaturated fatty acids do not contain a maximal number of hydrogen atoms, but they do contain some double bonds between adjacent carbon atoms; a double bond results in a bend in the string of carbons of approximately 30 degrees (Figure 5.1.2).

Thus, if saturated fatty acids, with their straight tails, are compressed by decreasing temperatures, they press in on each other, making a dense and fairly rigid membrane. If unsaturated fatty acids are compressed, the “kinks” in their tails elbow adjacent phospholipid molecules away, maintaining some space between the phospholipid molecules. This “elbow room” helps to maintain fluidity in the membrane at temperatures at which membranes with saturated fatty acid tails in their phospholipids would “freeze” or solidify. The relative fluidity of the membrane is particularly important in a cold environment. A cold environment tends to compress membranes composed largely of saturated fatty acids, making them less fluid and more susceptible to rupturing. Many organisms (fish are one example) are capable of adapting to cold environments by changing the proportion of unsaturated fatty acids in their membranes in response to the lowering of the temperature.

Link to Learning



Visit this site to see animations of the fluidity and mosaic quality of membranes.

Animals have an additional membrane constituent that assists in maintaining fluidity. Cholesterol, which lies alongside the phospholipids in the membrane, tends to dampen the effects of temperature on the membrane. Thus, this lipid functions as a buffer, preventing lower temperatures from inhibiting fluidity and preventing increased temperatures from increasing fluidity too much. Thus, cholesterol extends, in both directions, the range of temperature in which the membrane is appropriately fluid and consequently functional. Cholesterol also serves other functions, such as organizing clusters of transmembrane proteins into lipid rafts.

Table **5.1.1**: The Components and Functions of the Plasma Membrane.

Component	Location
Phospholipid	Main fabric of the membrane
Cholesterol	Attached between phospholipids and between the two phospholipid layers
Integral proteins (for example, integrins)	Embedded within the phospholipid layer(s). May or may not penetrate through both layers
Peripheral proteins	On the inner or outer surface of the phospholipid bilayer; not embedded within the phospholipids
Carbohydrates (components of glycoproteins and glycolipids)	Generally attached to proteins on the outside membrane layer

Career Connection: Immunologist

The variations in peripheral proteins and carbohydrates that affect a cell's recognition sites are of prime interest in immunology. These changes are taken into consideration in vaccine development. Many infectious diseases, such as smallpox, polio, diphtheria, and tetanus, were conquered by the use of vaccines.

Immunologists are the physicians and scientists who research and develop vaccines, as well as treat and study allergies or other immune problems. Some immunologists study and treat autoimmune problems (diseases in which a person's immune system attacks his or her own cells or tissues, such as lupus) and immunodeficiencies, whether acquired (such as acquired immunodeficiency syndrome, or AIDS) or hereditary (such as severe combined immunodeficiency, or SCID). Immunologists are called in to help treat organ transplantation patients, who must have their immune systems suppressed so that their bodies will not reject a transplanted organ. Some immunologists work to understand natural immunity and the effects of a person's

environment on it. Others work on questions about how the immune system affects diseases such as cancer. In the past, the importance of having a healthy immune system in preventing cancer was not at all understood.

To work as an immunologist, a PhD or MD is required. In addition, immunologists undertake at least 2–3 years of training in an accredited program and must pass an examination given by the American Board of Allergy and Immunology. Immunologists must possess knowledge of the functions of the human body as they relate to issues beyond immunization, and knowledge of pharmacology and medical technology, such as medications, therapies, test materials, and surgical procedures.

Summary

The modern understanding of the plasma membrane is referred to as the fluid mosaic model. The plasma membrane is composed of a bilayer of phospholipids, with their hydrophobic, fatty acid tails in contact with each other. The landscape of the membrane is studded with proteins, some of which span the membrane. Some of these proteins serve to transport materials into or out of the cell. Carbohydrates are attached to some of the proteins and lipids on the outward-facing surface of the membrane, forming complexes that function to identify the cell to other cells. The fluid nature of the membrane is due to temperature, the configuration of the fatty acid tails (some kinked by double bonds), the presence of cholesterol embedded in the membrane, and the mosaic nature of the proteins and protein-carbohydrate combinations, which are not firmly fixed in place. Plasma membranes enclose and define the borders of cells, but rather than being a static bag, they are dynamic and constantly in flux.

Glossary

amphiphilic
: molecule possessing a polar or charged area and a nonpolar or uncharged area capable of interacting with both hydrophilic and hydrophobic environments

fluid mosaic model
: describes the structure of the plasma membrane as a mosaic of components including phospholipids, cholesterol, proteins, glycoproteins, and glycolipids (sugar chains attached to proteins or lipids, respectively), resulting in a fluid character (fluidity)

glycolipid
: combination of carbohydrates and lipids

glycoprotein
: combination of carbohydrates and proteins

hydrophilic
: molecule with the ability to bond with water; “water-loving”

hydrophobic
: molecule that does not have the ability to bond with water; “water-hating”

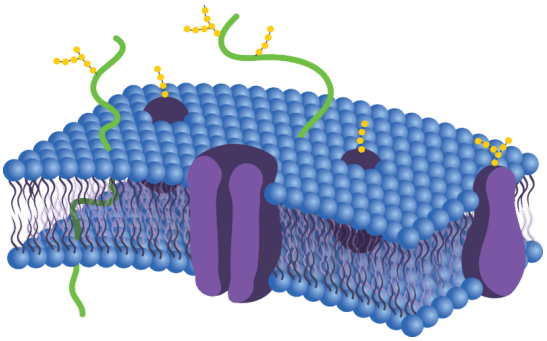
integral protein
: protein integrated into the membrane structure that interacts extensively with the hydrocarbon chains of membrane lipids and often spans the membrane; these proteins can be removed only by the disruption of the membrane by detergents

peripheral protein
: protein found at the surface of a plasma membrane either on its exterior or interior side; these proteins can be removed (washed off of the membrane) by a high-salt wash

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5.2: Phospholipids- The Membrane's Foundation



All cells have a plasma membrane. This membrane surrounds the cell. So what is its role?

Can molecules enter and leave the cell? Yes. Can anything or everything enter or leave? No. So, what determines what can go in or out? Is it the nucleus? The DNA? Or the plasma membrane?

The Plasma Membrane

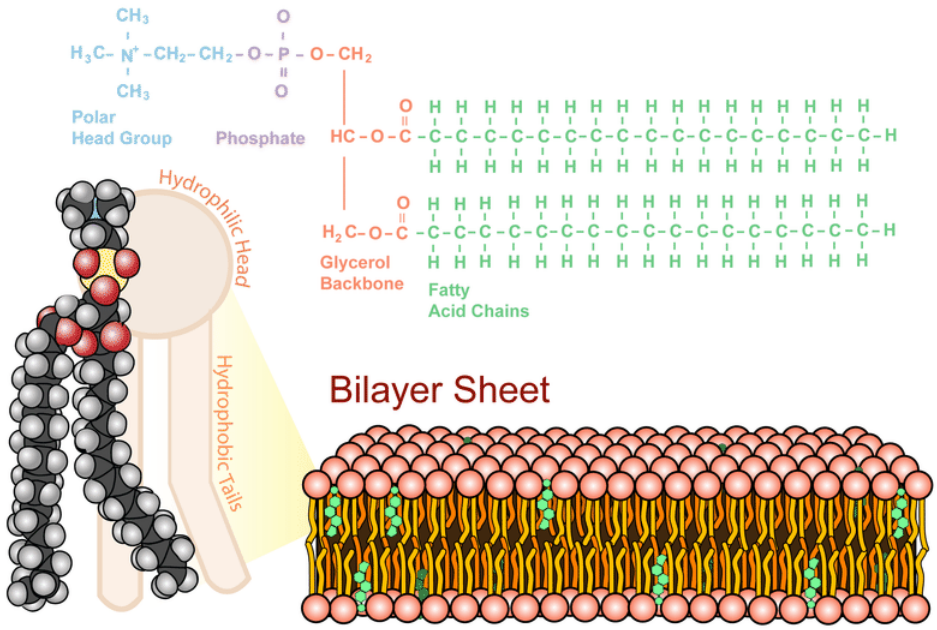
The **plasma membrane** (also known as the **cell membrane**) forms a barrier between the cytoplasm inside the cell and the environment outside the cell. It protects and supports the cell and also controls everything that enters and leaves the cell. It allows only certain substances to pass through, while keeping others in or out. The ability to allow only certain molecules in or out of the cell is referred to as selective permeability or **semipermeability**. To understand how the plasma membrane controls what crosses into or out of the cell, you need to know its composition.

The plasma membrane is discussed at http://www.youtube.com/watch?v=-aSfoB8Cmic (6:16).

A Phospholipid Bilayer

The plasma membrane is composed mainly of phospholipids, which consist of fatty acids and alcohol. The phospholipids in the plasma membrane are arranged in two layers, called a**phospholipid bilayer**. As shown in **Figure** below, each phospholipid molecule has a head and two tails. The head “loves” water (**hydrophilic**) and the tails “hate” water (**hydrophobic**). The water-hating tails are on the interior of the membrane, whereas the water-loving heads point outwards, toward either the cytoplasm or the fluid that surrounds the cell.

Molecules that are hydrophobic can easily pass through the plasma membrane, if they are small enough, because they are water-hating like the interior of the membrane. Molecules that are hydrophilic, on the other hand, cannot pass through the plasma membrane—at least not without help—because they are water-loving like the exterior of the membrane, and are therefore excluded from the interior of the membrane.



Phospholipid Bilayer. The phospholipid bilayer consists of two layers of phospholipids, with a hydrophobic, or water-hating, interior and a hydrophilic, or water-loving, exterior. The hydrophilic (polar) head group and hydrophobic tails (fatty acid chains) are depicted in the single phospholipid molecule. The polar head group and fatty acid chains are attached by a 3-carbon glycerol unit.

See *Insights into cell membranes via dish detergent* at http://ed.ted.com/lessons/insights-into-cell-membranes-via-dish-detergent-ethan-perlstein for additional information on the cell membrane.

Summary

- The plasma membrane forms a barrier between the cytoplasm and the environment outside the cell. The plasma membrane has selective permeability.
- The plasma membrane is primarily composed of phospholipids arranged in a bilayer, with the hydrophobic tails on the interior of the membrane, and the hydrophilic heads pointing outwards.

Explore More

Use these resources to answer the questions that follow.

Explore More I

- **Construction of the Cell Membrane** at http://www.wisc-online.com/Objects/ViewObject.aspx?ID=AP1101.

1. What are the two main components of the cell membrane?
2. Describe the types of proteins that live in the cell membrane.
3. Describe the orientation of the phospholipid molecule in the cell membrane.

Explore More II

- **Cell Membranes** at http://johnkyrk.com/cellmembrane.html.

1. Are *all* cells surrounded by a membrane?
2. Why are phospholipids considered an amphipathic molecule?
3. What is a glycolipid?
4. Describe the role of cholesterol in the cell membrane.

Explore More III

- http://www.hippocampus.org/Biology → Non-Majors Biology → Search: **Plasma Membrane Structure**

1. What are the roles of the plasma membrane?
2. What are the functions of proteins associated with the cell membrane?
3. Why is the structure of the cell membrane described as "fluid mosaic"?

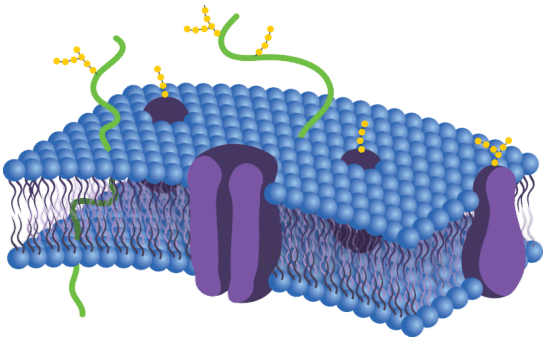
Review

1. Describe the role of the plasma membrane.
2. What is meant by semipermeability?
3. Describe the composition of the plasma membrane.
4. Explain why hydrophobic molecules can easily cross the plasma membrane, while hydrophilic molecules cannot.

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5.3: Proteins- Multifunctional Components



Can anything or everything move in or out of the cell?

No. It is the semipermeable plasma membrane that determines what can enter and leave the cell. So, if not everything can cross the membrane, how do certain things get across?

Membrane Proteins

The plasma membrane contains molecules other than phospholipids, primarily other lipids and proteins. The green molecules in **Figure** below, for example, are the lipid cholesterol. Molecules of cholesterol help the plasma membrane keep its shape. Many of the proteins in the plasma membrane assist other substances in crossing the membrane.

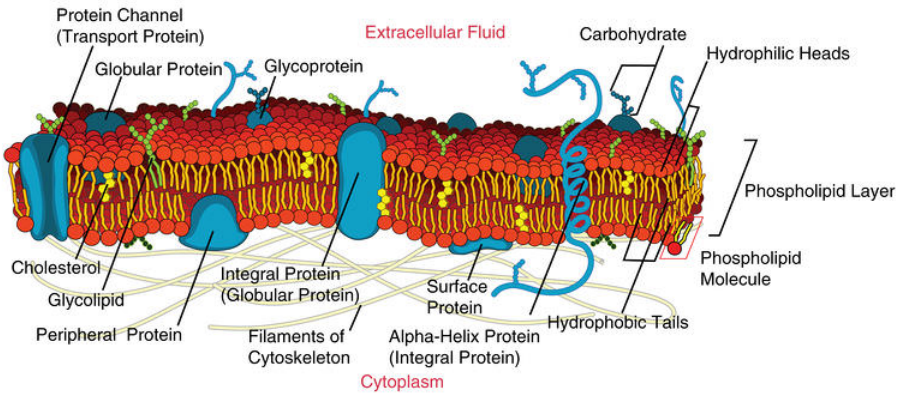
The plasma membranes also contain certain types of proteins. A **membrane protein** is a protein molecule that is attached to, or associated with, the membrane of a cell or an organelle. Membrane proteins can be put into two groups based on how the protein is associated with the membrane.

Integral membrane proteins are permanently embedded within the plasma membrane. They have a range of important functions. Such functions include channeling or transporting molecules across the membrane. Other integral proteins act as cell receptors. Integral membrane proteins can be classified according to their relationship with the bilayer:

- Transmembrane proteins span the entire plasma membrane. Transmembrane proteins are found in all types of biological membranes.
- Integral monotopic proteins are permanently attached to the membrane from only one side.

Some integral membrane proteins are responsible for cell adhesion (sticking of a cell to another cell or surface). On the outside of cell membranes and attached to some of the proteins are carbohydrate chains that act as labels that identify the cell type. Shown in **Figure** below are two different types of membrane proteins and associated molecules.

Peripheral membrane proteins are proteins that are only temporarily associated with the membrane. They can be easily removed, which allows them to be involved in cell signaling. Peripheral proteins can also be attached to integral membrane proteins, or they can stick into a small portion of the lipid bilayer by themselves. Peripheral membrane proteins are often associated with ion channels and transmembrane receptors. Most peripheral membrane proteins are hydrophilic.



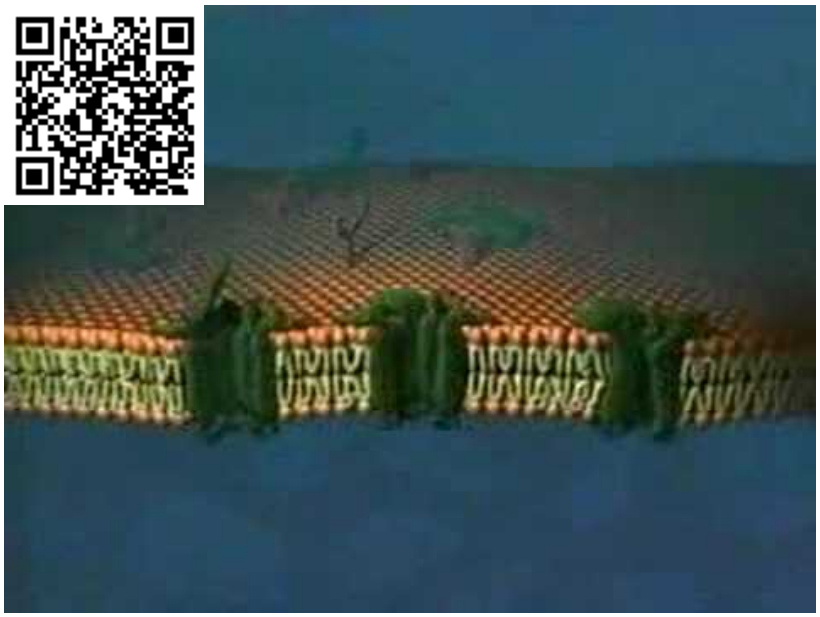
Some of the membrane proteins make up a major transport system that moves molecules and ions through the polar phospholipid bilayer.

The Fluid Mosaic Model

In 1972 S.J. Singer and G.L. Nicolson proposed the now widely accepted **Fluid Mosaic Model**of the structure of cell membranes. The model proposes that integral membrane proteins are embedded in the phospholipid bilayer, as seen in **Figure** above. Some of these proteins extend all the way through the bilayer, and some only partially across it. These membrane proteins act as transport proteins and receptors proteins.

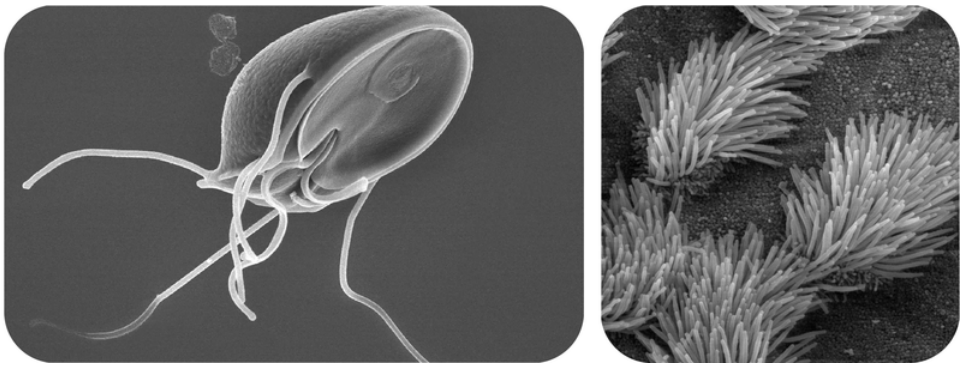
Their model also proposed that the membrane behaves like a fluid, rather than a solid. The proteins and lipids of the membrane move around the membrane, much like buoys in water. Such movement causes a constant change in the "mosaic pattern" of the plasma membrane.

A further description of the Fluid Mosaic Model can be viewed athttp://www.youtube.com/watch?v=Qqsf_UJcfBc (1:27).



Extensions of the Plasma Membrane

The plasma membrane may have extensions, such as whip-like **flagella** or brush-like **cilia**. In single-celled organisms, like those shown in **Figure** below, the membrane extensions may help the organisms move. In multicellular organisms, the extensions have other functions. For example, the cilia on human lung cells sweep foreign particles and mucus toward the mouth and nose.



Flagella and Cilia. Cilia and flagella are extensions of the plasma membrane of many cells.

Summary

- The plasma membrane has many proteins that assist other substances in crossing the membrane.
- The Fluid Mosaic Model depicts the biological nature of the plasma membrane.
- Cilia and flagella are extensions of the plasma membrane.

Explore More

Use these resources to answer the questions that follow.

Explore More I

- **Cell Membranes** at http://johnkyrk.com/cellmembrane.html.

1. What is the major role of many membrane proteins?
2. How much of a cell's genetic material may code for membrane proteins?
3. What are transmembrane proteins, and what is their main function?
4. How can a protein "tunnel" form through the membrane?
5. How can a protein "channel" form through the membrane?

Explore More II

- **Construction of the Cell Membrane** at http://www.wisc-online.com/Objects/ViewObject.aspx?ID=AP1101.

1. How may water molecules enter the cell?
2. How may ions enter the cell?
3. What type(s) of protein(s) identify the cell?
4. What molecule is found in the membrane of animal cells but not plant cells?

Review

1. What is the main difference between the two main types of proteins associated with the plasma membrane?
2. What are two functions of integral membrane proteins?
3. Discuss the Fluid Mosaic Model.
4. What are flagella and cilia?

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- **2.6: Membrane Proteins** by CK12 is licensed CK-12. Original source: http://www.ck12.org/book/CK-12-Biology-Concepts.

5.4: Passive Transport Across Membranes

Plasma membranes must allow certain substances to enter and leave a cell, while preventing harmful material from entering and essential material from leaving. In other words, plasma membranes are selectively permeable—they allow some substances through but not others. If they were to lose this selectivity, the cell would no longer be able to sustain itself, and it would be destroyed. Some cells require larger amounts of specific substances than do other cells; they must have a way of obtaining these materials from the extracellular fluids. This may happen passively, as certain materials move back and forth, or the cell may have special mechanisms that ensure transport. Most cells expend most of their energy, in the form of adenosine triphosphate (ATP), to create and maintain an uneven distribution of ions on the opposite sides of their membranes. The structure of the plasma membrane contributes to these functions, but it also presents some problems.

The most direct forms of membrane transport are passive. Passive transport is a naturally occurring phenomenon and does not require the cell to expend energy to accomplish the movement. In passive transport, substances move from an area of higher concentration to an area of lower concentration in a process called diffusion. A physical space in which there is a different concentration of a single substance is said to have a concentration gradient.

Selective Permeability

Plasma membranes are asymmetric, meaning that despite the mirror image formed by the phospholipids, the interior of the membrane is not identical to the exterior of the membrane. Integral proteins that act as channels or pumps work in one direction. Carbohydrates, attached to lipids or proteins, are also found on the exterior surface of the plasma membrane. These carbohydrate complexes help the cell bind substances that the cell needs in the extracellular fluid. This adds considerably to the selective nature of plasma membranes.

Recall that plasma membranes have hydrophilic and hydrophobic regions. This characteristic helps the movement of certain materials through the membrane and hinders the movement of others. Lipid-soluble material can easily slip through the hydrophobic lipid core of the membrane. Substances such as the fat-soluble vitamins A, D, E, and K readily pass through the plasma membranes in the digestive tract and other tissues. Fat-soluble drugs also gain easy entry into cells and are readily transported into the body’s tissues and organs. Molecules of oxygen and carbon dioxide have no charge and pass through by simple diffusion.

Polar substances, with the exception of water, present problems for the membrane. While some polar molecules connect easily with the outside of a cell, they cannot readily pass through the lipid core of the plasma membrane. Additionally, whereas small ions could easily slip through the spaces in the mosaic of the membrane, their charge prevents them from doing so. Ions such as sodium, potassium, calcium, and chloride must have a special means of penetrating plasma membranes. Simple sugars and amino acids also need help with transport across plasma membranes.

Diffusion

Diffusion is a passive process of transport. A single substance tends to move from an area of high concentration to an area of low concentration until the concentration is equal across the space. You are familiar with diffusion of substances through the air. For example, think about someone opening a bottle of perfume in a room filled with people. The perfume is at its highest concentration in the bottle and is at its lowest at the edges of the room. The perfume vapor will diffuse, or spread away, from the bottle, and gradually, more and more people will smell the perfume as it spreads. Materials move within the cell’s cytosol by diffusion, and certain materials move through the plasma membrane by diffusion (Figure **5.4.1**). Diffusion expends no energy. Rather the different concentrations of materials in different areas are a form of potential energy, and diffusion is the dissipation of that potential energy as materials move down their concentration gradients, from high to low.

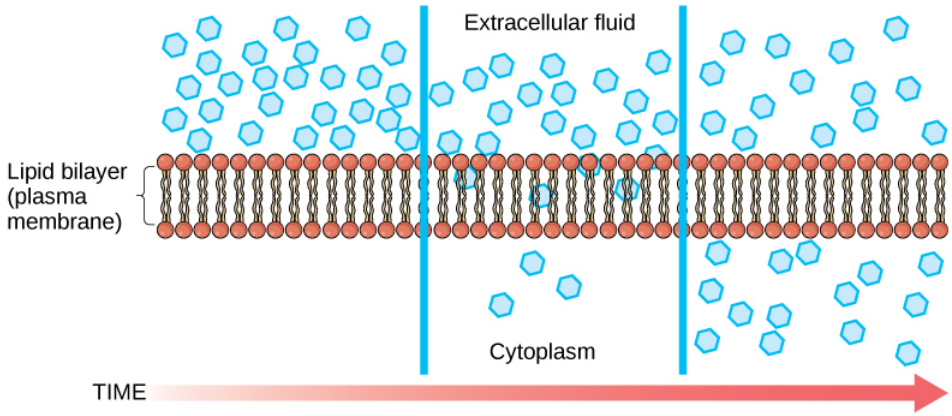


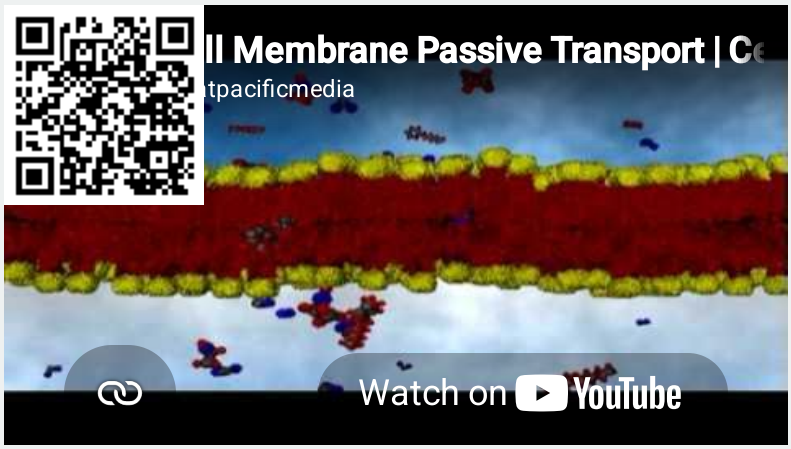
Figure 5.4.1: Diffusion through a permeable membrane follows the concentration gradient of a substance, moving the substance from an area of high concentration to one of low concentration. (credit: modification of work by Mariana Ruiz Villarreal)

Each separate substance in a medium, such as the extracellular fluid, has its own concentration gradient, independent of the concentration gradients of other materials. Additionally, each substance will diffuse according to that gradient.

Several factors affect the rate of diffusion.

- Extent of the concentration gradient: The greater the difference in concentration, the more rapid the diffusion. The closer the distribution of the material gets to equilibrium, the slower the rate of diffusion becomes.
- Mass of the molecules diffusing: More massive molecules move more slowly, because it is more difficult for them to move between the molecules of the substance they are moving through; therefore, they diffuse more slowly.
- Temperature: Higher temperatures increase the energy and therefore the movement of the molecules, increasing the rate of diffusion.
- Solvent density: As the density of the solvent increases, the rate of diffusion decreases. The molecules slow down because they have a more difficult time getting through the denser medium.

CONCEPT IN ACTION



For an animation of the diffusion process in action, view this short video on cell membrane transport.

Facilitated transport

In facilitated transport, also called facilitated diffusion, material moves across the plasma membrane with the assistance of transmembrane proteins down a concentration gradient (from high to low concentration) without the expenditure of cellular energy. However, the substances that undergo facilitated transport would otherwise not diffuse easily or quickly across the plasma membrane. The solution to moving polar substances and other substances across the plasma membrane rests in the proteins that span its surface. The material being transported is first attached to protein or glycoprotein receptors on the exterior surface of the plasma membrane. This allows the material that is needed by the cell to be removed from the extracellular fluid. The substances are

then passed to specific integral proteins that facilitate their passage, because they form channels or pores that allow certain substances to pass through the membrane. The integral proteins involved in facilitated transport are collectively referred to as transport proteins, and they function as either channels for the material or carriers.

Osmosis

Osmosis is the diffusion of water through a semipermeable membrane according to the concentration gradient of water across the membrane. Whereas diffusion transports material across membranes and within cells, osmosis transports *only water* across a membrane and the membrane limits the diffusion of solutes in the water. Osmosis is a special case of diffusion. Water, like other substances, moves from an area of higher concentration to one of lower concentration. Imagine a beaker with a semipermeable membrane, separating the two sides or halves (Figure **5.4.2**). On both sides of the membrane, the water level is the same, but there are different concentrations on each side of a dissolved substance, or solute, that cannot cross the membrane. If the volume of the water is the same, but the concentrations of solute are different, then there are also different concentrations of water, the solvent, on either side of the membrane.

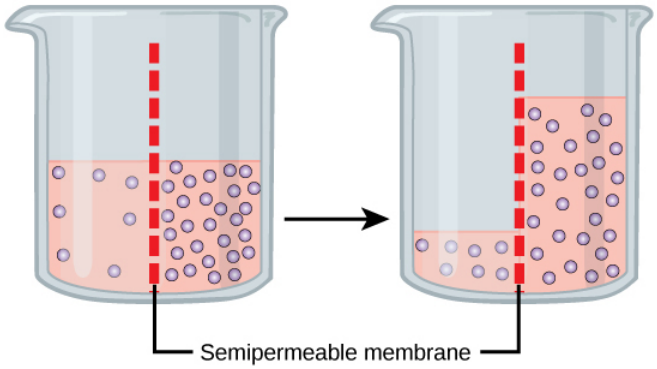


Figure 5.4.2: In osmosis, water always moves from an area of higher concentration (of water) to one of lower concentration (of water). In this system, the solute cannot pass through the selectively permeable membrane.

A principle of diffusion is that the molecules move around and will spread evenly throughout the medium if they can. However, only the material capable of getting through the membrane will diffuse through it. In this example, the solute cannot diffuse through the membrane, but the water can. Water has a concentration gradient in this system. Therefore, water will diffuse down its concentration gradient, crossing the membrane to the side where it is less concentrated. This diffusion of water through the membrane—osmosis—will continue until the concentration gradient of water goes to zero. Osmosis proceeds constantly in living systems.

Tonicity

Tonicity describes the amount of solute in a solution. The measure of the tonicity of a solution, or the total amount of solutes dissolved in a specific amount of solution, is called its osmolarity. Three terms—hypotonic, isotonic, and hypertonic—are used to relate the osmolarity of a cell to the osmolarity of the extracellular fluid that contains the cells. In a hypotonic solution, such as tap water, the extracellular fluid has a lower concentration of solutes than the fluid inside the cell, and water enters the cell. (In living systems, the point of reference is always the cytoplasm, so the prefix *hypo-* means that the extracellular fluid has a lower concentration of solutes, or a lower osmolarity, than the cell cytoplasm.) It also means that the extracellular fluid has a higher concentration of water than does the cell. In this situation, water will follow its concentration gradient and enter the cell. This may cause an animal cell to burst, or lyse.

In a hypertonic solution (the prefix *hyper-* refers to the extracellular fluid having a higher concentration of solutes than the cell's cytoplasm), the fluid contains less water than the cell does, such as seawater. Because the cell has a lower concentration of solutes, the water will leave the cell. In effect, the solute is drawing the water out of the cell. This may cause an animal cell to shrivel, or crenate.

In an isotonic solution, the extracellular fluid has the same osmolarity as the cell. If the concentration of solutes of the cell matches that of the extracellular fluid, there will be no net movement of water into or out of the cell. Blood cells in hypertonic, isotonic, and hypotonic solutions take on characteristic appearances (Figure **5.4.3**).

ART CONNECTION

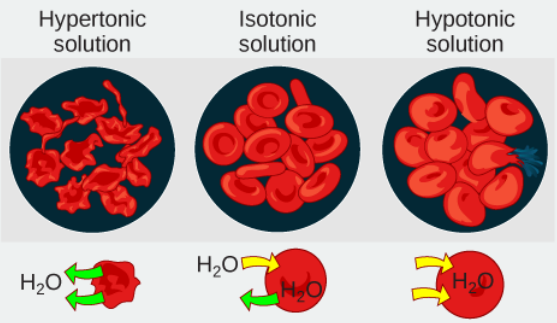


Figure 5.4.3: Osmotic pressure changes the shape of red blood cells in hypertonic, isotonic, and hypotonic solutions. (credit: modification of work by Mariana Ruiz Villarreal)

A doctor injects a patient with what the doctor thinks is isotonic saline solution. The patient dies, and autopsy reveals that many red blood cells have been destroyed. Do you think the solution the doctor injected was really isotonic?

Some organisms, such as plants, fungi, bacteria, and some protists, have cell walls that surround the plasma membrane and prevent cell lysis. The plasma membrane can only expand to the limit of the cell wall, so the cell will not lyse. In fact, the cytoplasm in plants is always slightly hypertonic compared to the cellular environment, and water will always enter a cell if water is available. This influx of water produces turgor pressure, which stiffens the cell walls of the plant (Figure **5.4.4**). In nonwoody plants, turgor pressure supports the plant. If the plant cells become hypertonic, as occurs in drought or if a plant is not watered adequately, water will leave the cell. Plants lose turgor pressure in this condition and wilt.

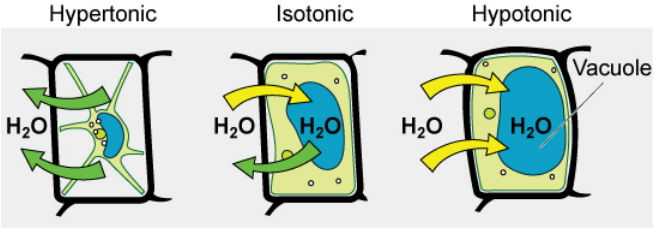


Figure 5.4.4: The turgor pressure within a plant cell depends on the tonicity of the solution that it is bathed in. (credit: modification of work by Mariana Ruiz Villarreal)

Section Summary

The passive forms of transport, diffusion and osmosis, move material of small molecular weight. Substances diffuse from areas of high concentration to areas of low concentration, and this process continues until the substance is evenly distributed in a system. In solutions of more than one substance, each type of molecule diffuses according to its own concentration gradient. Many factors can affect the rate of diffusion, including concentration gradient, the sizes of the particles that are diffusing, and the temperature of the system.

In living systems, diffusion of substances into and out of cells is mediated by the plasma membrane. Some materials diffuse readily through the membrane, but others are hindered, and their passage is only made possible by protein channels and carriers. The chemistry of living things occurs in aqueous solutions, and balancing the concentrations of those solutions is an ongoing problem. In living systems, diffusion of some substances would be slow or difficult without membrane proteins.

Art Connections

Figure **5.4.3**: A doctor injects a patient with what he thinks is isotonic saline solution. The patient dies, and autopsy reveals that many red blood cells have been destroyed. Do you think the solution the doctor injected was really isotonic?

Answer

No, it must have been hypotonic, as a hypotonic solution would cause water to enter the cells, thereby making them burst.

Glossary

concentration gradient
an area of high concentration across from an area of low concentration

diffusion
a passive process of transport of low-molecular weight material down its concentration gradient

facilitated transport
a process by which material moves down a concentration gradient (from high to low concentration) using integral membrane proteins

hypertonic
describes a solution in which extracellular fluid has higher osmolarity than the fluid inside the cell

hypotonic
describes a solution in which extracellular fluid has lower osmolarity than the fluid inside the cell

isotonic
describes a solution in which the extracellular fluid has the same osmolarity as the fluid inside the cell

osmolarity
the total amount of substances dissolved in a specific amount of solution

osmosis
the transport of water through a semipermeable membrane from an area of high water concentration to an area of low water concentration across a membrane

passive transport
a method of transporting material that does not require energy

selectively permeable
the characteristic of a membrane that allows some substances through but not others

solute
a substance dissolved in another to form a solution

tonicity
the amount of solute in a solution.

Contributors and Attributions

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SECTION OVERVIEW

5.5: Active Transport Across Membranes

5.5.1: Active Transport I

5.5.2: Active Transport II

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5.5.1: Active Transport I

Active transport:

Active transport is the pumping of molecules or ions through a membrane **against** their concentration gradient. It requires a transmembrane protein (usually a complex of them) called a transporter and energy. The source of this energy is **ATP**.

The energy of ATP may be used directly or indirectly.

- **Direct Active Transport.** Some transporters bind ATP directly and use the energy of its hydrolysis to drive active transport.
- **Indirect Active Transport.** Other transporters use the energy already stored in the gradient of a directly-pumped **ion**. Direct active transport of the ion establishes a concentration gradient. When this is relieved by facilitated diffusion, the energy released can be harnessed to the pumping of some other ion or molecule.

Direct Active Transport

The Na^+/K^+ ATPase

The cytosol of animal cells contains a concentration of potassium ions (K^+) as much as 20 times higher than that in the extracellular fluid. Conversely, the extracellular fluid contains a concentration of sodium ions (Na^+) as much as 10 times greater than that within the cell. These concentration gradients are established by the active transport of both ions. And, in fact, the same transporter, called the Na^+/K^+ ATPase, does both jobs. It uses the energy from the hydrolysis of ATP to

- actively transport 3 Na^+ ions out of the cell
- for each 2 K^+ ions pumped into the cell.

This accomplishes several vital functions:

- It helps establish a net charge across the plasma membrane with the interior of the cell being negatively charged with respect to the exterior. This **resting potential** prepares nerve and muscle cells for the propagation of action potentials leading to nerve impulses and muscle contraction.
- The accumulation of sodium ions outside of the cell draws water out of the cell and thus enables it to maintain osmotic balance (otherwise it would swell and burst from the inward diffusion of water).
- The gradient of sodium ions is harnessed to provide the energy to run several types of indirect pumps.

The crucial roles of the Na^+/K^+ ATPase are reflected in the fact that almost one-third of all the energy generated by the mitochondria in animal cells is used just to run this pump.

The H^+/K^+ ATPase

The parietal cells of your stomach use this pump to secrete gastric juice. These cells transport protons (H^+) from a concentration of about 4 x 10^{-8} M within the cell to a concentration of about 0.15 M in the gastric juice (giving it a pH close to 1). Small wonder that parietal cells are stuffed with mitochondria and uses huge amounts of **ATP** as they carry out this three-million fold concentration of protons.

The Ca^{2+} ATPases

A Ca^{2+} ATPase is located in the **plasma membrane** of all eukaryotic cells. It uses the energy provided by one molecule of ATP to pump one Ca^{2+} ion out of the cell. The activity of these pumps helps to maintain the ~20,000-fold concentration gradient of Ca^{2+} between the cytosol (~ 100 nM) and the ECF (~ 20 mM). In resting skeletal muscle, there is a much higher concentration of calcium ions (Ca^{2+}) in the sarcoplasmic reticulum than in the cytosol. Activation of the muscle fiber allows some of this Ca^{2+} to pass by facilitated diffusion into the cytosol where it triggers contraction.

After contraction, this Ca^{2+} is pumped back into the sarcoplasmic reticulum. This is done by another Ca^{2+} ATPase that uses the energy from each molecule of ATP to pump 2 Ca^{2+} ions.

Pumps **1. - 3.** are designated **P-type ion transporters** because they use the same basic mechanism: a conformational change in the proteins as they are reversibly phosphorylated by ATP. And all three pumps can be made to run backward. That is, if the pumped ions are allowed to diffuse back through the membrane complex, ATP can be synthesized from ADP and inorganic phosphate.

ABC Transporters

ABC ("**A**TP-**B**inding **C**assette") transporters are transmembrane proteins that

- expose a ligand-binding domain at one surface and a
- ATP-binding domain at the other surface.

The ligand-binding domain is usually restricted to a single type of molecule.

The ATP bound to its domain provides the energy to pump the ligand across the membrane.

The human genome contains 48 genes for ABC transporters. Some examples:

- **CFTR** — the cystic fibrosis transmembrane conductance regulator
- **TAP**, the transporter associated with antigen processing
- The transporter that liver cells use to pump the salts of bile acids out into the bile.
- ABC transporters that pump chemotherapeutic drugs out of cancer cells thus reducing their effectiveness.

ABC transporters must have evolved early in the history of life. The ATP-binding domains in archaea, eubacteria, and eukaryotes all share a homologous structure, the ATP-binding "cassette".

Indirect Active Transport

Indirect active transport uses the downhill flow of an ion to pump some other molecule or ion against its gradient. The driving ion is usually sodium (Na^+) with its gradient established by the Na^+/K^+ ATPase.

Symport Pumps

In this type of indirect active transport, the driving ion (Na^+) and the pumped molecule pass through the membrane pump in the **same** direction. Examples:

- **The Na^+/glucose transporter**. This transmembrane protein allows sodium ions and glucose to enter the cell together. The sodium ions flow **down** their concentration gradient while the glucose molecules are pumped **up** theirs. Later the sodium is pumped back out of the cell by the Na^+/K^+ ATPase. The Na^+/glucose transporter is used to actively transport glucose out of the intestine and also out of the kidney tubules and back into the blood.
- All the **amino acids** can be actively transported, for example out of the kidney tubules and into the blood, by sodium-driven symport pumps.
- Sodium-driven symport pumps also return **neurotransmitters** to the presynaptic neuron.
- **The Na^+/iodide transporter**. This symporter pumps iodide ions into the cells of the thyroid gland (for the manufacture of thyroxine) and also into the cells of the mammary gland (to supply the baby's need for iodide).
- The **permease** encoded by the lac operon of *E. coli* that transports lactose into the cell.

Antiport Pumps

In antiport pumps, the driving ion (again, usually sodium) diffuses through the pump in one direction providing the energy for the active transport of some other molecule or ion in the opposite direction. **Example**:

Ca^{2+} ions are pumped out of cells by sodium-driven antiport pumps. Antiport pumps in the vacuole of some plants harness the outward facilitated diffusion of protons (themselves pumped into the vacuole by a H^+ ATPase) to the active inward transport of sodium ions. This sodium/proton antiport pump enables the plant to sequester sodium ions in its vacuole. Transgenic tomato plants that overexpress this sodium/proton antiport pump are able to thrive in saline soils too salty for conventional tomatoes. Antiport pumps to the active inward transport of nitrate ions ($NO3^-$)

Some inherited ion-channel diseases

A growing number of human diseases have been discovered to be caused by inherited mutations in genes encoding channels.

Examples:

- **Chloride-channel** diseases
  - cystic fibrosis

- inherited tendency to kidney stones (caused by a different kind of chloride channel than the one involved in cystic fibrosis)

- **Potassium-channel** diseases
  - the majority of cases of **long QT syndrome**, an inherited disorder of the heartbeat
  - a rare, inherited tendency to epileptic seizures in the newborn
  - several types of inherited **deafness**
- **Sodium-channel** diseases
  - inherited tendency to certain types of muscle spasms
  - Liddle's syndrome. Inadequate sodium transport out of the kidneys, because of a mutant sodium channel, leads to elevated **osmotic pressure** of the blood and resulting hypertension (high blood pressure)

Osmosis

Osmosis is a special term used for the diffusion of water through cell membranes. Although water is a polar molecule, it is able to pass through the lipid bilayer of the plasma membrane. Aquaporins — transmembrane proteins that form hydrophilic channels — greatly accelerate the process, but even without these, water is still able to get through. Water passes by diffusion from a region of higher to a region of lower concentration. Note that this refers to the concentration of water, NOT the concentration of any solutes present in the water. Water is never transported actively; that is, it never moves against its concentration gradient. However, the concentration of water can be altered by the active transport of solutes and in this way the movement of water in and out of the cell can be controlled. **Example**: the reabsorption of water from the kidney tubules back into the blood depends on the water following behind the active transport of Na^+.

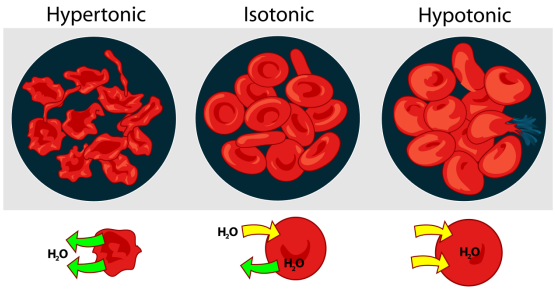


Figure 3.23.3: Osmosis effect on blood cells in different solutions. (Public domain; Ladyofhats).

- **Hypotonic solutions:** If the concentration of water in the medium surrounding a cell is greater than that of the cytosol, the medium is said to be **hypotonic**. Water enters the cell by osmosis. A red blood cell placed in a hypotonic solution (e.g., pure water) bursts immediately ("hemolysis") from the influx of water. Plant cells and bacterial cells avoid bursting in hypotonic surroundings by their strong cell walls. These allow the buildup of **turgor** within the cell. When the turgor pressure equals the osmotic pressure, osmosis ceases.
- **Isotonic solutions**: When red blood cells are placed in a 0.9% salt solution, they neither gain nor lose water by osmosis. Such a solution is said to be **isotonic**. The extracellular fluid (ECF) of mammalian cells is isotonic to their cytoplasm. This balance must be actively maintained because of the large number of organic molecules dissolved in the cytosol but not present in the ECF. These organic molecules exert an osmotic effect that, if not compensated for, would cause the cell to take in so much water that it would swell and might even burst. This fate is avoided by pumping sodium ions out of the cell with the Na^+/K^+ ATPase.
- **Hypertonic solutions:** If red cells are placed in sea water (about 3% salt), they lose water by osmosis and the cells shrivel up. Sea water is **hypertonic** to their cytosol. Similarly, if a plant tissue is placed in sea water, the cell contents shrink away from the rigid cell wall. This is called **plasmolysis**. Sea water is also hypertonic to the ECF of most marine vertebrates. To avoid fatal dehydration, these animals (e.g., bony fishes like the cod) must continuously drink sea water and then desalt it by pumping ions out of their gills by active transport.

Marine birds, which may pass long periods of time away from fresh water, and sea turtles use a similar device. They, too, drink salt water to take care of their water needs and use metabolic energy to desalt it. In the herring gull, shown here, the salt is extracted by two glands in the head and released (in a very concentrated solution — it is saltier than the blood) to the outside through the nostrils. Marine snakes use a similar desalting mechanism.

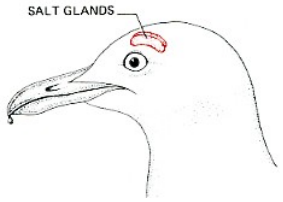


Figure 3.23.4: herring gull salt glands

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5.5.2: Active Transport II

Active transport mechanisms require the use of the cell's energy, usually in the form of adenosine triphosphate (ATP). If a substance must move into the cell against its concentration gradient, that is, if the concentration of the substance inside the cell must be greater than its concentration in the extracellular fluid, the cell must use energy to move the substance. Some active transport mechanisms move small-molecular weight material, such as ions, through the membrane.

In addition to moving small ions and molecules through the membrane, cells also need to remove and take in larger molecules and particles. Some cells are even capable of engulfing entire unicellular microorganisms. You might have correctly hypothesized that the uptake and release of large particles by the cell requires energy. A large particle, however, cannot pass through the membrane, even with energy supplied by the cell.

Electrochemical Gradient

We have discussed simple concentration gradients—differential concentrations of a substance across a space or a membrane—but in living systems, gradients are more complex. Because cells contain proteins, most of which are negatively charged, and because ions move into and out of cells, there is an electrical gradient, a difference of charge, across the plasma membrane. The interior of living cells is electrically negative with respect to the extracellular fluid in which they are bathed; at the same time, cells have higher concentrations of potassium (K^+) and lower concentrations of sodium (Na^+) than does the extracellular fluid. Thus, in a living cell, the concentration gradient and electrical gradient of Na^+ promotes diffusion of the ion into the cell, and the electrical gradient of Na^+ (a positive ion) tends to drive it inward to the negatively charged interior. The situation is more complex, however, for other elements such as potassium. The electrical gradient of K^+ promotes diffusion of the ion *into* the cell, but the concentration gradient of K^+ promotes diffusion *out* of the cell (Figure 5.5.2.1). The combined gradient that affects an ion is called its electrochemical gradient, and it is especially important to muscle and nerve cells.

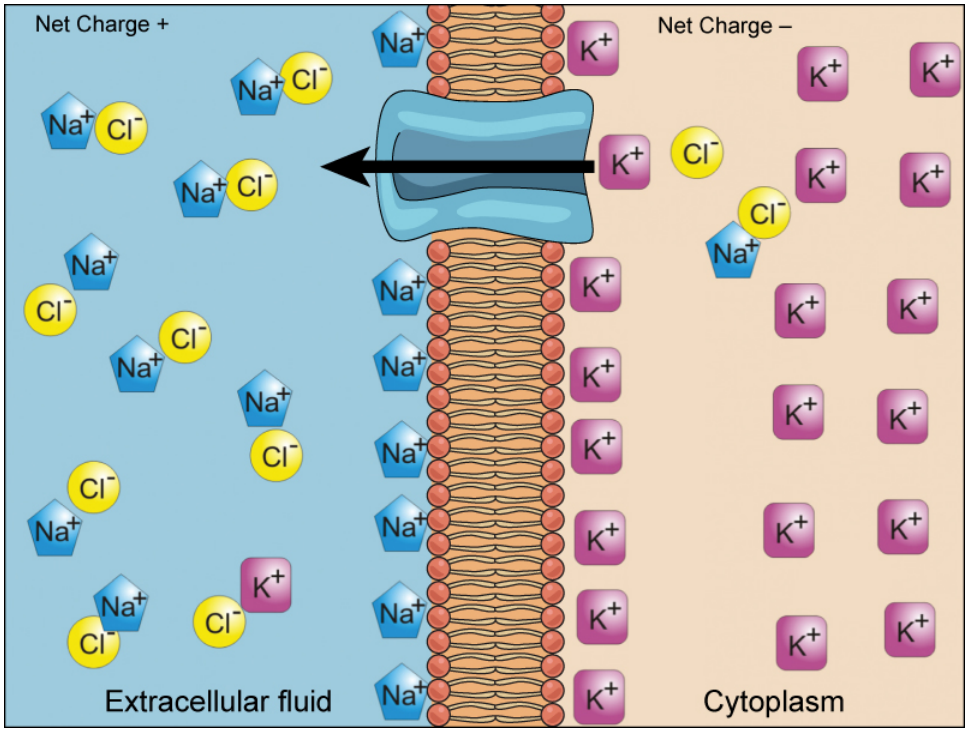


Figure 5.5.2.1: Electrochemical gradients arise from the combined effects of concentration gradients and electrical gradients. (credit: modification of work by "Synaptitude"/Wikimedia Commons)

Moving Against a Gradient

To move substances against a concentration or an electrochemical gradient, the cell must use energy. This energy is harvested from ATP that is generated through cellular metabolism. Active transport mechanisms, collectively called pumps or carrier proteins, work against electrochemical gradients. With the exception of ions, small substances constantly pass through plasma membranes.

Active transport maintains concentrations of ions and other substances needed by living cells in the face of these passive changes. Much of a cell's supply of metabolic energy may be spent maintaining these processes. Because active transport mechanisms depend on cellular metabolism for energy, they are sensitive to many metabolic poisons that interfere with the supply of ATP.

Two mechanisms exist for the transport of small-molecular weight material and macromolecules. Primary active transport moves ions across a membrane and creates a difference in charge across that membrane. The primary active transport system uses ATP to move a substance, such as an ion, into the cell, and often at the same time, a second substance is moved out of the cell. The sodium-potassium pump, an important pump in animal cells, expends energy to move potassium ions into the cell and a different number of sodium ions out of the cell (Figure **5.5.2.2**). The action of this pump results in a concentration and charge difference across the membrane.

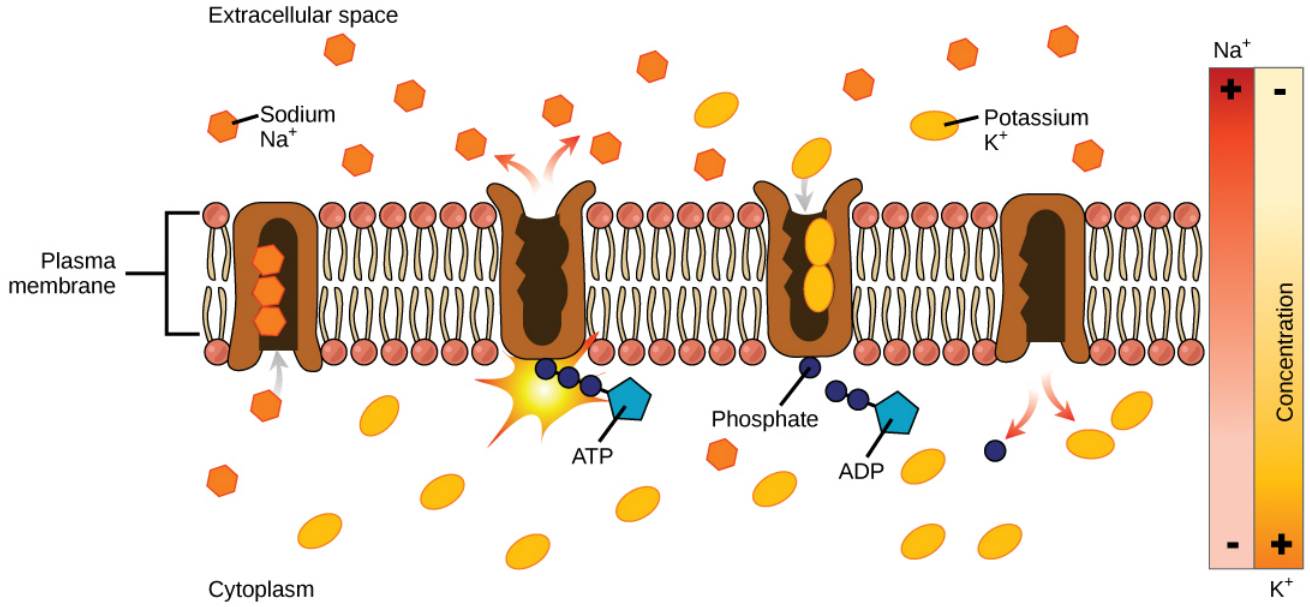


Figure 5.5.2.2: The sodium-potassium pump moves potassium and sodium ions across the plasma membrane. (credit: modification of work by Mariana Ruiz Villarreal)

Secondary active transport describes the movement of material using the energy of the electrochemical gradient established by primary active transport. Using the energy of the electrochemical gradient created by the primary active transport system, other substances such as amino acids and glucose can be brought into the cell through membrane channels. ATP itself is formed through secondary active transport using a hydrogen ion gradient in the mitochondrion.

Endocytosis

Endocytosis is a type of active transport that moves particles, such as large molecules, parts of cells, and even whole cells, into a cell. There are different variations of endocytosis, but all share a common characteristic: The plasma membrane of the cell invaginates, forming a pocket around the target particle. The pocket pinches off, resulting in the particle being contained in a newly created vacuole that is formed from the plasma membrane.

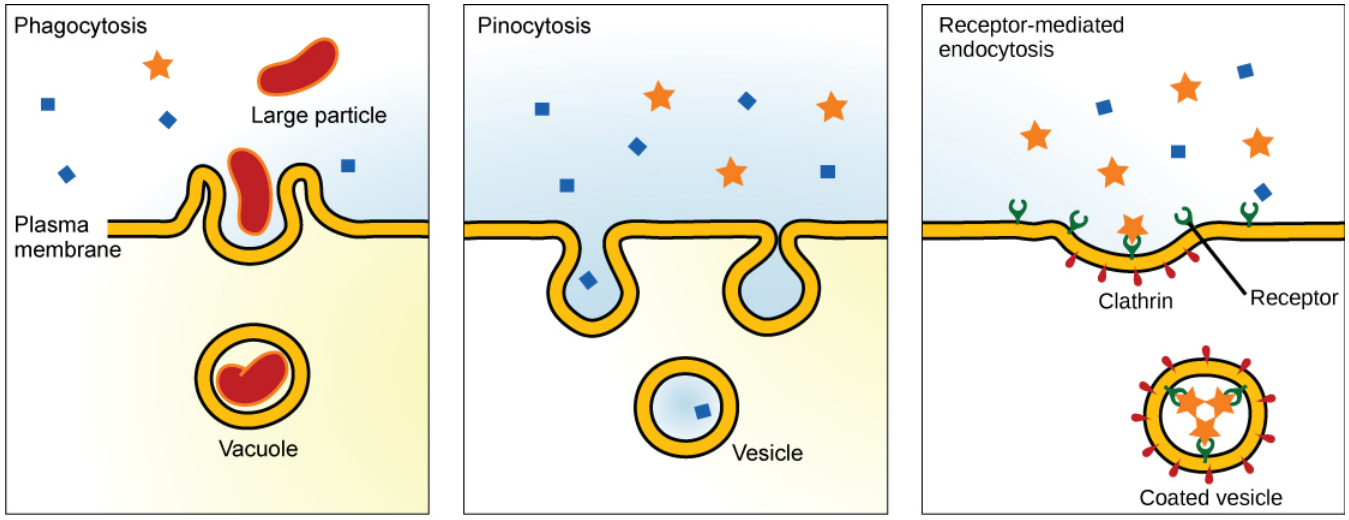


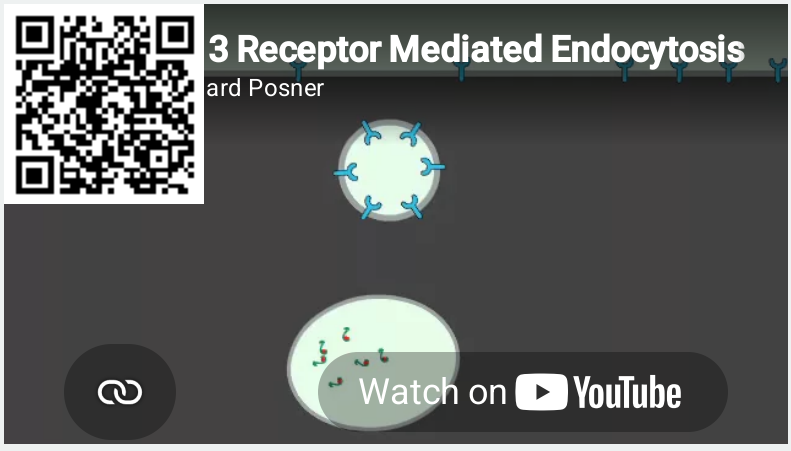
Figure 5.5.2.3: Three variations of endocytosis are shown. (a) In one form of endocytosis, phagocytosis, the cell membrane surrounds the particle and pinches off to form an intracellular vacuole. (b) In another type of endocytosis, pinocytosis, the cell membrane surrounds a small volume of fluid and pinches off, forming a vesicle. (c) In receptor-mediated endocytosis, uptake of substances by the cell is targeted to a single type of substance that binds at the receptor on the external cell membrane. (credit: modification of work by Mariana Ruiz Villarreal)

Phagocytosis is the process by which large particles, such as cells, are taken in by a cell. For example, when microorganisms invade the human body, a type of white blood cell called a neutrophil removes the invader through this process, surrounding and engulfing the microorganism, which is then destroyed by the neutrophil (Figure 5.5.2.3).

A variation of endocytosis is called pinocytosis. This literally means “cell drinking” and was named at a time when the assumption was that the cell was purposefully taking in extracellular fluid. In reality, this process takes in solutes that the cell needs from the extracellular fluid (Figure 5.5.2.3).

A targeted variation of endocytosis employs binding proteins in the plasma membrane that are specific for certain substances (Figure 5.5.2.3). The particles bind to the proteins and the plasma membrane invaginates, bringing the substance and the proteins into the cell. If passage across the membrane of the target of receptor-mediated endocytosis is ineffective, it will not be removed from the tissue fluids or blood. Instead, it will stay in those fluids and increase in concentration. Some human diseases are caused by a failure of receptor-mediated endocytosis. For example, the form of cholesterol termed low-density lipoprotein or LDL (also referred to as “bad” cholesterol) is removed from the blood by receptor-mediated endocytosis. In the human genetic disease familial hypercholesterolemia, the LDL receptors are defective or missing entirely. People with this condition have life-threatening levels of cholesterol in their blood, because their cells cannot clear the chemical from their blood.

CONCEPT IN ACTION



See receptor-mediated endocytosis animation in action.

Exocytosis

In contrast to these methods of moving material into a cell is the process of exocytosis. Exocytosis is the opposite of the processes discussed above in that its purpose is to expel material from the cell into the extracellular fluid. A particle enveloped in membrane fuses with the interior of the plasma membrane. This fusion opens the membranous envelope to the exterior of the cell, and the particle is expelled into the extracellular space (Figure 5.5.2.4).

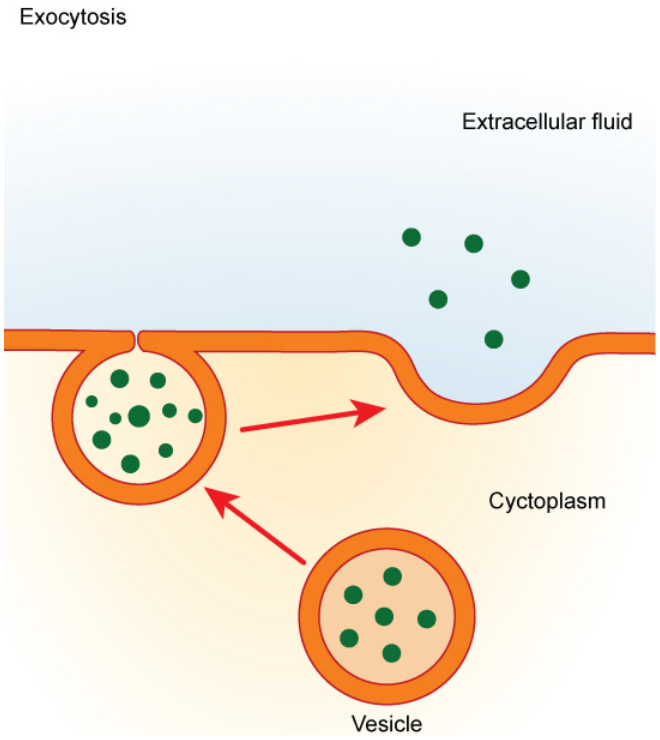


Figure 5.5.2.4: In exocytosis, a vesicle migrates to the plasma membrane, binds, and releases its contents to the outside of the cell. (credit: modification of work by Mariana Ruiz Villarreal)

Section Summary

The combined gradient that affects an ion includes its concentration gradient and its electrical gradient. Living cells need certain substances in concentrations greater than they exist in the extracellular space. Moving substances up their electrochemical gradients requires energy from the cell. Active transport uses energy stored in ATP to fuel the transport. Active transport of small molecular-size material uses integral proteins in the cell membrane to move the material—these proteins are analogous to pumps. Some pumps, which carry out primary active transport, couple directly with ATP to drive their action. In secondary transport, energy from primary transport can be used to move another substance into the cell and up its concentration gradient.

Endocytosis methods require the direct use of ATP to fuel the transport of large particles such as macromolecules; parts of cells or whole cells can be engulfed by other cells in a process called phagocytosis. In phagocytosis, a portion of the membrane invaginates and flows around the particle, eventually pinching off and leaving the particle wholly enclosed by an envelope of plasma membrane. Vacuoles are broken down by the cell, with the particles used as food or dispatched in some other way. Pinocytosis is a similar process on a smaller scale. The cell expels waste and other particles through the reverse process, exocytosis. Wastes are moved outside the cell, pushing a membranous vesicle to the plasma membrane, allowing the vesicle to fuse with the membrane and incorporating itself into the membrane structure, releasing its contents to the exterior of the cell.

Glossary

active transport

the method of transporting material that requires energy

electrochemical gradient

a gradient produced by the combined forces of the electrical gradient and the chemical gradient

endocytosis

a type of active transport that moves substances, including fluids and particles, into a cell

exocytosis

a process of passing material out of a cell

phagocytosis

a process that takes macromolecules that the cell needs from the extracellular fluid; a variation of endocytosis

pinocytosis

a process that takes solutes that the cell needs from the extracellular fluid; a variation of endocytosis

receptor-mediated endocytosis

a variant of endocytosis that involves the use of specific binding proteins in the plasma membrane for specific molecules or particles

Contributors and Attributions

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5.6: Bulk Transport by Endocytosis and Exocytosis

Skills to Develop

- Describe endocytosis, including phagocytosis, pinocytosis, and receptor-mediated endocytosis
- Understand the process of exocytosis

In addition to moving small ions and molecules through the membrane, cells also need to remove and take in larger molecules and particles (see Table **5.6.1** for examples). Some cells are even capable of engulfing entire unicellular microorganisms. You might have correctly hypothesized that the uptake and release of large particles by the cell requires energy. A large particle, however, cannot pass through the membrane, even with energy supplied by the cell.

Endocytosis

Endocytosis is a type of active transport that moves particles, such as large molecules, parts of cells, and even whole cells, into a cell. There are different variations of endocytosis, but all share a common characteristic: The plasma membrane of the cell invaginates, forming a pocket around the target particle. The pocket pinches off, resulting in the particle being contained in a newly created intracellular vesicle formed from the plasma membrane.

Phagocytosis

Phagocytosis (the condition of "cell eating") is the process by which large particles, such as cells or relatively large particles, are taken in by a cell. For example, when microorganisms invade the human body, a type of white blood cell called a neutrophil will remove the invaders through this process, surrounding and engulfing the microorganism, which is then destroyed by the neutrophil (Figure **5.6.1**).

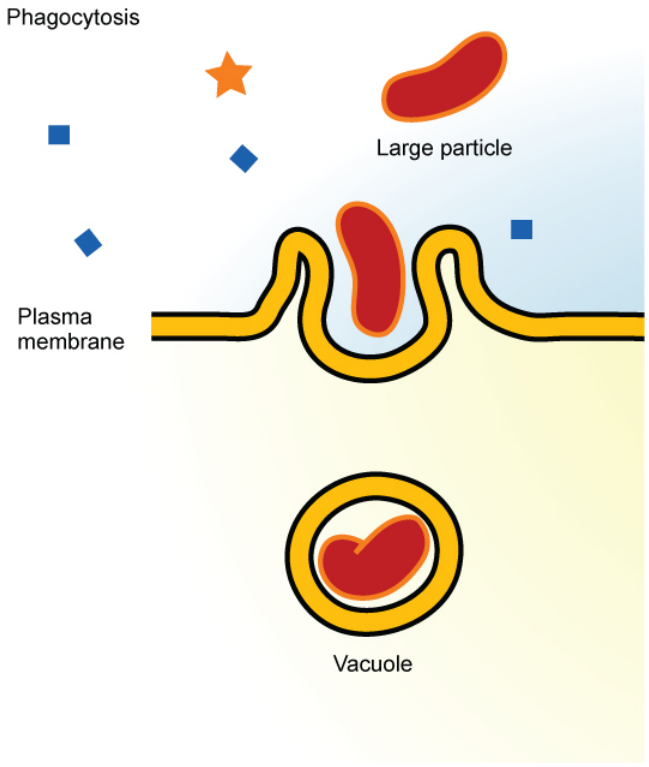


Figure **5.6.1**: In phagocytosis, the cell membrane surrounds the particle and engulfs it. (credit: Mariana Ruiz Villareal)

In preparation for phagocytosis, a portion of the inward-facing surface of the plasma membrane becomes coated with a protein called clathrin, which stabilizes this section of the membrane. The coated portion of the membrane then extends from the body of the cell and surrounds the particle, eventually enclosing it. Once the vesicle containing the particle is enclosed within the cell, the clathrin disengages from the membrane and the vesicle merges with a lysosome for the breakdown of the material in the newly

formed compartment (endosome). When accessible nutrients from the degradation of the vesicular contents have been extracted, the newly formed endosome merges with the plasma membrane and releases its contents into the extracellular fluid. The endosomal membrane again becomes part of the plasma membrane.

Pinocytosis

A variation of endocytosis is called pinocytosis. This literally means “cell drinking” and was named at a time when the assumption was that the cell was purposefully taking in extracellular fluid. In reality, this is a process that takes in molecules, including water, which the cell needs from the extracellular fluid. Pinocytosis results in a much smaller vesicle than does phagocytosis, and the vesicle does not need to merge with a lysosome (Figure 5.6.2).

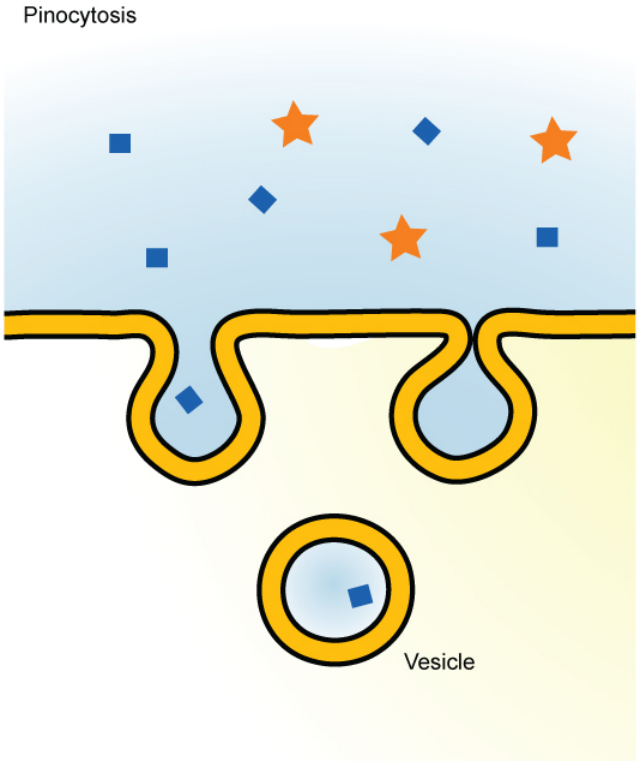


Figure 5.6.2: In pinocytosis, the cell membrane invaginates, surrounds a small volume of fluid, and pinches off. (credit: Mariana Ruiz Villareal)

A variation of pinocytosis is called potocytosis. This process uses a coating protein, called caveolin, on the cytoplasmic side of the plasma membrane, which performs a similar function to clathrin. The cavities in the plasma membrane that form the vacuoles have membrane receptors and lipid rafts in addition to caveolin. The vacuoles or vesicles formed in caveolae (singular caveola) are smaller than those in pinocytosis. Potocytosis is used to bring small molecules into the cell and to transport these molecules through the cell for their release on the other side of the cell, a process called transcytosis.

Receptor-mediated Endocytosis

A targeted variation of endocytosis employs receptor proteins in the plasma membrane that have a specific binding affinity for certain substances (Figure 5.6.3).

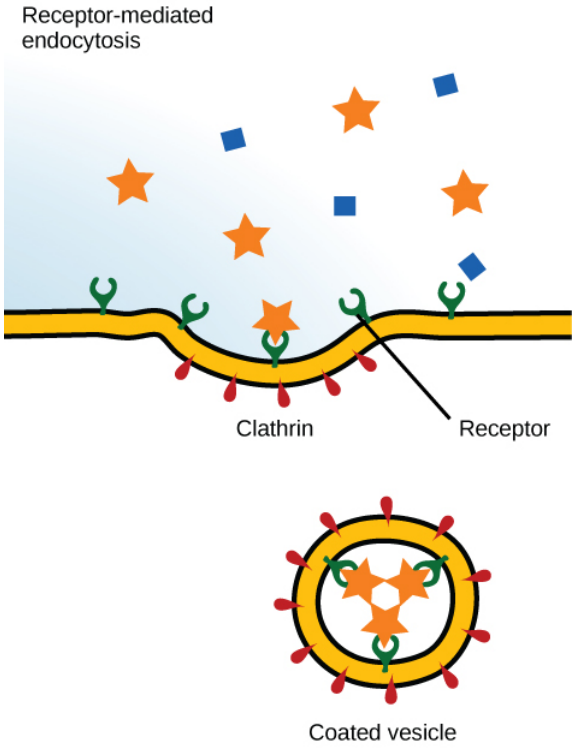
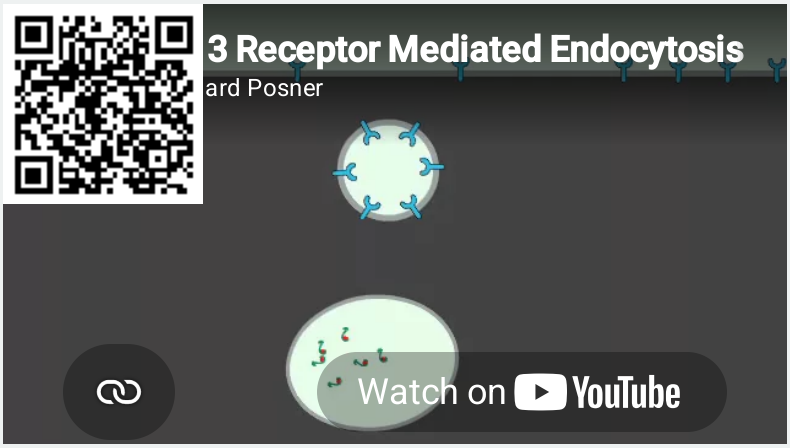


Figure 5.6.3: In receptor-mediated endocytosis, uptake of substances by the cell is targeted to a single type of substance that binds to the receptor on the external surface of the cell membrane. (credit: modification of work by Mariana Ruiz Villareal)

In receptor-mediated endocytosis, as in phagocytosis, clathrin is attached to the cytoplasmic side of the plasma membrane. If uptake of a compound is dependent on receptor-mediated endocytosis and the process is ineffective, the material will not be removed from the tissue fluids or blood. Instead, it will stay in those fluids and increase in concentration. Some human diseases are caused by the failure of receptor-mediated endocytosis. For example, the form of cholesterol termed low-density lipoprotein or LDL (also referred to as “bad” cholesterol) is removed from the blood by receptor-mediated endocytosis. In the human genetic disease familial hypercholesterolemia, the LDL receptors are defective or missing entirely. People with this condition have life-threatening levels of cholesterol in their blood, because their cells cannot clear LDL particles from their blood.

Although receptor-mediated endocytosis is designed to bring specific substances that are normally found in the extracellular fluid into the cell, other substances may gain entry into the cell at the same site. Flu viruses, diphtheria, and cholera toxin all have sites that cross-react with normal receptor-binding sites and gain entry into cells.

Link to Learning



Video 5.6.1: See receptor-mediated endocytosis in action, and click on different parts for a focused animation.

Exocytosis

The reverse process of moving material into a cell is the process of exocytosis. Exocytosis is the opposite of the processes discussed above in that its purpose is to expel material from the cell into the extracellular fluid. Waste material is enveloped in a membrane and fuses with the interior of the plasma membrane. This fusion opens the membranous envelope on the exterior of the cell, and the waste material is expelled into the extracellular space (Figure 5.6.4). Other examples of cells releasing molecules via exocytosis include the secretion of proteins of the extracellular matrix and secretion of neurotransmitters into the synaptic cleft by synaptic vesicles.

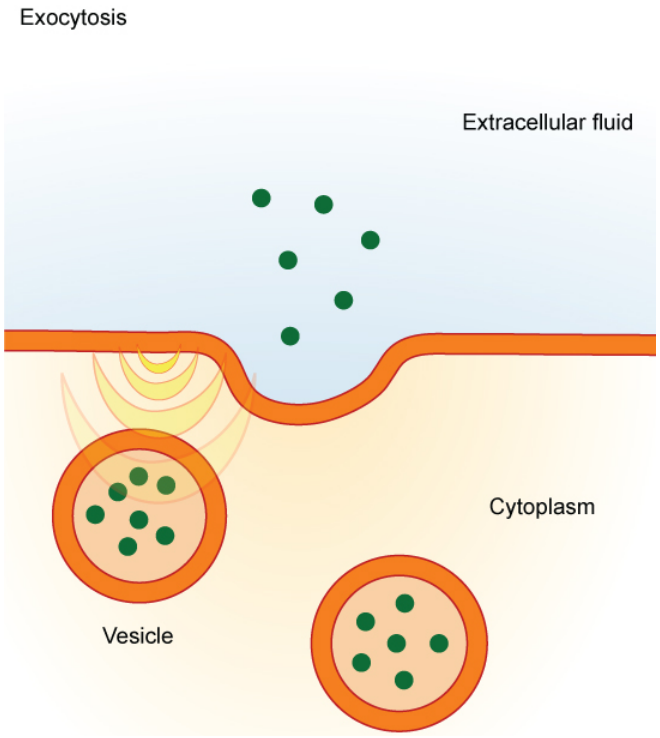


Figure 5.6.4: In exocytosis, vesicles containing substances fuse with the plasma membrane. The contents are then released to the exterior of the cell. (credit: modification of work by Mariana Ruiz Villareal)

Table 5.6.1: Methods of transport, Energy requirements and types of Material transported.

Transport Method	Active/Passive	Material Transported
Diffusion	Passive	Small-molecular weight material
Osmosis	Passive	Water
Facilitated transport/diffusion	Passive	Sodium, potassium, calcium, glucose
Primary active transport	Active	Sodium, potassium, calcium
Secondary active transport	Active	Amino acids, lactose
Phagocytosis	Active	Large macromolecules, whole cells, or cellular structures
Pinocytosis and potocytosis	Active	Small molecules (liquids/water)
Receptor-mediated endocytosis	Active	Large quantities of macromolecules

Summary

Active transport methods require the direct use of ATP to fuel the transport. Large particles, such as macromolecules, parts of cells, or whole cells, can be engulfed by other cells in a process called phagocytosis. In phagocytosis, a portion of the membrane

invaginates and flows around the particle, eventually pinching off and leaving the particle entirely enclosed by an envelope of plasma membrane. Vesicle contents are broken down by the cell, with the particles either used as food or dispatched. Pinocytosis is a similar process on a smaller scale. The plasma membrane invaginates and pinches off, producing a small envelope of fluid from outside the cell. Pinocytosis imports substances that the cell needs from the extracellular fluid. The cell expels waste in a similar but reverse manner: it pushes a membranous vacuole to the plasma membrane, allowing the vacuole to fuse with the membrane and incorporate itself into the membrane structure, releasing its contents to the exterior.

Glossary

caveolin
: protein that coats the cytoplasmic side of the plasma membrane and participates in the process of liquid update by potocytosis

clathrin
: protein that coats the inward-facing surface of the plasma membrane and assists in the formation of specialized structures, like coated pits, for phagocytosis

endocytosis
: type of active transport that moves substances, including fluids and particles, into a cell

exocytosis
: process of passing bulk material out of a cell

pinocytosis
: a variation of endocytosis that imports macromolecules that the cell needs from the extracellular fluid

potocytosis
: variation of pinocytosis that uses a different coating protein (caveolin) on the cytoplasmic side of the plasma membrane

receptor-mediated endocytosis
: variation of endocytosis that involves the use of specific binding proteins in the plasma membrane for specific molecules or particles, and clathrin-coated pits that become clathrin-coated vesicles

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CHAPTER OVERVIEW

6: Energy and Metabolism

6.1: The Flow of Energy in Living Systems

6.1.1: The Role of Energy and Metabolism

6.1.2: Types of Energy

6.2: The Laws of Thermodynamics and Free Energy

6.2.1: Free Energy

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6.2.3: The Second Law of Thermodynamics

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6.3: Adenosine Triphosphate -ATP The Energy Currency of Cells

6.4: Enzymes- Biological Catalysts

6.5: Metabolism- The Chemical Description of Cell Function

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SECTION OVERVIEW

6.1: The Flow of Energy in Living Systems

6.1.1: The Role of Energy and Metabolism

6.1.2: Types of Energy

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6.1.1: The Role of Energy and Metabolism

Learning Objectives

- Explain the importance of metabolism

Energy and Metabolism

All living organisms need energy to grow and reproduce, maintain their structures, and respond to their environments. Metabolism is the set of life-sustaining chemical processes that enables organisms transform the chemical energy stored in molecules into energy that can be used for cellular processes. Animals consume food to replenish energy; their metabolism breaks down the carbohydrates, lipids, proteins, and nucleic acids to provide chemical energy for these processes. Plants convert light energy from the sun into chemical energy stored in molecules during the process of photosynthesis.

Bioenergetics and Chemical Reactions

Scientists use the term bioenergetics to discuss the concept of energy flow through living systems such as cells. Cellular processes such as the building and breaking down of complex molecules occur through step-by-step chemical reactions. Some of these chemical reactions are spontaneous and release energy, whereas others require energy to proceed. All of the chemical reactions that take place inside cells, including those that use energy and those that release energy, are the cell's metabolism.

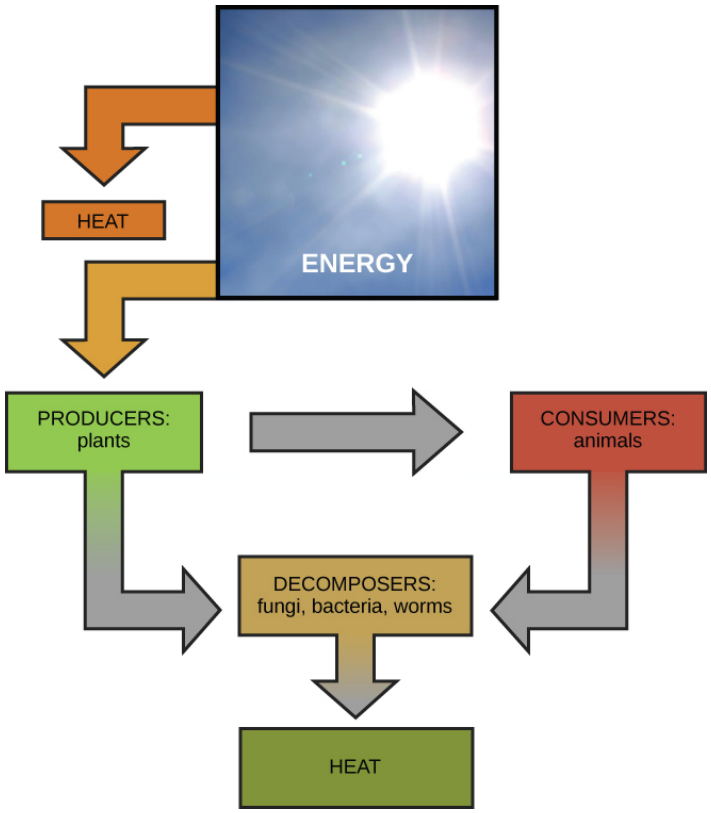


Figure **6.1.1.1**: Most energy comes from the sun, either directly or indirectly: Most life forms on earth get their energy from the sun. Plants use photosynthesis to capture sunlight, and herbivores eat those plants to obtain energy. Carnivores eat the herbivores, and decomposers digest plant and animal matter.

Cellular Metabolism

Every task performed by living organisms requires energy. Energy is needed to perform heavy labor and exercise, but humans also use a great deal of energy while thinking and even while sleeping. For every action that requires energy, many chemical reactions take place to provide chemical energy to the systems of the body, including muscles, nerves, heart, lungs, and brain.

The living cells of every organism constantly use energy to survive and grow. Cells break down complex carbohydrates into simple sugars that the cell can use for energy. Muscle cells may consumer energy to build long muscle proteins from small amino acid molecules. Molecules can be modified and transported around the cell or may be distributed to the entire organism. Just as energy is required to both build and demolish a building, energy is required for both the synthesis and breakdown of molecules.

Many cellular process require a steady supply of energy provided by the cell's metabolism. Signaling molecules such as hormones and neurotransmitters must be synthesized and then transported between cells. Pathogenic bacteria and viruses are ingested and broken down by cells. Cells must also export waste and toxins to stay healthy, and many cells must swim or move surrounding materials via the beating motion of cellular appendages like cilia and flagella.



Figure **6.1.1.1**: Eating provides energy for activities like flight: A hummingbird needs energy to maintain prolonged periods of flight. The hummingbird obtains its energy from taking in food and transforming the nutrients into energy through a series of biochemical reactions. The flight muscles in birds are extremely efficient in energy production.

Key Points

- All living organisms need energy to grow and reproduce, maintain their structures, and respond to their environments; metabolism is the set of the processes that makes energy available for cellular processes.
- Metabolism is a combination of chemical reactions that are spontaneous and release energy and chemical reactions that are non-spontaneous and require energy in order to proceed.
- Living organisms must take in energy via food, nutrients, or sunlight in order to carry out cellular processes.
- The transport, synthesis, and breakdown of nutrients and molecules in a cell require the use of energy.

Key Terms

- **metabolism**: the complete set of chemical reactions that occur in living cells
- **bioenergetics**: the study of the energy transformations that take place in living organisms
- **energy**: the capacity to do work

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6.1.2: Types of Energy

Learning Objectives

- Differentiate between types of energy

Energy is a property of objects which can be transferred to other objects or converted into different forms, but cannot be created or destroyed. Organisms use energy to survive, grow, respond to stimuli, reproduce, and for every type of biological process. The potential energy stored in molecules can be converted to chemical energy, which can ultimately be converted to kinetic energy, enabling an organism to move. Eventually, most of energy used by organisms is transformed into heat and dissipated.

Kinetic Energy

Energy associated with objects in motion is called kinetic energy. For example, when an airplane is in flight, the airplane is moving through air very quickly—doing work to enact change on its surroundings. The jet engines are converting potential energy in fuel to the kinetic energy of movement. A wrecking ball can perform a large amount of damage, even when moving slowly. However, a still wrecking ball cannot perform any work and therefore has no kinetic energy. A speeding bullet, a walking person, the rapid movement of molecules in the air that produces heat, and electromagnetic radiation, such as sunlight, all have kinetic energy.

Potential Energy

What if that same motionless wrecking ball is lifted two stories above a car with a crane? If the suspended wrecking ball is not moving, is there energy associated with it? Yes, the wrecking ball has energy because the wrecking ball has the potential to do work. This form of energy is called potential energy because it is possible for that object to do work in a given state.

Objects transfer their energy between potential and kinetic states. As the wrecking ball hangs motionlessly, it has 0%0% kinetic and 100%100%potential energy. Once the ball is released, its kinetic energy increases as the ball picks up speed. At the same time, the ball loses potential energy as it nears the ground. Other examples of potential energy include the energy of water held behind a dam or a person about to skydive out of an airplane.



Figure **6.1.2.1**: Potential energy vs. kinetic energy: Water behind a dam has potential energy. Moving water, such as in a waterfall or a rapidly flowing river, has kinetic energy.

Chemical Energy

Potential energy is not only associated with the location of matter, but also with the structure of matter. A spring on the ground has potential energy if it is compressed, as does a rubber band that is pulled taut. The same principle applies to molecules. On a chemical level, the bonds that hold the atoms of molecules together have potential energy. This type of potential energy is called chemical energy, and like all potential energy, it can be used to do work.

For example, chemical energy is contained in the gasoline molecules that are used to power cars. When gas ignites in the engine, the bonds within its molecules are broken, and the energy released is used to drive the pistons. The potential energy stored within chemical bonds can be harnessed to perform work for biological processes. Different metabolic processes break down organic molecules to release the energy for an organism to grow and survive.

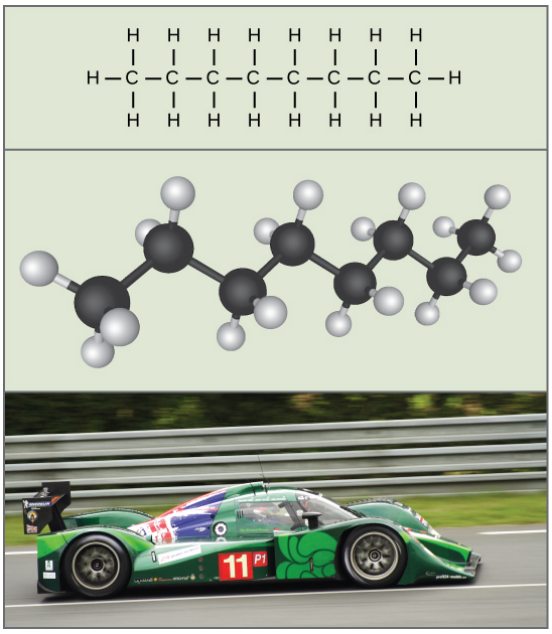


Figure **6.1.2.1**: Chemical energy: The molecules in gasoline (octane, the chemical formula shown) contain chemical energy. This energy is transformed into kinetic energy that allows a car to race on a racetrack.

Key Points

- All organisms use different forms of energy to power the biological processes that allow them to grow and survive.
- Kinetic energy is the energy associated with objects in motion.
- Potential energy is the type of energy associated with an object's potential to do work.
- Chemical energy is the type of energy released from the breakdown of chemical bonds and can be harnessed for metabolic processes.

Key Terms

- **chemical energy**: The net potential energy liberated or absorbed during the course of a chemical reaction.
- **potential energy**: Energy possessed by an object because of its position (in a gravitational or electric field), or its condition (as a stretched or compressed spring, as a chemical reactant, or by having rest mass).
- **kinetic energy**: The energy possessed by an object because of its motion, equal to one half the mass of the body times the square of its velocity.

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SECTION OVERVIEW

6.2: The Laws of Thermodynamics and Free Energy

6.2.1: Free Energy

6.2.2: The First Law of Thermodynamics

6.2.3: The Second Law of Thermodynamics

6.2.4: Activation Energy

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6.2.1: Free Energy

Learning Objectives

- Discuss the concept of free energy.

Free Energy

Since chemical reactions release energy when energy-storing bonds are broken, how is the energy associated with chemical reactions quantified and expressed? How can the energy released from one reaction be compared to that of another reaction?

A measurement of free energy is used to quantitate these energy transfers. Free energy is called Gibbs free energy (G) after Josiah Willard Gibbs, the scientist who developed the measurement. Recall that according to the second law of thermodynamics, all energy transfers involve the loss of some amount of energy in an unusable form such as heat, resulting in entropy. Gibbs free energy specifically refers to the energy associated with a chemical reaction that is available after accounting for entropy. In other words, Gibbs free energy is usable energy or energy that is available to do work.

Calculating ΔG

Every chemical reaction involves a change in free energy, called delta G (ΔG). The change in free energy can be calculated for any system that undergoes a change, such as a chemical reaction. To calculate ΔG, subtract the amount of energy lost to entropy (denoted as ΔS) from the total energy change of the system. This total energy change in the system is called enthalpy and is denoted as ΔH. The formula for calculating ΔG is as follows, where the symbol T refers to absolute temperature in Kelvin (degrees Celsius + 273): $G=\Delta H-T\Delta S$.

The standard free energy change of a chemical reaction is expressed as an amount of energy per mole of the reaction product (either in kilojoules or kilocalories, kJ/mol or kcal/mol; 1 kJ = 0.239 kcal) under standard pH, temperature, and pressure conditions. Standard pH, temperature, and pressure conditions are generally calculated at pH 7.0 in biological systems, 25 degrees Celsius, and 100 kilopascals (1 atm pressure), respectively. It is important to note that cellular conditions vary considerably from these standard conditions; therefore, standard calculated ΔG values for biological reactions will be different inside the cell.

Endergonic and Exergonic Reactions

If energy is released during a chemical reaction, then the resulting value from the above equation will be a negative number. In other words, reactions that release energy have a $\Delta G < 0$. A negative ΔG also means that the products of the reaction have less free energy than the reactants because they gave off some free energy during the reaction. Reactions that have a negative ΔG and, consequently, release free energy, are called exergonic reactions. Exergonic means energy is exiting the system. These reactions are also referred to as spontaneous reactions because they can occur without the addition of energy into the system. Understanding which chemical reactions are spontaneous and release free energy is extremely useful for biologists because these reactions can be harnessed to perform work inside the cell. An important distinction must be drawn between the term spontaneous and the idea of a chemical reaction that occurs immediately. Contrary to the everyday use of the term, a spontaneous reaction is not one that suddenly or quickly occurs. The rusting of iron is an example of a spontaneous reaction that occurs slowly, little by little, over time.

If a chemical reaction requires an input of energy rather than releasing energy, then the ΔG for that reaction will be a positive value. In this case, the products have more free energy than the reactants. Thus, the products of these reactions can be thought of as energy-storing molecules. These chemical reactions are called endergonic reactions; they are non-spontaneous. An endergonic reaction will not take place on its own without the addition of free energy.

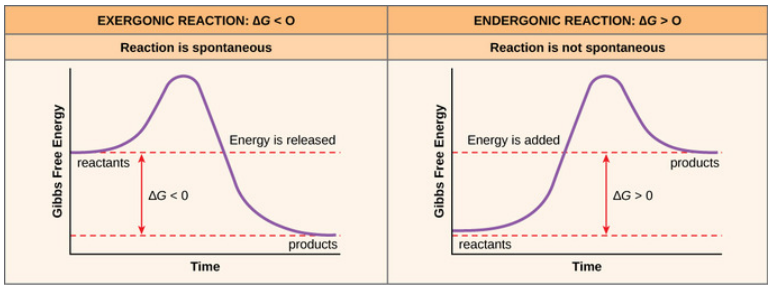


Figure **6.2.1.1**: Exergonic and Endergonic Reactions: Exergonic and endergonic reactions result in changes in Gibbs free energy. Exergonic reactions release energy; endergonic reactions require energy to proceed.

Free Energy and Biological Processes

In a living cell, chemical reactions are constantly moving towards equilibrium, but never reach it. A living cell is an open system: materials pass in and out, the cell recycles the products of certain chemical reactions into other reactions, and chemical equilibrium is never reached. In this way, living organisms are in a constant energy-requiring, uphill battle against equilibrium and entropy.

When complex molecules, such as starches, are built from simpler molecules, such as sugars, the anabolic process requires energy. Therefore, the chemical reactions involved in anabolic processes are endergonic reactions. On the other hand, the catabolic process of breaking sugar down into simpler molecules releases energy in a series of exergonic reactions. As in the example of rust above, the breakdown of sugar involves spontaneous reactions, but these reactions don't occur instantaneously. An important concept in the study of metabolism and energy is that of chemical equilibrium. Most chemical reactions are reversible. They can proceed in both directions, releasing energy into their environment in one direction, and absorbing it from the environment in the other direction.



Figure **6.2.1.1**: Endergonic and Exergonic Processes: Shown are some examples of endergonic processes (ones that require energy) and exergonic processes (ones that release energy). These include (a) a compost pile decomposing, (b) a chick hatching from a fertilized egg, (c) sand art being destroyed, and (d) a ball rolling down a hill.

Key Points

- Every chemical reaction involves a change in free energy, called delta G (ΔG).
- To calculate ΔG, subtract the amount of energy lost to entropy (ΔS) from the total energy change of the system; this total energy change in the system is called enthalpy (ΔH): $\Delta G = \Delta H - T\Delta S$.
- Endergonic reactions require an input of energy; the ΔG for that reaction will be a positive value.
- Exergonic reactions release free energy; the ΔG for that reaction will be a negative value.

Key Terms

- **exergonic reaction**: A chemical reaction where the change in the Gibbs free energy is negative, indicating a spontaneous reaction
- **endergonic reaction**: A chemical reaction in which the standard change in free energy is positive, and energy is absorbed
- **Gibbs free energy**: The difference between the enthalpy of a system and the product of its entropy and absolute temperature

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6.2.2: The First Law of Thermodynamics

Learning Objectives

- Describe the first law of thermodynamics

Thermodynamics is the study of heat energy and other types of energy, such as work, and the various ways energy is transferred within chemical systems. “Thermo-” refers to heat, while “dynamics” refers to motion.

The First Law of Thermodynamics

The first law of thermodynamics deals with the total amount of energy in the universe. The law states that this total amount of energy is constant. In other words, there has always been, and always will be, exactly the same amount of energy in the universe.

Energy exists in many different forms. According to the first law of thermodynamics, energy can be transferred from place to place or changed between different forms, but it cannot be created or destroyed. The transfers and transformations of energy take place around us all the time. For instance, light bulbs transform electrical energy into light energy, and gas stoves transform chemical energy from natural gas into heat energy. Plants perform one of the most biologically useful transformations of energy on Earth: they convert the energy of sunlight into the chemical energy stored within organic molecules.

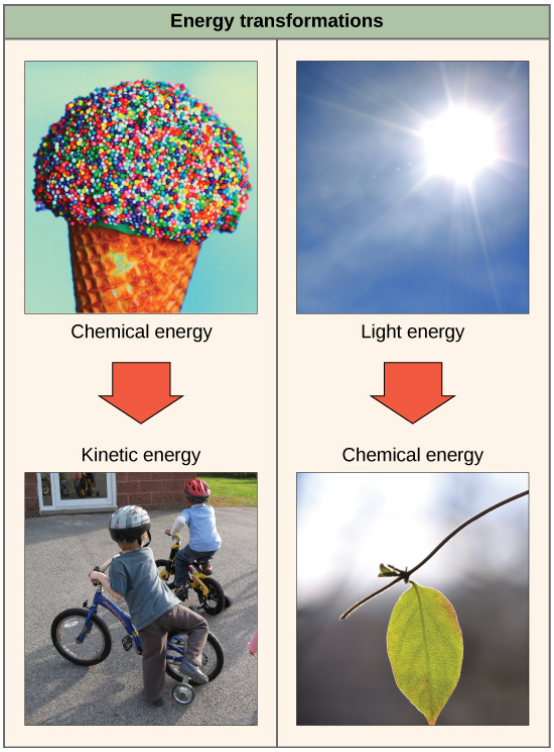


Figure **6.2.2.1**: The first law of thermodynamics: Shown are two examples of energy being transferred from one system to another and transformed from one form to another. Humans can convert the chemical energy in food, like this ice cream cone, into kinetic energy by riding a bicycle. Plants can convert electromagnetic radiation (light energy) from the sun into chemical energy.

The System and Surroundings

Thermodynamics often divides the universe into two categories: the system and its surroundings. In chemistry, the system almost always refers to a given chemical reaction and the container in which it takes place. The first law of thermodynamics tells us that energy can neither be created nor destroyed, so we know that the energy that is absorbed in an endothermic chemical reaction must have been lost from the surroundings. Conversely, in an exothermic reaction, the heat that is released in the reaction is given off and absorbed by the surroundings. Stated mathematically, we have:

$\Delta E = \Delta E_{sys} + \Delta E_{surr} = 0$

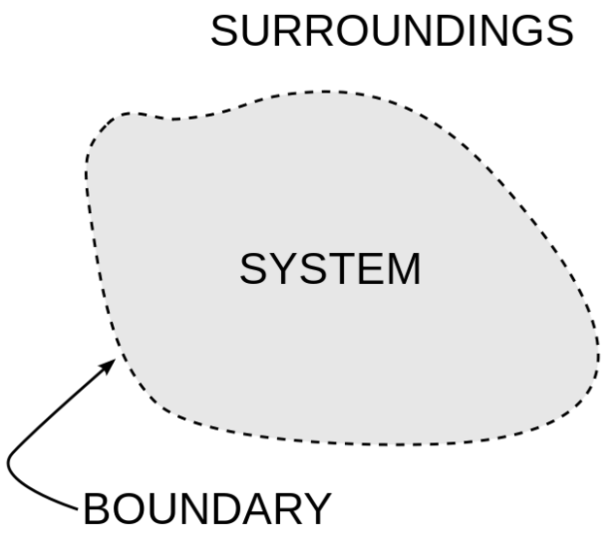


Figure **6.2.2.1**: The system and surroundings: A basic diagram showing the fundamental distinction between the system and its surroundings in thermodynamics.

Heat and Work

We know that chemical systems can either absorb heat from their surroundings, if the reaction is endothermic, or release heat to their surroundings, if the reaction is exothermic. However, chemical reactions are often used to do work instead of just exchanging heat. For instance, when rocket fuel burns and causes a space shuttle to lift off from the ground, the chemical reaction, by propelling the rocket, is doing work by applying a force over a distance.

If you've ever witnessed a video of a space shuttle lifting off, the chemical reaction that occurs also releases tremendous amounts of heat and light. Another useful form of the first law of thermodynamics relates heat and work for the change in energy of the internal system:

$$\Delta E_{sys}=Q+W$$

While this formulation is more commonly used in physics, it is still important to know for chemistry.



Figure **6.2.2.1**: Rocket launch: The powerful chemical reaction propelling the rocket lets off tremendous heat to the surroundings and does work on the surroundings (the rocket) as well.

Key Points

- According to the first law of thermodynamics, the total amount of energy in the universe is constant.
- Energy can be transferred from place to place or transformed into different forms, but it cannot be created or destroyed.

- Living organisms have evolved to obtain energy from their surroundings in forms that they can transfer or transform into usable energy to do work.

Key Terms

- **first law of thermodynamics**: A version of the law of conservation of energy, specialized for thermodynamical systems, that states that the energy of an isolated system is constant and can neither be created nor destroyed.
- **work**: A measure of energy expended by moving an object, usually considered to be force times distance. No work is done if the object does not move.

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6.2.3: The Second Law of Thermodynamics

Learning Objectives

- Explain how living organisms can increase their order despite the second law of thermodynamics

The Second Law of Thermodynamics

A living cell ‘s primary tasks of obtaining, transforming, and using energy to do work may seem simple enough, but they are more problematic than they appear. The second law of thermodynamics explains why: No energy transfers or transformations in the universe are completely efficient. In every energy transfer, some amount of energy is lost in a form that is unusable. In most cases, this energy is in the form of heat. Thermodynamically, heat energy is defined as the energy transferred from one system to another that is not doing work. For example, when an airplane flies through the air, some of the energy of the flying plane is lost as heat energy due to friction with the surrounding air. This friction heats the air by temporarily increasing the speed of air molecules. Likewise, some energy is lost in the form of heat during cellular metabolic reactions. This is good for warm-blooded creatures like us because heat energy helps to maintain our body temperature. Strictly speaking, no energy transfer is completely efficient because some energy is lost in an unusable form.

Entropy

An important concept in physical systems is disorder (also known as randomness). The more energy that is lost by a system to its surroundings, the less ordered and more random the system is. Scientists define the measure of randomness or disorder within a system as entropy. High entropy means high disorder and low energy. To better understand entropy, remember that it requires energy to maintain structure. For example, think about an ice cube. It is made of water molecules bound together in an orderly lattice. This arrangement takes energy to maintain. When the ice cube melts and becomes water, its molecules are more disordered, in a random arrangement as opposed to a structure. Overall, there is less energy in the system inside the molecular bonds. Therefore, water can be said to have greater entropy than ice.

This holds true for solids, liquids, and gases in general. Solids have the highest internal energy holding them together and therefore the lowest entropy. Liquids are more disordered and it takes less energy to hold them together. Therefore they are higher in entropy than solids, but lower than gases, which are so disordered that they have the highest entropy and lowest amount of energy spent holding them together.

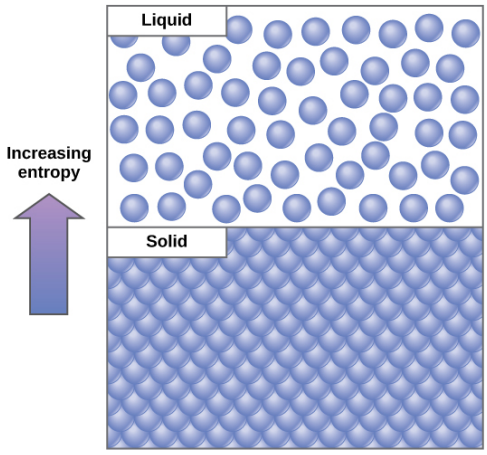


Figure **6.2.3.1**: Entropy: Entropy is a measure of randomness or disorder in a system. Gases have higher entropy than liquids, and liquids have higher entropy than solids.

Entropy changes also occur in chemical reactions. In an exergonic chemical reaction where energy is released, entropy increases because the final products have less energy inside them holding their chemical bonds together. That energy has been lost to the environment, usually in the form of heat.

All physical systems can be thought of in this way. Living things are highly ordered, requiring constant energy input to be maintained in a state of low entropy. As living systems take in energy-storing molecules and transform them through chemical

reactions, they lose some amount of usable energy in the process because no reaction is completely efficient. They also produce waste and by-products that are not useful energy sources. This process increases the entropy of the system's surroundings. Since all energy transfers result in the loss of some usable energy, the second law of thermodynamics states that every energy transfer or transformation increases the entropy of the universe. Even though living things are highly ordered and maintain a state of low entropy, the entropy of the universe in total is constantly increasing due to the loss of usable energy with each energy transfer that occurs. Essentially, living things are in a continuous uphill battle against this constant increase in universal entropy.

Key Points

- During energy transfer, some amount of energy is lost in the form of unusable heat energy.
- Because energy is lost in an unusable form, no energy transfer is completely efficient.
- The more energy that is lost by a system to its surroundings, the less ordered and more random the system is.
- Entropy is a measure of randomness and disorder; high entropy means high disorder and low energy.
- As chemical reactions reach a state of equilibrium, entropy increases; and as molecules at a high concentration in one place diffuse and spread out, entropy also increases.

Key Terms

- **second law of thermodynamics**: Every energy transfer or transformation increases the entropy of the universe since all energy transfers result in the loss of some usable energy.
- **entropy**: A measure of randomness and disorder in a system.

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6.2.4: Activation Energy

Learning Objectives

- Discuss the concept of activation energy

Many chemical reactions, and almost all biochemical reactions do not occur spontaneously and must have an initial input of energy (called the activation energy) to get started. Activation energy must be considered when analyzing both endergonic and exergonic reactions. Exergonic reactions have a net release of energy, but they still require a small amount of energy input before they can proceed with their energy-releasing steps. This small amount of energy input necessary for all chemical reactions to occur is called the activation energy (or free energy of activation) and is abbreviated E_A.

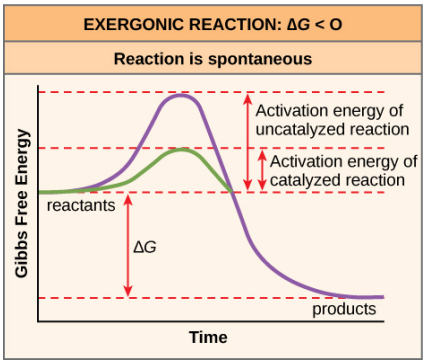


Figure **6.2.4.1**: Activation energy: Activation energy is the energy required for a reaction to proceed; it is lower if the reaction is catalyzed. The horizontal axis of this diagram describes the sequence of events in time.

Activation Energy in Chemical Reactions

Why would an energy-releasing, negative ΔG reaction actually require some energy to proceed? The reason lies in the steps that take place during a chemical reaction. During chemical reactions, certain chemical bonds are broken and new ones are formed. For example, when a glucose molecule is broken down, bonds between the carbon atoms of the molecule are broken. Since these are energy-storing bonds, they release energy when broken. However, to get them into a state that allows the bonds to break, the molecule must be somewhat contorted. A small energy input is required to achieve this contorted state, which is called the *transition state*: it is a high-energy, unstable state. For this reason, reactant molecules don't last long in their transition state, but very quickly proceed to the next steps of the chemical reaction.

Cells will at times couple an exergonic reaction ($\Delta G<0$) with endergonic reactions ($\Delta G>0$), allowing them to proceed. This spontaneous shift from one reaction to another is called energy coupling. The free energy released from the exergonic reaction is absorbed by the
endergonic reaction. One example of energy coupling using ATP involves a transmembrane ion pump that is extremely important for cellular function.

Free Energy Diagrams

Free energy diagrams illustrate the energy profiles for a given reaction. Whether the reaction is exergonic ($\Delta G<0$) or endergonic ($\Delta G>0$) determines whether the products in the diagram will exist at a lower or higher energy state than the reactants. However, the measure of the activation energy is *independent* of the reaction's ΔG. In other words, at a given temperature, the activation energy depends on the nature of the chemical transformation that takes place, but not on the relative energy state of the reactants and products.

Although the image above discusses the concept of activation energy within the context of the exergonic forward reaction, the same principles apply to the reverse reaction, which must be endergonic. Notice that the activation energy for the reverse reaction is larger than for the forward reaction.

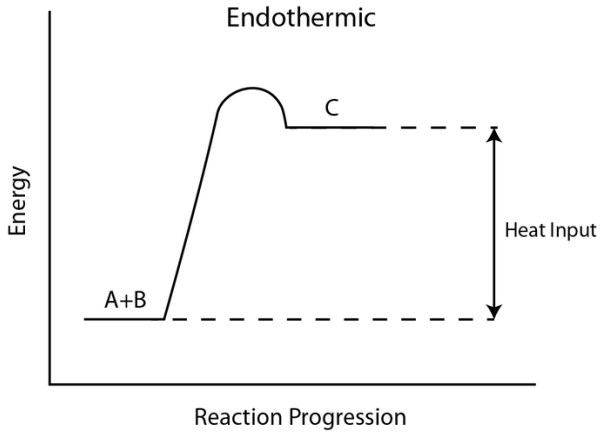


Figure **6.2.4.1**: Activation energy in an endergonic reaction: In this endergonic reaction, activation energy is still required to transform the reactants A + B into the product C. This figure implies that the activation energy is in the form of heat energy.

Heat Energy

The source of the activation energy needed to push reactions forward is typically heat energy from the surroundings. Heat energy (the total bond energy of reactants or products in a chemical reaction) speeds up the motion of molecules, increasing the frequency and force with which they collide. It also moves atoms and bonds within the molecule slightly, helping them reach their transition state. For this reason, heating up a system will cause chemical reactants within that system to react more frequently. Increasing the pressure on a system has the same effect. Once reactants have absorbed enough heat energy from their surroundings to reach the transition state, the reaction will proceed.

The activation energy of a particular reaction determines the rate at which it will proceed. The higher the activation energy, the slower the chemical reaction will be. The example of iron rusting illustrates an inherently slow reaction. This reaction occurs slowly over time because of its high E_A. Additionally, the burning of many fuels, which is strongly exergonic, will take place at a negligible rate unless their activation energy is overcome by sufficient heat from a spark. Once they begin to burn, however, the chemical reactions release enough heat to continue the burning process, supplying the activation energy for surrounding fuel molecules.

Like these reactions outside of cells, the activation energy for most cellular reactions is too high for heat energy to overcome at efficient rates. In other words, in order for important cellular reactions to occur at significant rates (number of reactions per unit time), their activation energies must be lowered; this is referred to as catalysis. This is a very good thing as far as living cells are concerned. Important macromolecules, such as proteins, DNA, and RNA, store considerable energy, and their breakdown is exergonic. If cellular temperatures alone provided enough heat energy for these exergonic reactions to overcome their activation barriers, the essential components of a cell would disintegrate.

The Arrhenius Equation

The Arrhenius equations relates the rate of a chemical reaction to the magnitude of the activation energy:

$$k=Ae^{E_a/RT}$$

where

- k is the reaction rate coefficient or constant
- A is the frequency factor of the reaction. It is determined experimentally.
- R is the Universal Gas constant
- T is the temperature in Kelvin

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Key Points

- Reactions require an input of energy to initiate the reaction; this is called the activation energy (E_A).
- Activation energy is the amount of energy required to reach the transition state.
- The source of the activation energy needed to push reactions forward is typically heat energy from the surroundings.
- For cellular reactions to occur fast enough over short time scales, their activation energies are lowered by molecules called catalysts.
- Enzymes are catalysts.

Key Terms

- **activation energy**: The minimum energy required for a reaction to occur.
- **catalysis**: The increase in the rate of a chemical reaction by lowering its activation energy.
- **transition state**: An intermediate state during a chemical reaction that has a higher energy than the reactants or the products.

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6.3: Adenosine Triphosphate -ATP The Energy Currency of Cells

Skills to Develop

- Explain the role of ATP as the cellular energy currency
- Describe how energy is released through hydrolysis of ATP

Even exergonic, energy-releasing reactions require a small amount of activation energy in order to proceed. However, consider endergonic reactions, which require much more energy input, because their products have more free energy than their reactants. Within the cell, where does energy to power such reactions come from? The answer lies with an energy-supplying molecule called adenosine triphosphate, or ATP. ATP is a small, relatively simple molecule (Figure **6.3.1**), but within some of its bonds, it contains the potential for a quick burst of energy that can be harnessed to perform cellular work. This molecule can be thought of as the primary energy currency of cells in much the same way that money is the currency that people exchange for things they need. ATP is used to power the majority of energy-requiring cellular reactions.

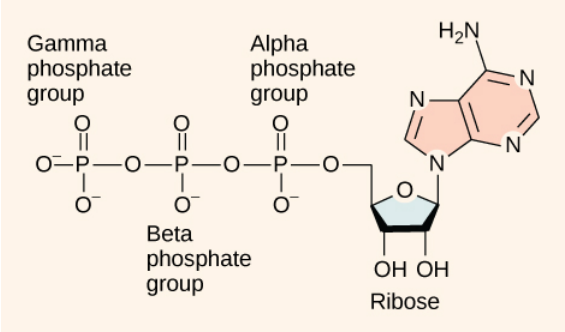


Figure **6.3.1**: ATP is the primary energy currency of the cell. It has an adenosine backbone with three phosphate groups attached.

As its name suggests, adenosine triphosphate is comprised of adenosine bound to three phosphate groups (Figure **6.3.1**). Adenosine is a nucleoside consisting of the nitrogenous base adenine and a five-carbon sugar, ribose. The three phosphate groups, in order of closest to furthest from the ribose sugar, are labeled alpha, beta, and gamma. Together, these chemical groups constitute an energy powerhouse. However, not all bonds within this molecule exist in a particularly high-energy state. Both bonds that link the phosphates are equally high-energy bonds (phosphoanhydride bonds) that, when broken, release sufficient energy to power a variety of cellular reactions and processes. These high-energy bonds are the bonds between the second and third (or beta and gamma) phosphate groups and between the first and second phosphate groups. The reason that these bonds are considered "high-energy" is because the products of such bond breaking—adenosine diphosphate (ADP) and one inorganic phosphate group (P_i)—have considerably lower free energy than the reactants: ATP and a water molecule. Because this reaction takes place with the use of a water molecule, it is considered a hydrolysis reaction. In other words, ATP is hydrolyzed into ADP in the following reaction:

$$\mathbf{ATP + H_2O \rightarrow ADP + P_i + free\ energy}$$

Like most chemical reactions, the hydrolysis of ATP to ADP is reversible. The reverse reaction regenerates ATP from ADP + P_i. Indeed, cells rely on the regeneration of ATP just as people rely on the regeneration of spent money through some sort of income. Since ATP hydrolysis releases energy, ATP regeneration must require an input of free energy. The formation of ATP is expressed in this equation:

$$\mathbf{ADP + P_i + free\ energy \rightarrow ATP + H_2O}$$

Two prominent questions remain with regard to the use of ATP as an energy source. Exactly how much free energy is released with the hydrolysis of ATP, and how is that free energy used to do cellular work? The calculated ΔG for the hydrolysis of one mole of ATP into ADP and P_i is −7.3 kcal/mole (−30.5 kJ/mol). Since this calculation is true under standard conditions, it would be expected that a different value exists under cellular conditions. In fact, the ΔG for the hydrolysis of one mole of ATP in a living cell is almost double the value at standard conditions: 14 kcal/mol (−57 kJ/mol).

ATP is a highly unstable molecule. Unless quickly used to perform work, ATP spontaneously dissociates into ADP + P_i, and the free energy released during this process is lost as heat. The second question posed above, that is, how the energy released by ATP

hydrolysis is used to perform work inside the cell, depends on a strategy called energy coupling. Cells couple the exergonic reaction of ATP hydrolysis with endergonic reactions, allowing them to proceed. One example of energy coupling using ATP involves a transmembrane ion pump that is extremely important for cellular function. This sodium-potassium pump (Na^+/K^+ pump) drives sodium out of the cell and potassium into the cell (Figure **6.3.2**). A large percentage of a cell's ATP is spent powering this pump, because cellular processes bring a great deal of sodium into the cell and potassium out of the cell. The pump works constantly to stabilize cellular concentrations of sodium and potassium. In order for the pump to turn one cycle (exporting three Na^+ ions and importing two K^+ ions), one molecule of ATP must be hydrolyzed. When ATP is hydrolyzed, its gamma phosphate doesn't simply float away, but is actually transferred onto the pump protein. This process of a phosphate group binding to a molecule is called phosphorylation. As with most cases of ATP hydrolysis, a phosphate from ATP is transferred onto another molecule. In a phosphorylated state, the Na^+/K^+ pump has more free energy and is triggered to undergo a conformational change. This change allows it to release Na^+ to the outside of the cell. It then binds extracellular K^+, which, through another conformational change, causes the phosphate to detach from the pump. This release of phosphate triggers the K^+ to be released to the inside of the cell. Essentially, the energy released from the hydrolysis of ATP is coupled with the energy required to power the pump and transport Na^+ and K^+ ions. ATP performs cellular work using this basic form of energy coupling through phosphorylation.

Art Connection

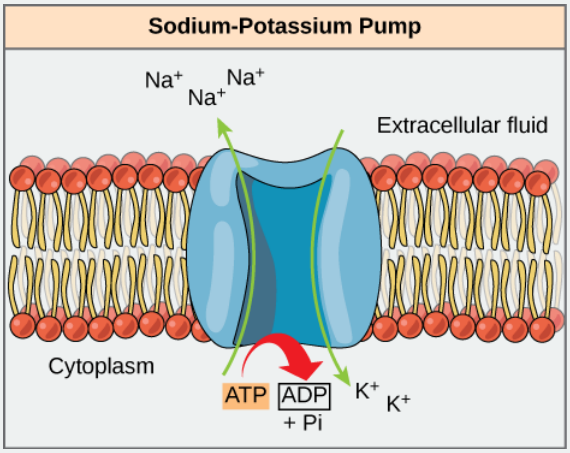


Figure **6.3.2**: The sodium-potassium pump is an example of energy coupling. The energy derived from exergonic ATP hydrolysis is used to pump sodium and potassium ions across the cell membrane.

The hydrolysis of one ATP molecule releases 7.3 kcal/mol of energy ($\Delta G = -7.3$ kcal/mol of energy). If it takes 2.1 kcal/mol of energy to move one Na^+ across the membrane ($\Delta G = +2.1$ kcal/mol of energy), how many sodium ions could be moved by the hydrolysis of one ATP molecule?

Often during cellular metabolic reactions, such as the synthesis and breakdown of nutrients, certain molecules must be altered slightly in their conformation to become substrates for the next step in the reaction series. One example is during the very first steps of cellular respiration, when a molecule of the sugar glucose is broken down in the process of glycolysis. In the first step of this process, ATP is required for the phosphorylation of glucose, creating a high-energy but unstable intermediate. This phosphorylation reaction powers a conformational change that allows the phosphorylated glucose molecule to be converted to the phosphorylated sugar fructose. Fructose is a necessary intermediate for glycolysis to move forward. Here, the exergonic reaction of ATP hydrolysis is coupled with the endergonic reaction of converting glucose into a phosphorylated intermediate in the pathway. Once again, the energy released by breaking a phosphate bond within ATP was used for the phosphorylation of another molecule, creating an unstable intermediate and powering an important conformational change.

Link to Learning



See an interactive animation of the ATP-producing glycolysis process at this site.

Summary

ATP is the primary energy-supplying molecule for living cells. ATP is made up of a nucleotide, a five-carbon sugar, and three phosphate groups. The bonds that connect the phosphates (phosphoanhydride bonds) have high-energy content. The energy released from the hydrolysis of ATP into ADP + P_i is used to perform cellular work. Cells use ATP to perform work by coupling the exergonic reaction of ATP hydrolysis with endergonic reactions. ATP donates its phosphate group to another molecule via a process known as phosphorylation. The phosphorylated molecule is at a higher-energy state and is less stable than its unphosphorylated form, and this added energy from the addition of the phosphate allows the molecule to undergo its endergonic reaction.

Art Connections

Figure **6.3.2**: The hydrolysis of one ATP molecule releases 7.3 kcal/mol of energy (ΔG = −7.3 kcal/mol of energy). If it takes 2.1 kcal/mol of energy to move one Na^+ across the membrane (ΔG = +2.1 kcal/mol of energy), how many sodium ions could be moved by the hydrolysis of one ATP molecule?

Answer

Three sodium ions could be moved by the hydrolysis of one ATP molecule. The ΔG of the coupled reaction must be negative. Movement of three sodium ions across the membrane will take 6.3 kcal of energy (2.1 kcal × 3 Na^+ ions = 6.3 kcal). Hydrolysis of ATP provides 7.3 kcal of energy, more than enough to power this reaction. Movement of four sodium ions across the membrane, however, would require 8.4 kcal of energy, more than one ATP molecule can provide.

Glossary

ATP

adenosine triphosphate, the cell’s energy currency

phosphoanhydride bond

bond that connects phosphates in an ATP molecule

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6.4: Enzymes- Biological Catalysts

Skills to Develop

- Describe the role of enzymes in metabolic pathways
- Explain how enzymes function as molecular catalysts
- Discuss enzyme regulation by various factors

A substance that helps a chemical reaction to occur is a catalyst, and the special molecules that catalyze biochemical reactions are called enzymes. Almost all enzymes are proteins, made up of chains of amino acids, and they perform the critical task of lowering the activation energies of chemical reactions inside the cell. Enzymes do this by binding to the reactant molecules, and holding them in such a way as to make the chemical bond-breaking and bond-forming processes take place more readily. It is important to remember that enzymes don't change the ΔG of a reaction. In other words, they don't change whether a reaction is exergonic (spontaneous) or endergonic. This is because they don't change the free energy of the reactants or products. They only reduce the activation energy required to reach the transition state (Figure **6.4.1**).

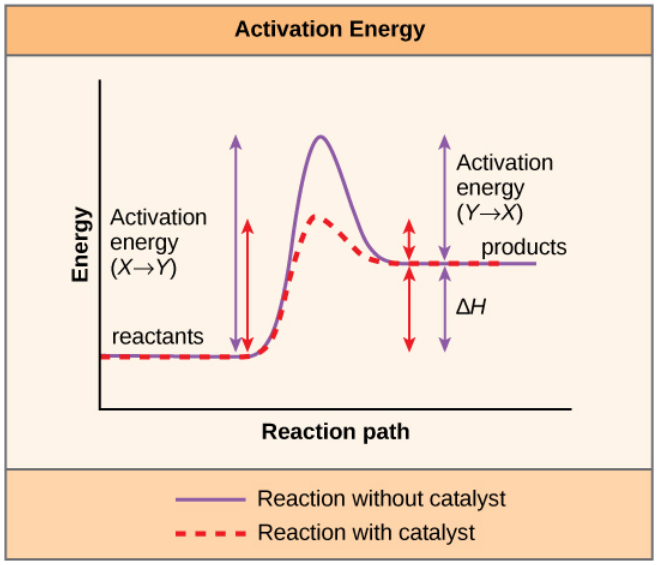


Figure **6.4.1**: Enzymes lower the activation energy of the reaction but do not change the free energy of the reaction.

Enzyme Active Site and Substrate Specificity

The chemical reactants to which an enzyme binds are the enzyme's substrates. There may be one or more substrates, depending on the particular chemical reaction. In some reactions, a single-reactant substrate is broken down into multiple products. In others, two substrates may come together to create one larger molecule. Two reactants might also enter a reaction, both become modified, and leave the reaction as two products. The location within the enzyme where the substrate binds is called the enzyme's active site. The active site is where the "action" happens, so to speak. Since enzymes are proteins, there is a unique combination of amino acid residues (also called side chains, or R groups) within the active site. Each residue is characterized by different properties. Residues can be large or small, weakly acidic or basic, hydrophilic or hydrophobic, positively or negatively charged, or neutral. The unique combination of amino acid residues, their positions, sequences, structures, and properties, creates a very specific chemical environment within the active site. This specific environment is suited to bind, albeit briefly, to a specific chemical substrate (or substrates). Due to this jigsaw puzzle-like match between an enzyme and its substrates (which adapts to find the best fit between the transition state and the active site), enzymes are known for their specificity. The "best fit" results from the shape and the amino acid functional group's attraction to the substrate. There is a specifically matched enzyme for each substrate and, thus, for each chemical reaction; however, there is flexibility as well.

The fact that active sites are so perfectly suited to provide specific environmental conditions also means that they are subject to influences by the local environment. It is true that increasing the environmental temperature generally increases reaction rates, enzyme-catalyzed or otherwise. However, increasing or decreasing the temperature outside of an optimal range can affect chemical

bonds within the active site in such a way that they are less well suited to bind substrates. High temperatures will eventually cause enzymes, like other biological molecules, to denature, a process that changes the natural properties of a substance. Likewise, the pH of the local environment can also affect enzyme function. Active site amino acid residues have their own acidic or basic properties that are optimal for catalysis. These residues are sensitive to changes in pH that can impair the way substrate molecules bind. Enzymes are suited to function best within a certain pH range, and, as with temperature, extreme pH values (acidic or basic) of the environment can cause enzymes to denature.

Induced Fit and Enzyme Function

For many years, scientists thought that enzyme-substrate binding took place in a simple "lock-and-key" fashion. This model asserted that the enzyme and substrate fit together perfectly in one instantaneous step. However, current research supports a more refined view called induced fit (Figure **6.4.2**). The induced-fit model expands upon the lock-and-key model by describing a more dynamic interaction between enzyme and substrate. As the enzyme and substrate come together, their interaction causes a mild shift in the enzyme's structure that confirms an ideal binding arrangement between the enzyme and the transition state of the substrate. This ideal binding maximizes the enzyme's ability to catalyze its reaction.

When an enzyme binds its substrate, an enzyme-substrate complex is formed. This complex lowers the activation energy of the reaction and promotes its rapid progression in one of many ways. On a basic level, enzymes promote chemical reactions that involve more than one substrate by bringing the substrates together in an optimal orientation. The appropriate region (atoms and bonds) of one molecule is juxtaposed to the appropriate region of the other molecule with which it must react. Another way in which enzymes promote the reaction of their substrates is by creating an optimal environment within the active site for the reaction to occur. Certain chemical reactions might proceed best in a slightly acidic or non-polar environment. The chemical properties that emerge from the particular arrangement of amino acid residues within an active site create the perfect environment for an enzyme's specific substrates to react.

You've learned that the activation energy required for many reactions includes the energy involved in manipulating or slightly contorting chemical bonds so that they can easily break and allow others to reform. Enzymatic action can aid this process. The enzyme-substrate complex can lower the activation energy by contorting substrate molecules in such a way as to facilitate bond-breaking, helping to reach the transition state. Finally, enzymes can also lower activation energies by taking part in the chemical reaction itself. The amino acid residues can provide certain ions or chemical groups that actually form covalent bonds with substrate molecules as a necessary step of the reaction process. In these cases, it is important to remember that the enzyme will always return to its original state at the completion of the reaction. One of the hallmark properties of enzymes is that they remain ultimately unchanged by the reactions they catalyze. After an enzyme is done catalyzing a reaction, it releases its product(s).

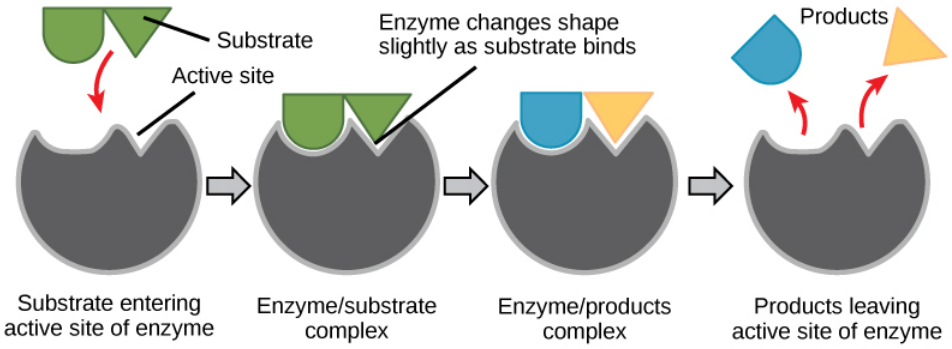


Figure **6.4.2**: According to the induced-fit model, both enzyme and substrate undergo dynamic conformational changes upon binding. The enzyme contorts the substrate into its transition state, thereby increasing the rate of the reaction.

Control of Metabolism Through Enzyme Regulation

It would seem ideal to have a scenario in which all of the enzymes encoded in an organism's genome existed in abundant supply and functioned optimally under all cellular conditions, in all cells, at all times. In reality, this is far from the case. A variety of mechanisms ensure that this does not happen. Cellular needs and conditions vary from cell to cell, and change within individual cells over time. The required enzymes and energetic demands of stomach cells are different from those of fat storage cells, skin

cells, blood cells, and nerve cells. Furthermore, a digestive cell works much harder to process and break down nutrients during the time that closely follows a meal compared with many hours after a meal. As these cellular demands and conditions vary, so do the amounts and functionality of different enzymes.

Since the rates of biochemical reactions are controlled by activation energy, and enzymes lower and determine activation energies for chemical reactions, the relative amounts and functioning of the variety of enzymes within a cell ultimately determine which reactions will proceed and at which rates. This determination is tightly controlled. In certain cellular environments, enzyme activity is partly controlled by environmental factors, like pH and temperature. There are other mechanisms through which cells control the activity of enzymes and determine the rates at which various biochemical reactions will occur.

Regulation of Enzymes by Molecules

Enzymes can be regulated in ways that either promote or reduce their activity. There are many different kinds of molecules that inhibit or promote enzyme function, and various mechanisms exist for doing so. In some cases of enzyme inhibition, for example, an inhibitor molecule is similar enough to a substrate that it can bind to the active site and simply block the substrate from binding. When this happens, the enzyme is inhibited through competitive inhibition, because an inhibitor molecule competes with the substrate for active site binding (Figure **6.4.3**). On the other hand, in noncompetitive inhibition, an inhibitor molecule binds to the enzyme in a location other than an allosteric site and still manages to block substrate binding to the active site.

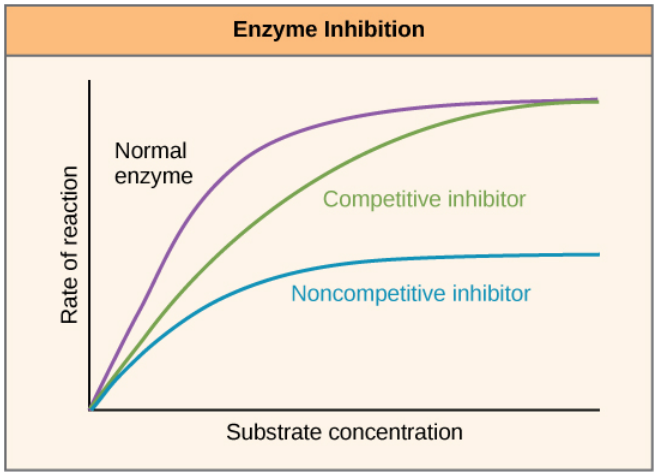


Figure **6.4.3**: Competitive and noncompetitive inhibition affect the rate of reaction differently. Competitive inhibitors affect the initial rate but do not affect the maximal rate, whereas noncompetitive inhibitors affect the maximal rate.

Some inhibitor molecules bind to enzymes in a location where their binding induces a conformational change that reduces the affinity of the enzyme for its substrate. This type of inhibition is called allosteric inhibition (Figure **6.4.4**). Most allosterically regulated enzymes are made up of more than one polypeptide, meaning that they have more than one protein subunit. When an allosteric inhibitor binds to an enzyme, all active sites on the protein subunits are changed slightly such that they bind their substrates with less efficiency. There are allosteric activators as well as inhibitors. Allosteric activators bind to locations on an enzyme away from the active site, inducing a conformational change that increases the affinity of the enzyme's active site(s) for its substrate(s).

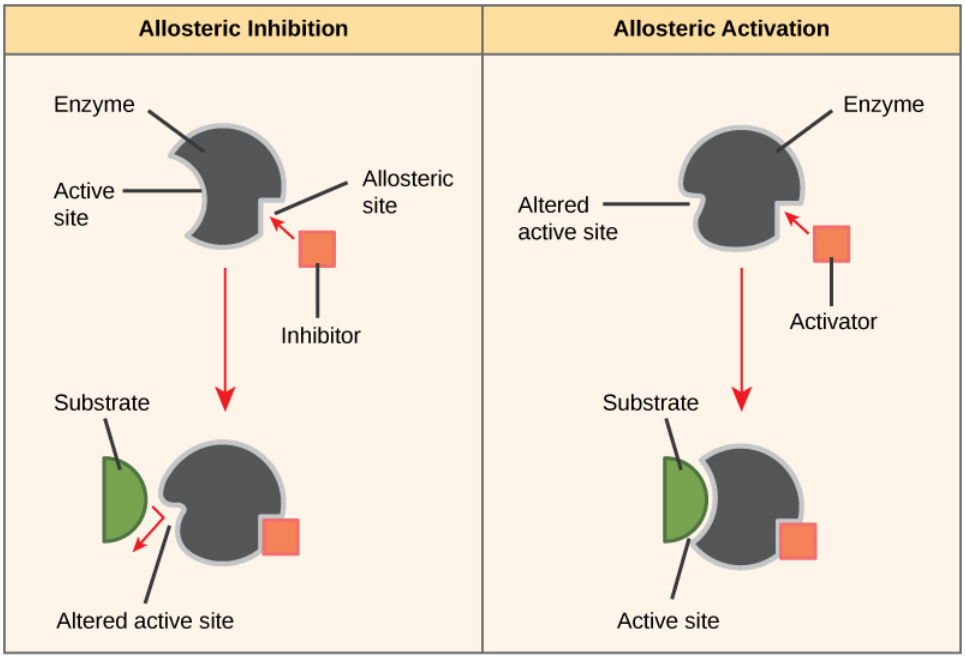


Figure 6.4.4: Allosteric inhibitors modify the active site of the enzyme so that substrate binding is reduced or prevented. In contrast, allosteric activators modify the active site of the enzyme so that the affinity for the substrate increases.

Everyday Connection: Drug Discovery by Looking for Inhibitors of Key Enzymes in Specific Pathways



Figure 6.4.5: Have you ever wondered how pharmaceutical drugs are developed? (credit: Deborah Austin)

Enzymes are key components of metabolic pathways. Understanding how enzymes work and how they can be regulated is a key principle behind the development of many of the pharmaceutical drugs (Figure 6.4.5) on the market today. Biologists working in this field collaborate with other scientists, usually chemists, to design drugs.

Consider statins for example—which is the name given to the class of drugs that reduces cholesterol levels. These compounds are essentially inhibitors of the enzyme HMG-CoA reductase. HMG-CoA reductase is the enzyme that synthesizes cholesterol from lipids in the body. By inhibiting this enzyme, the levels of cholesterol synthesized in the body can be reduced. Similarly, acetaminophen, popularly marketed under the brand name Tylenol, is an inhibitor of the enzyme cyclooxygenase. While it is effective in providing relief from fever and inflammation (pain), its mechanism of action is still not completely understood.

How are drugs developed? One of the first challenges in drug development is identifying the specific molecule that the drug is intended to target. In the case of statins, HMG-CoA reductase is the drug target. Drug targets are identified through painstaking research in the laboratory. Identifying the target alone is not sufficient; scientists also need to know how the target acts inside the cell and which reactions go awry in the case of disease. Once the target and the pathway are identified, then the actual process of drug design begins. During this stage, chemists and biologists work together to design and synthesize molecules that can either block or activate a particular reaction. However, this is only the beginning: both if and when a drug prototype is

successful in performing its function, then it must undergo many tests from in vitro experiments to clinical trials before it can get FDA approval to be on the market.

Many enzymes don't work optimally, or even at all, unless bound to other specific non-protein helper molecules, either temporarily through ionic or hydrogen bonds or permanently through stronger covalent bonds. Two types of helper molecules are cofactors and coenzymes. Binding to these molecules promotes optimal conformation and function for their respective enzymes. Cofactors are inorganic ions such as iron (Fe++) and magnesium (Mg++). One example of an enzyme that requires a metal ion as a cofactor is the enzyme that builds DNA molecules, DNA polymerase, which requires bound zinc ion (Zn++) to function. Coenzymes are organic helper molecules, with a basic atomic structure made up of carbon and hydrogen, which are required for enzyme action. The most common sources of coenzymes are dietary vitamins (Figure **6.4.6**). Some vitamins are precursors to coenzymes and others act directly as coenzymes. Vitamin C is a coenzyme for multiple enzymes that take part in building the important connective tissue component, collagen. An important step in the breakdown of glucose to yield energy is catalysis by a multi-enzyme complex called pyruvate dehydrogenase. Pyruvate dehydrogenase is a complex of several enzymes that actually requires one cofactor (a magnesium ion) and five different organic coenzymes to catalyze its specific chemical reaction. Therefore, enzyme function is, in part, regulated by an abundance of various cofactors and coenzymes, which are supplied primarily by the diets of most organisms.

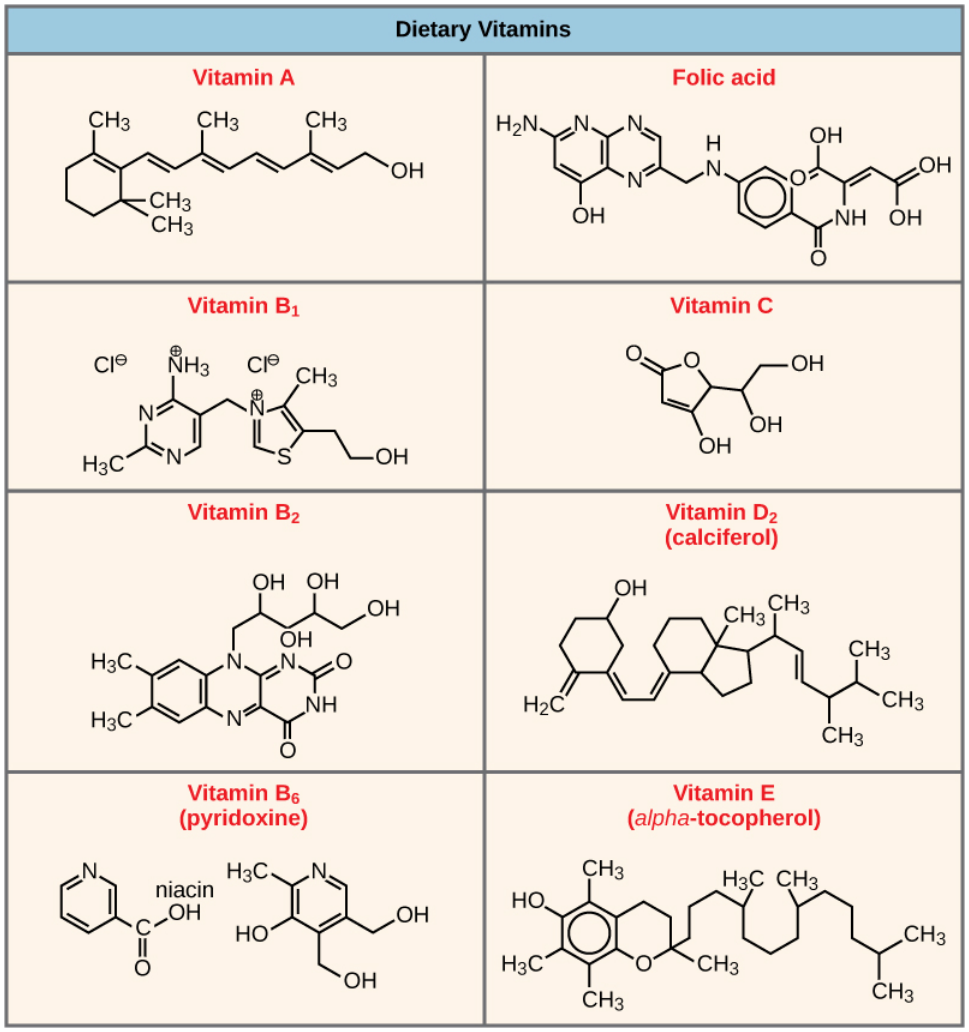


Figure **6.4.6**: Vitamins are important coenzymes or precursors of coenzymes, and are required for enzymes to function properly. Multivitamin capsules usually contain mixtures of all the vitamins at different percentages.

Enzyme Compartmentalization

In eukaryotic cells, molecules such as enzymes are usually compartmentalized into different organelles. This allows for yet another level of regulation of enzyme activity. Enzymes required only for certain cellular processes can be housed separately along with

their substrates, allowing for more efficient chemical reactions. Examples of this sort of enzyme regulation based on location and proximity include the enzymes involved in the latter stages of cellular respiration, which take place exclusively in the mitochondria, and the enzymes involved in the digestion of cellular debris and foreign materials, located within lysosomes.

Feedback Inhibition in Metabolic Pathways

Molecules can regulate enzyme function in many ways. A major question remains, however: What are these molecules and where do they come from? Some are cofactors and coenzymes, ions, and organic molecules, as you've learned. What other molecules in the cell provide enzymatic regulation, such as allosteric modulation, and competitive and noncompetitive inhibition? The answer is that a wide variety of molecules can perform these roles. Some of these molecules include pharmaceutical and non-pharmaceutical drugs, toxins, and poisons from the environment. Perhaps the most relevant sources of enzyme regulatory molecules, with respect to cellular metabolism, are the products of the cellular metabolic reactions themselves. In a most efficient and elegant way, cells have evolved to use the products of their own reactions for feedback inhibition of enzyme activity. Feedback inhibition involves the use of a reaction product to regulate its own further production (Figure **6.4.7**). The cell responds to the abundance of specific products by slowing down production during anabolic or catabolic reactions. Such reaction products may inhibit the enzymes that catalyzed their production through the mechanisms described above.

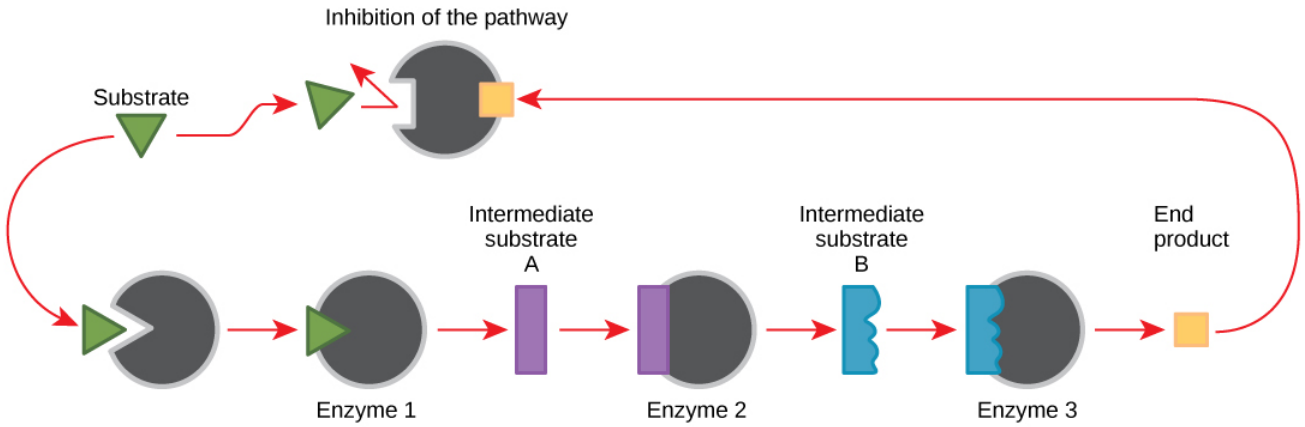


Figure **6.4.7**: Metabolic pathways are a series of reactions catalyzed by multiple enzymes. Feedback inhibition, where the end product of the pathway inhibits an upstream step, is an important regulatory mechanism in cells.

The production of both amino acids and nucleotides is controlled through feedback inhibition. Additionally, ATP is an allosteric regulator of some of the enzymes involved in the catabolic breakdown of sugar, the process that produces ATP. In this way, when ATP is abundant, the cell can prevent its further production. Remember that ATP is an unstable molecule that can spontaneously dissociate into ADP. If too much ATP were present in a cell, much of it would go to waste. On the other hand, ADP serves as a positive allosteric regulator (an allosteric activator) for some of the same enzymes that are inhibited by ATP. Thus, when relative levels of ADP are high compared to ATP, the cell is triggered to produce more ATP through the catabolism of sugar.

Summary

Enzymes are chemical catalysts that accelerate chemical reactions at physiological temperatures by lowering their activation energy. Enzymes are usually proteins consisting of one or more polypeptide chains. Enzymes have an active site that provides a unique chemical environment, made up of certain amino acid R groups (residues). This unique environment is perfectly suited to convert particular chemical reactants for that enzyme, called substrates, into unstable intermediates called transition states. Enzymes and substrates are thought to bind with an induced fit, which means that enzymes undergo slight conformational adjustments upon substrate contact, leading to full, optimal binding. Enzymes bind to substrates and catalyze reactions in four different ways: bringing substrates together in an optimal orientation, compromising the bond structures of substrates so that bonds can be more easily broken, providing optimal environmental conditions for a reaction to occur, or participating directly in their chemical reaction by forming transient covalent bonds with the substrates.

Enzyme action must be regulated so that in a given cell at a given time, the desired reactions are being catalyzed and the undesired reactions are not. Enzymes are regulated by cellular conditions, such as temperature and pH. They are also regulated through their

location within a cell, sometimes being compartmentalized so that they can only catalyze reactions under certain circumstances. Inhibition and activation of enzymes via other molecules are other important ways that enzymes are regulated. Inhibitors can act competitively, noncompetitively, or allosterically; noncompetitive inhibitors are usually allosteric. Activators can also enhance the function of enzymes allosterically. The most common method by which cells regulate the enzymes in metabolic pathways is through feedback inhibition. During feedback inhibition, the products of a metabolic pathway serve as inhibitors (usually allosteric) of one or more of the enzymes (usually the first committed enzyme of the pathway) involved in the pathway that produces them.

Glossary

active site
specific region of the enzyme to which the substrate binds

allosteric inhibition
inhibition by a binding event at a site different from the active site, which induces a conformational change and reduces the affinity of the enzyme for its substrate

coenzyme
small organic molecule, such as a vitamin or its derivative, which is required to enhance the activity of an enzyme

cofactor
inorganic ion, such as iron and magnesium ions, required for optimal regulation of enzyme activity

competitive inhibition
type of inhibition in which the inhibitor competes with the substrate molecule by binding to the active site of the enzyme

denature
process that changes the natural properties of a substance

feedback inhibition
effect of a product of a reaction sequence to decrease its further production by inhibiting the activity of the first enzyme in the pathway that produces it

induced fit
dynamic fit between the enzyme and its substrate, in which both components modify their structures to allow for ideal binding

substrate
molecule on which the enzyme acts

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6.5: Metabolism- The Chemical Description of Cell Function

All living things must have an unceasing supply of energy and matter. The transformation of this energy and matter within the body is called **metabolism**.

Catabolism and Anabolism

Catabolism is **destructive metabolism**. Typically, in catabolism, larger organic molecules are broken down into smaller constituents. This usually occurs with the release of energy (usually as ATP). Anabolism is **constructive metabolism**. Typically, in anabolism, small precursor molecules are assembled into larger organic molecules. This always requires the input of energy (often as ATP).

Autotrophic vs. Heterotrophic Nutrition

Green plants, algae, and some bacteria are **autotrophs** ("self-feeders"). Most of them use the energy of sunlight to assemble inorganic precursors, chiefly carbon dioxide and water, into the array of organic macromolecules of which they are made. The process is **photosynthesis**. Photosynthesis makes the ATP needed for the anabolic reactions in the cell. All other organisms, including ourselves, are **heterotrophs**. We secure all our energy from organic molecules taken in from our surroundings ("food"). Although heterotrophs may feed partially (as most of us do) or exclusively on other heterotrophs, all the food molecules come ultimately from autotrophs. We may eat beef but the steer ate grass. Heterotrophs degrade some of the organic molecules they take in (catabolism) to make the ATP that they need to synthesize the others into the macromolecules of which they are made (anabolism).

How humans (and other animals) do it

Humans are heterotrophs. We are totally dependent on ingested preformed organic molecules to meet all our **energy** needs. We are also dependent on preformed organic molecules as the building blocks to meet our **anabolic** needs.

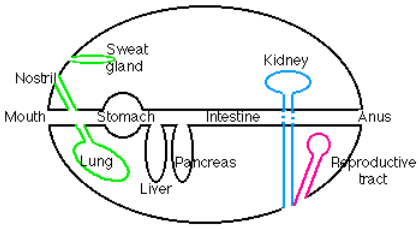


Figure 6.5.1: Human Topology

The steps for converting food to energy in animals:

1. **Ingestion**: taking food within the body (although as the figure shows, it is still topologically in the external world, not the internal).
2. **Digestion:** The enzyme-catalyzed hydrolysis of polysaccharides (e.g., starch) to sugars, proteins to amino acids, fats to fatty acids and glycerol, and nucleic acids to nucleotides.
3. **Absorption** into the body and transport to the cells.
4. **Absorption** into cells.

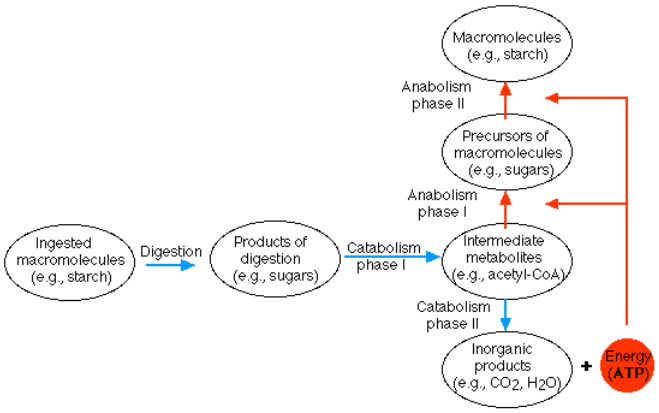


Figure 6.5.2: Metabolic Pathways

Within cells, these molecules are further degraded into still simpler molecules containing two to four carbon atoms. These fragments (**acetyl-CoA** for example) face one of two alternatives. They may proceed up various metabolic pathways and serve as the building blocks of, for example, sugars and fatty acids. From these will be assembled the macromolecules of the cell (e.g., polysaccharides, fats, proteins, and nucleic acids). Alternatively, the molecules in this pool of two- to four-carbon fragments may be still further degraded — ultimately to simple inorganic molecules such as carbon dioxide (CO_2), H_2O, and ammonia (NH_3). This phase of catabolism releases large amounts of energy (in the form of **ATP**). One use to which this energy is put is to run the anabolic activities of the cell.

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SECTION OVERVIEW

7.1: Overview of Respiration

7.1.1: Transforming Chemical Energy

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7.1.3: ATP in Metabolism

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7.1.1: Transforming Chemical Energy

Learning Objectives

- Discuss the importance of cellular respiration

Introduction: Cellular Respiration

An electrical energy plant converts energy from one form to another form that can be more easily used. For example, geothermal energy plants start with underground thermal energy (heat) and transform it into electrical energy that will be transported to homes and factories.



Figure **7.1.1.1**: Energy Plant: This geothermal energy plant transforms thermal energy from deep in the ground into electrical energy, which can be easily used.

Like a generating plant, living organisms must take in energy from their environment and convert it into to a form their cells can use. Organisms ingest large molecules, like carbohydrates, proteins, and fats, and convert them into smaller molecules like carbon dioxide and water. This process is called cellular respiration, a form of catabolism, and makes energy available for the cell to use. The energy released by cellular respiration is temporarily captured by the formation of adenosine triphosphate (ATP) within the cell. ATP is the principle form of stored energy used for cellular functions and is frequently referred to as the energy currency of the cell.

The nutrients broken down through cellular respiration lose electrons throughout the process and are said to be oxidized. When oxygen is used to help drive the oxidation of nutrients the process is called aerobic respiration. Aerobic respiration is common among the eukaryotes, including humans, and takes place mostly within the mitochondria. Respiration occurs within the cytoplasm of prokaryotes. Several prokaryotes and a few eukaryotes use an inorganic molecule other than oxygen to drive the oxidation of their nutrients in a process called anaerobic respiration. Electron acceptors for anaerobic respiration include nitrate, sulfate, carbon dioxide, and several metal ions.

The energy released during cellular respiration is then used in other biological processes. These processes build larger molecules that are essential to an organism's survival, such as amino acids, DNA, and proteins. Because they synthesize new molecules, these processes are examples of anabolism.

Key Points

- Organisms ingest organic molecules like the carbohydrate glucose to obtain the energy needed for cellular functions.
- The energy in glucose can be extracted in a series of chemical reactions known as cellular respiration.
- Cellular respiration produces energy in the form of ATP, which is the universal energy currency for cells.

Key Terms

- **aerobic respiration**: the process of converting the biochemical energy in nutrients to ATP in the presence of oxygen
- **adenosine triphosphate**: a multifunctional nucleoside triphosphate used in cells as a coenzyme, often called the "molecular unit of energy currency" in intracellular energy transfer
- **cellular respiration**: the set of the metabolic reactions and processes that take place in the cells of organisms to convert biochemical energy from nutrients into adenosine triphosphate (ATP)

- **catabolism**: the breakdown of large molecules into smaller ones usually accompanied by the release of energy

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7.1.2: Electrons and Energy

Learning Objectives

- Describe the role played by electrons in energy production and storage

Electrons and Energy

The removal of an electron from a molecule via a process called oxidation results in a decrease in the potential energy stored in the oxidized compound. When oxidation occurs in the cell, the electron (sometimes as part of a hydrogen atom) does not remain unbonded in the cytoplasm. Instead, the electron shifts to a second compound, reducing the second compound (oxidation of one species always occurs in tandem with reduction of another).

The shift of an electron from one compound to another removes some potential energy from the first compound (the oxidized compound) and increases the potential energy of the second compound (the reduced compound). The transfer of electrons between molecules via oxidation and reduction is important because most of the energy stored in atoms is in the form of high-energy electrons; it is this energy that is used to fuel cellular functions. The transfer of energy in the form of electrons allows the cell to transfer and use energy in an incremental fashion: in small packages rather than as a single, destructive burst.

Electron carriers

In living systems, a small class of molecules functions as electron shuttles: they bind and carry high-energy electrons between compounds in cellular pathways. The principal electron carriers we will consider are derived from the vitamin B group, which are derivatives of nucleotides. These compounds can be easily reduced (that is, they accept electrons) or oxidized (they lose electrons). Nicotinamide adenine dinucleotide (NAD) is derived from vitamin B3, niacin. NAD^+ is the oxidized form of niacin; NADH is the reduced form after it has accepted two electrons and a proton (which together are the equivalent of a hydrogen atom with an extra electron). It is noteworthy that NAD^+ *must* accept two electrons at once; it cannot serve as a one-electron carrier.

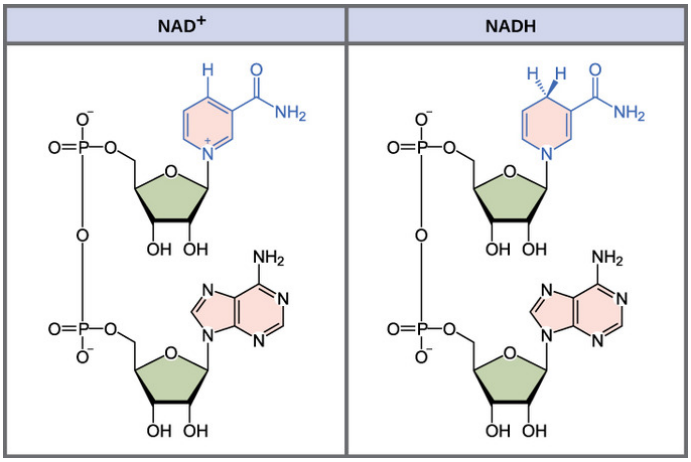


Figure **7.1.2.1**: The structure of NADH and NAD+: The oxidized form of the electron carrier (NAD+) is shown on the left and the reduced form (NADH) is shown on the right. The nitrogenous base in NADH has one more hydrogen ion and two more electrons than in NAD+.

NAD^+ can accept electrons from an organic molecule according to the general equation:

RH (Reducing agent) + NAD^+ (Oxidizing agent) → NADH (Reduced) + R (Oxidized)

When electrons are added to a compound, the compound is reduced. A compound that reduces another is called a reducing agent. In the above equation, RH is a reducing agent and NAD^+ is reduced to NADH. When electrons are removed from a compound, the compound is oxidized. In the above equation, NAD^+ is an oxidizing agent and RH is oxidized to R. The molecule NADH is critical for cellular respiration and other metabolic pathways.

Similarly, flavin adenine dinucleotide (FAD^+) is derived from vitamin B_2, also called riboflavin. Its reduced form is $FADH_2$. A second variation of NAD, NADP, contains an extra phosphate group. Both NAD^+ and FAD^+ are extensively used in energy

extraction from sugars, and NADP plays an important role in anabolic reactions and photosynthesis.

Key Points

- When electrons are added to a compound, the compound is reduced; a compound that reduces another is called a reducing agent.
- When electrons are removed from a compound, the compound is considered oxidized; a compound that oxidizes another is called an oxidizing agent.
- The transfer of energy in the form of electrons allows the cell to transfer and use energy in an incremental fashion.
- The principle electron carriers are NAD+ and NADH because they can be easily oxidized and reduced, respectively.
- NAD+ is the oxidized form of the niacin and NADH is the reduced form after it has accepted two electrons and a proton.

Key Terms

- **oxidation**: A reaction in which the atoms of an element lose electrons and the valence of the element increases.
- **reduction**: A reaction in which electrons are gained and valence is reduced; often by the removal of oxygen or the addition of hydrogen.
- **nicotinamide adenine dinucleotide**: (NAD) An organic coenzyme involved in biological oxidation and reduction reactions.
- **electron shuttle**: molecules that bind and carry high-energy electrons between compounds in cellular pathways

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7.1.3: ATP in Metabolism

Learning Objectives

- Compare the two methods by which cells utilize ATP for energy.

ATP in Living Systems

A living cell cannot store significant amounts of free energy. Excess free energy would result in an increase of heat in the cell, which would lead to excessive thermal motion that could damage and then destroy the cell. Rather, a cell must be able to handle that energy in a way that enables the cell to store energy safely and release it for use as needed. Living cells accomplish this by using the compound adenosine triphosphate (ATP). ATP is often called the "energy currency" of the cell and can be used to fill any energy need of the cell.

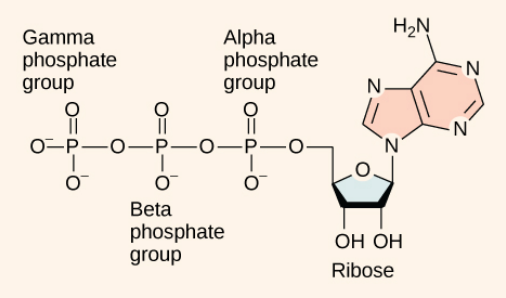


Figure **7.1.3.1**: Adenosine triphosphate.: ATP (adenosine triphosphate) has three phosphate groups that can be removed by hydrolysis to form ADP (adenosine diphosphate) or AMP (adenosine monophosphate).The negative charges on the phosphate group naturally repel each other, requiring energy to bond them together and releasing energy when these bonds are broken.

ATP Structure and Function

The core of ATP is a molecule of adenosine monophosphate (AMP), which is composed of an adenine molecule bonded to a ribose molecule and to a single phosphate group. Ribose is a five-carbon sugar found in RNA, and AMP is one of the nucleotides in RNA. The addition of a second phosphate group to this core molecule results in the formation of adenosine diphosphate (ADP); the addition of a third phosphate group forms adenosine triphosphate (ATP).

The addition of a phosphate group to a molecule requires energy. Phosphate groups are negatively charged and, thus, repel one another when they are arranged in a series, as they are in ADP and ATP. This repulsion makes the ADP and ATP molecules inherently unstable. The release of one or two phosphate groups from ATP, a process called dephosphorylation, releases energy.

Energy from ATP

Hydrolysis is the process of breaking complex macromolecules apart. During hydrolysis, water is split, or lysed, and the resulting hydrogen atom (H^+) and a hydroxyl group (OH^-) are added to the larger molecule. The hydrolysis of ATP produces ADP, together with an inorganic phosphate ion (P_i), and the release of free energy. To carry out life processes, ATP is continuously broken down into ADP, and, like a rechargeable battery, ADP is continuously regenerated into ATP by the reattachment of a third phosphate group. Water, which was broken down into its hydrogen atom and hydroxyl group during ATP hydrolysis, is regenerated when a third phosphate is added to the ADP molecule, reforming ATP.

Obviously, energy must be infused into the system to regenerate ATP. In nearly every living thing on earth, the energy comes from the metabolism of glucose. In this way, ATP is a direct link between the limited set of exergonic pathways of glucose catabolism and the multitude of endergonic pathways that power living cells.

Phosphorylation

When ATP is broken down by the removal of its terminal phosphate group, energy is released and can be used to do work by the cell. Often the released phosphate is directly transferred to another molecule, such as a protein, activating it. For example, ATP supplies the energy to move the contractile muscle proteins during the mechanical work of muscle contraction. Recall the active

transport work of the sodium-potassium pump in cell membranes. Phosphorylation by ATP alters the structure of the integral protein that functions as the pump, changing its affinity for sodium and potassium. In this way, the cell performs work, using energy from ATP to pump ions against their electrochemical gradients.

Sometimes phosphorylation of an enzyme leads to its inhibition. For example, the pyruvate dehydrogenase (PDH) complex could be phosphorylated by pyruvate dehydrogenase kinase (PDHK). This reaction leads to inhibition of PDH and its inability to convert pyruvate into acetyl-CoA.

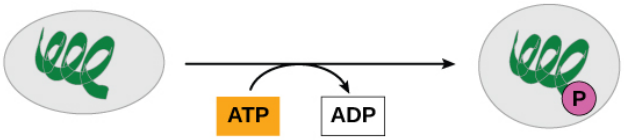


Figure **7.1.3.1**: Protein phosphorylation: In phosphorylation reactions, the gamma phosphate of ATP is attached to a protein.

Energy from ATP hydrolysis

The energy from ATP can also be used to drive chemical reactions by coupling ATP hydrolysis with another reaction process in an enzyme. In many cellular chemical reactions, enzymes bind to several substrates or reactants to form a temporary intermediate complex that allow the substrates and reactants to more readily react with each other. In reactions where ATP is involved, ATP is one of the substrates and ADP is a product. During an endergonic chemical reaction, ATP forms an intermediate complex with the substrate and enzyme in the reaction. This intermediate complex allows the ATP to transfer its third phosphate group, with its energy, to the substrate, a process called phosphorylation. Phosphorylation refers to the addition of the phosphate (~P). When the intermediate complex breaks apart, the energy is used to modify the substrate and convert it into a product of the reaction. The ADP molecule and a free phosphate ion are released into the medium and are available for recycling through cell metabolism. This is illustrated by the following generic reaction:

A + enzyme + ATP → [A enzyme −P] B + enzyme + ADP + phosphate ion

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Key Points

- Cells require a constant supply of energy to survive, but cannot store this energy as free energy as this would result in elevated temperatures and would destroy the cell.
- Cells store energy in the form of adenosine triphosphate, or ATP.
- Energy is released when the terminal phosphate group is removed from ATP.
- To utilize the energy stored as ATP, cells either couple ATP hydrolysis to an energetically unfavorable reaction to allow it to proceed or transfer one of the phosphate groups from ATP to a protein substrate, causing it to change conformations and hence energetic preference.

Key Terms

- **phosphorylation**: the addition of a phosphate group to a compound; often catalyzed by enzymes
- **adenosine triphosphate**: a multifunctional nucleoside triphosphate used in cells as a coenzyme, often called the “molecular unit of energy currency” in intracellular energy transfer
- **phosphate**: Any salt or ester of phosphoric acid

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SECTION OVERVIEW

7.2: Glycolysis- Splitting Glucose

7.2.1: Glycolysis

7.2.2: Glycolysis

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7.2.1: Glycolysis

Skills to Develop

- Describe the overall result in terms of molecules produced in the breakdown of glucose by glycolysis
- Compare the output of glycolysis in terms of ATP molecules and NADH molecules produced

You have read that nearly all of the energy used by living cells comes to them in the bonds of the sugar, glucose. Glycolysis is the first step in the breakdown of glucose to extract energy for cellular metabolism. Nearly all living organisms carry out glycolysis as part of their metabolism. The process does not use oxygen and is therefore anaerobic. Glycolysis takes place in the cytoplasm of both prokaryotic and eukaryotic cells. Glucose enters heterotrophic cells in two ways. One method is through secondary active transport in which the transport takes place against the glucose concentration gradient. The other mechanism uses a group of integral proteins called GLUT proteins, also known as glucose transporter proteins. These transporters assist in the facilitated diffusion of glucose.

Glycolysis begins with the six carbon ring-shaped structure of a single glucose molecule and ends with two molecules of a three-carbon sugar called pyruvate. Glycolysis consists of two distinct phases. The first part of the glycolysis pathway traps the glucose molecule in the cell and uses energy to modify it so that the six-carbon sugar molecule can be split evenly into the two three-carbon molecules. The second part of glycolysis extracts energy from the molecules and stores it in the form of ATP and NADH, the reduced form of NAD.

First Half of Glycolysis (Energy-Requiring Steps)

Step 1. The first step in glycolysis (Figure **7.2.1.1**) is catalyzed by hexokinase, an enzyme with broad specificity that catalyzes the phosphorylation of six-carbon sugars. Hexokinase phosphorylates glucose using ATP as the source of the phosphate, producing glucose-6-phosphate, a more reactive form of glucose. This reaction prevents the phosphorylated glucose molecule from continuing to interact with the GLUT proteins, and it can no longer leave the cell because the negatively charged phosphate will not allow it to cross the hydrophobic interior of the plasma membrane.

Step 2. In the second step of glycolysis, an isomerase converts glucose-6-phosphate into one of its isomers, fructose-6-phosphate. An isomerase is an enzyme that catalyzes the conversion of a molecule into one of its isomers. (This change from phosphoglucose to phosphofructose allows the eventual split of the sugar into two three-carbon molecules.).

Step 3. The third step is the phosphorylation of fructose-6-phosphate, catalyzed by the enzyme phosphofructokinase. A second ATP molecule donates a high-energy phosphate to fructose-6-phosphate, producing fructose-1,6-bisphosphate. In this pathway, phosphofructokinase is a rate-limiting enzyme. It is active when the concentration of ADP is high; it is less active when ADP levels are low and the concentration of ATP is high. Thus, if there is “sufficient” ATP in the system, the pathway slows down. This is a type of end product inhibition, since ATP is the end product of glucose catabolism.

Step 4. The newly added high-energy phosphates further destabilize fructose-1,6-bisphosphate. The fourth step in glycolysis employs an enzyme, aldolase, to cleave 1,6-bisphosphate into two three-carbon isomers: dihydroxyacetone-phosphate and glyceraldehyde-3-phosphate.

Step 5. In the fifth step, an isomerase transforms the dihydroxyacetone-phosphate into its isomer, glyceraldehyde-3-phosphate. Thus, the pathway will continue with two molecules of a single isomer. At this point in the pathway, there is a net investment of energy from two ATP molecules in the breakdown of one glucose molecule.

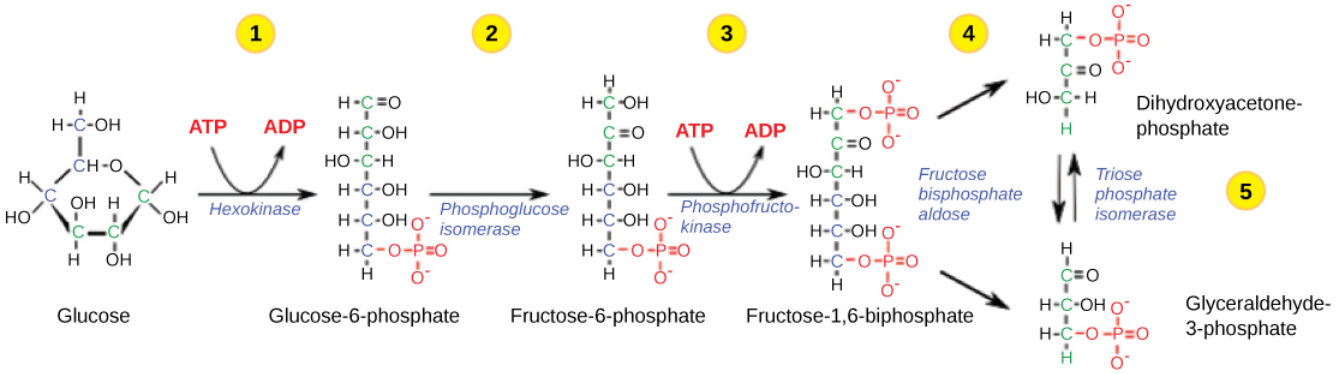


Figure **7.2.1.1**: The first half of glycolysis uses two ATP molecules in the phosphorylation of glucose, which is then split into two three-carbon molecules.

Second Half of Glycolysis (Energy-Releasing Steps)

So far, glycolysis has cost the cell two ATP molecules and produced two small, three-carbon sugar molecules. Both of these molecules will proceed through the second half of the pathway, and sufficient energy will be extracted to pay back the two ATP molecules used as an initial investment and produce a profit for the cell of two additional ATP molecules and two even higher-energy NADH molecules.

Step 6. The sixth step in glycolysis (Figure **7.2.1.2**) oxidizes the sugar (glyceraldehyde-3-phosphate), extracting high-energy electrons, which are picked up by the electron carrier NAD^+, producing NADH. The sugar is then phosphorylated by the addition of a second phosphate group, producing 1,3-bisphosphoglycerate. Note that the second phosphate group does not require another ATP molecule.

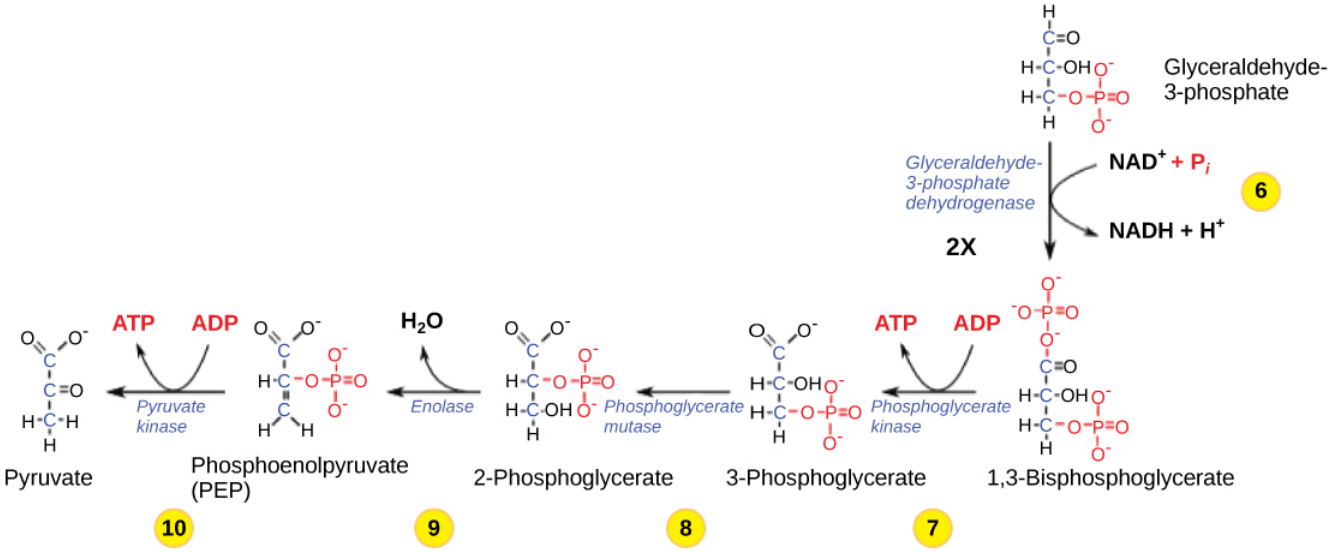


Figure **7.2.1.2**: The second half of glycolysis involves phosphorylation without ATP investment (step 6) and produces two NADH and four ATP molecules per glucose.

Here again is a potential limiting factor for this pathway. The continuation of the reaction depends upon the availability of the oxidized form of the electron carrier, NAD^+. Thus, NADH must be continuously oxidized back into NAD^+ in order to keep this step going. If NAD^+ is not available, the second half of glycolysis slows down or stops. If oxygen is available in the system, the NADH will be oxidized readily, though indirectly, and the high-energy electrons from the hydrogen released in this process will be used to produce ATP. In an environment without oxygen, an alternate pathway (fermentation) can provide the oxidation of NADH to NAD^+.

Step 7. In the seventh step, catalyzed by phosphoglycerate kinase (an enzyme named for the reverse reaction), 1,3-bisphosphoglycerate donates a high-energy phosphate to ADP, forming one molecule of ATP. (This is an example of substrate-level

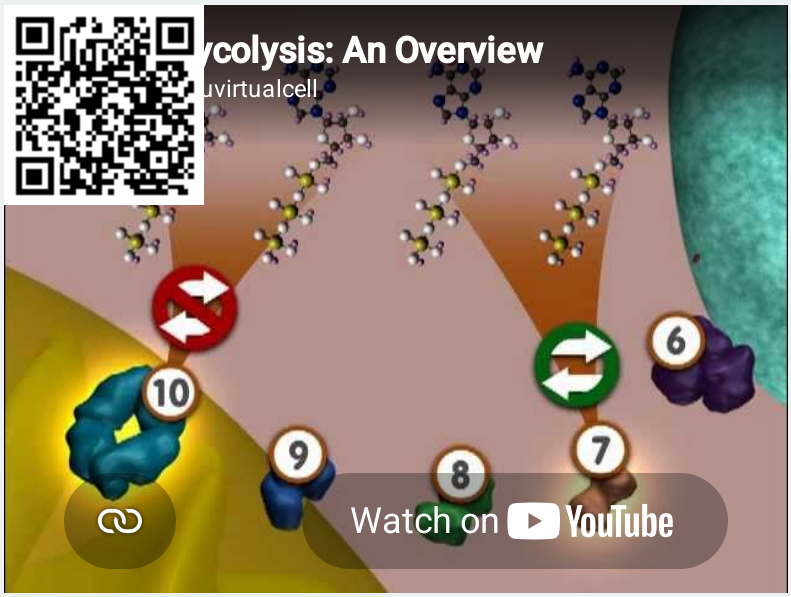
phosphorylation.) A carbonyl group on the 1,3-bisphosphoglycerate is oxidized to a carboxyl group, and 3-phosphoglycerate is formed.

Step 8. In the eighth step, the remaining phosphate group in 3-phosphoglycerate moves from the third carbon to the second carbon, producing 2-phosphoglycerate (an isomer of 3-phosphoglycerate). The enzyme catalyzing this step is a mutase (isomerase).

Step 9. Enolase catalyzes the ninth step. This enzyme causes 2-phosphoglycerate to lose water from its structure; this is a dehydration reaction, resulting in the formation of a double bond that increases the potential energy in the remaining phosphate bond and produces phosphoenolpyruvate (PEP).

Step 10. The last step in glycolysis is catalyzed by the enzyme pyruvate kinase (the enzyme in this case is named for the reverse reaction of pyruvate's conversion into PEP) and results in the production of a second ATP molecule by substrate-level phosphorylation and the compound pyruvic acid (or its salt form, pyruvate). Many enzymes in enzymatic pathways are named for the reverse reactions, since the enzyme can catalyze both forward and reverse reactions (these may have been described initially by the reverse reaction that takes place in vitro, under non-physiological conditions).

Link to Learning



Gain a better understanding of the breakdown of glucose by glycolysis by visiting this site to see the process in action.

Outcomes of Glycolysis

Glycolysis starts with glucose and ends with two pyruvate molecules, a total of four ATP molecules and two molecules of NADH. Two ATP molecules were used in the first half of the pathway to prepare the six-carbon ring for cleavage, so the cell has a net gain of two ATP molecules and 2 NADH molecules for its use. If the cell cannot catabolize the pyruvate molecules further, it will harvest only two ATP molecules from one molecule of glucose. Mature mammalian red blood cells are not capable of aerobic respiration—the process in which organisms convert energy in the presence of oxygen—and glycolysis is their sole source of ATP. If glycolysis is interrupted, these cells lose their ability to maintain their sodium-potassium pumps, and eventually, they die.

The last step in glycolysis will not occur if pyruvate kinase, the enzyme that catalyzes the formation of pyruvate, is not available in sufficient quantities. In this situation, the entire glycolysis pathway will proceed, but only two ATP molecules will be made in the second half. Thus, pyruvate kinase is a rate-limiting enzyme for glycolysis.

Summary

Glycolysis is the first pathway used in the breakdown of glucose to extract energy. It was probably one of the earliest metabolic pathways to evolve and is used by nearly all of the organisms on earth. Glycolysis consists of two parts: The first part prepares the six-carbon ring of glucose for cleavage into two three-carbon sugars. ATP is invested in the process during this half to energize the

separation. The second half of glycolysis extracts ATP and high-energy electrons from hydrogen atoms and attaches them to NAD^+. Two ATP molecules are invested in the first half and four ATP molecules are formed by substrate phosphorylation during the second half. This produces a net gain of two ATP and two NADH molecules for the cell.

Glossary

aerobic respiration
process in which organisms convert energy in the presence of oxygen

anaerobic
process that does not use oxygen

glycolysis
process of breaking glucose into two three-carbon molecules with the production of ATP and NADH

isomerase
enzyme that converts a molecule into its isomer

pyruvate
three-carbon sugar that can be decarboxylated and oxidized to make acetyl CoA, which enters the citric acid cycle under aerobic conditions; the end product of glycolysis

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7.2.2: Glycolysis

Even exergonic, energy-releasing reactions require a small amount of activation energy to proceed. However, consider endergonic reactions, which require much more energy input because their products have more free energy than their reactants. Within the cell, where does energy to power such reactions come from? The answer lies with an energy-supplying molecule called adenosine triphosphate, or ATP. ATP is a small, relatively simple molecule, but within its bonds contains the potential for a quick burst of energy that can be harnessed to perform cellular work. This molecule can be thought of as the primary energy currency of cells in the same way that money is the currency that people exchange for things they need. ATP is used to power the majority of energy-requiring cellular reactions.

ATP in Living Systems

A living cell cannot store significant amounts of free energy. Excess free energy would result in an increase of heat in the cell, which would denature enzymes and other proteins, and thus destroy the cell. Rather, a cell must be able to store energy safely and release it for use only as needed. Living cells accomplish this using ATP, which can be used to fill any energy need of the cell. How? It functions as a rechargeable battery.

When ATP is broken down, usually by the removal of its terminal phosphate group, energy is released. This energy is used to do work by the cell, usually by the binding of the released phosphate to another molecule, thus activating it. For example, in the mechanical work of muscle contraction, ATP supplies energy to move the contractile muscle proteins.

ATP Structure and Function

At the heart of ATP is a molecule of adenosine monophosphate (AMP), which is composed of an adenine molecule bonded to both a ribose molecule and a single phosphate group (Figure **7.2.2.1**). Ribose is a five-carbon sugar found in RNA and AMP is one of the nucleotides in RNA. The addition of a second phosphate group to this core molecule results in adenosine diphosphate (ADP); the addition of a third phosphate group forms adenosine triphosphate (ATP).

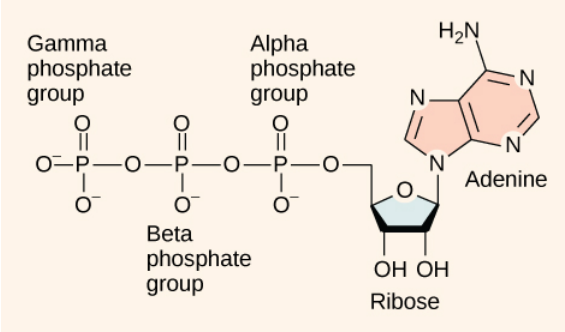


Figure 7.2.2.1: The structure of ATP shows the basic components of a two-ring adenine, five-carbon ribose, and three phosphate groups.

The addition of a phosphate group to a molecule requires a high amount of energy and results in a high-energy bond. Phosphate groups are negatively charged and thus repel one another when they are arranged in series, as they are in ADP and ATP. This repulsion makes the ADP and ATP molecules inherently unstable. The release of one or two phosphate groups from ATP, a process called hydrolysis, releases energy.

Glycolysis

You have read that nearly all of the energy used by living things comes to them in the bonds of the sugar, glucose. Glycolysis is the first step in the breakdown of glucose to extract energy for cell metabolism. Many living organisms carry out glycolysis as part of their metabolism. Glycolysis takes place in the cytoplasm of most prokaryotic and all eukaryotic cells.

Glycolysis begins with the six-carbon, ring-shaped structure of a single glucose molecule and ends with two molecules of a three-carbon sugar called pyruvate. Glycolysis consists of two distinct phases. In the first part of the glycolysis pathway, energy is used to make adjustments so that the six-carbon sugar molecule can be split evenly into two three-carbon pyruvate molecules. In the second part of glycolysis, ATP and nicotinamide-adenine dinucleotide (NADH) are produced (Figure **7.2.2.2**).

If the cell cannot catabolize the pyruvate molecules further, it will harvest only two ATP molecules from one molecule of glucose. For example, mature mammalian red blood cells are only capable of glycolysis, which is their sole source of ATP. If glycolysis is interrupted, these cells would eventually die.

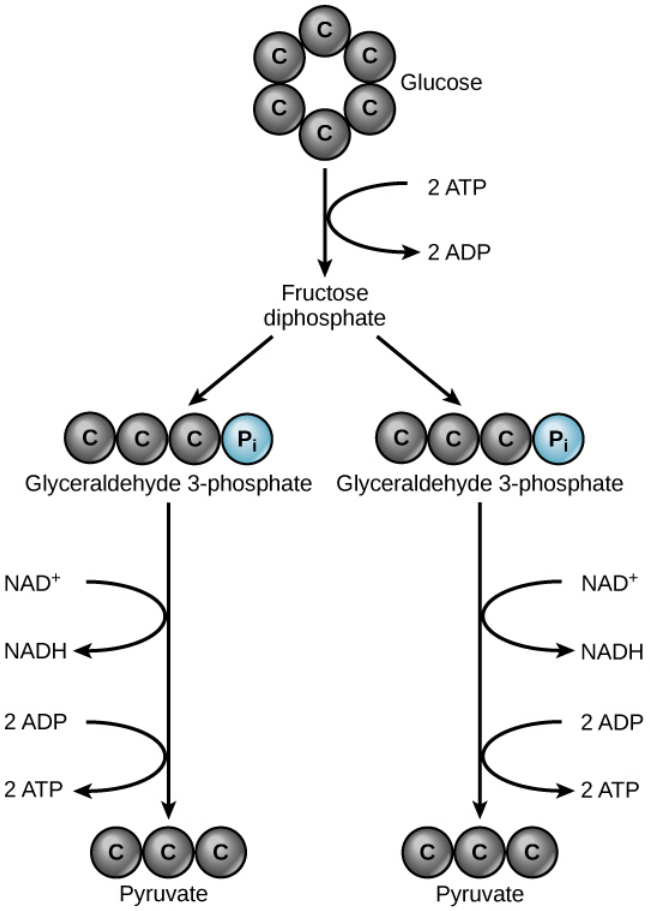


Figure 7.2.2.2: In glycolysis, a glucose molecule is converted into two pyruvate molecules.

Summary

ATP functions as the energy currency for cells. It allows cells to store energy briefly and transport it within itself to support endergonic chemical reactions. The structure of ATP is that of an RNA nucleotide with three phosphate groups attached. As ATP is used for energy, a phosphate group is detached, and ADP is produced. Energy derived from glucose catabolism is used to recharge ADP into ATP.

Glycolysis is the first pathway used in the breakdown of glucose to extract energy. Because it is used by nearly all organisms on earth, it must have evolved early in the history of life. Glycolysis consists of two parts: The first part prepares the six-carbon ring of glucose for separation into two three-carbon sugars. Energy from ATP is invested into the molecule during this step to energize the separation. The second half of glycolysis extracts ATP and high-energy electrons from hydrogen atoms and attaches them to NAD^+. Two ATP molecules are invested in the first half and four ATP molecules are formed during the second half. This produces a net gain of two ATP molecules per molecule of glucose for the cell.

Glossary

ATP

(also, adenosine triphosphate) the cell's energy currency

glycolysis

the process of breaking glucose into two three-carbon molecules with the production of ATP and NADH

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7.3: The Oxidation of Pyruvate Produces Acetyl-CoA

Learning Objectives

- Explain why cells break down pyruvate

Breakdown of Pyruvate

In order for pyruvate, the product of glycolysis, to enter the next pathway, it must undergo several changes to become acetyl Coenzyme A (acetyl CoA). Acetyl CoA is a molecule that is further converted to oxaloacetate, which enters the citric acid cycle (Krebs cycle). The conversion of pyruvate to acetyl CoA is a three-step process.

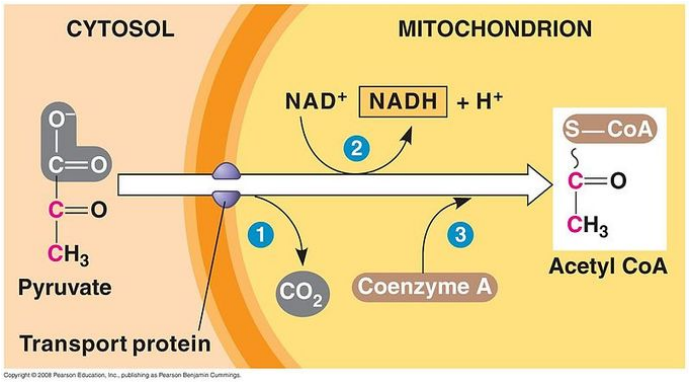


Figure **7.3.1**: Breakdown of Pyruvate: Each pyruvate molecule loses a carboxylic group in the form of carbon dioxide. The remaining two carbons are then transferred to the enzyme CoA to produce Acetyl CoA.

Step 1. A carboxyl group is removed from pyruvate, releasing a molecule of carbon dioxide into the surrounding medium. (Note: carbon dioxide is one carbon attached to two oxygen atoms and is one of the major end products of cellular respiration.) The result of this step is a two-carbon hydroxyethyl group bound to the enzyme pyruvate dehydrogenase; the lost carbon dioxide is the first of the six carbons from the original glucose molecule to be removed. This step proceeds twice for every molecule of glucose metabolized (remember: there are two pyruvate molecules produced at the end of glycolysis); thus, two of the six carbons will have been removed at the end of both of these steps.

Step 2. The hydroxyethyl group is oxidized to an acetyl group, and the electrons are picked up by NAD^+, forming NADH (the reduced form of NAD+). The high- energy electrons from NADH will be used later by the cell to generate ATP for energy.

Step 3. The enzyme-bound acetyl group is transferred to CoA, producing a molecule of acetyl CoA. This molecule of acetyl CoA is then further converted to be used in the next pathway of metabolism, the citric acid cycle.

Key Points

- In the conversion of pyruvate to acetyl CoA, each pyruvate molecule loses one carbon atom with the release of carbon dioxide.
- During the breakdown of pyruvate, electrons are transferred to NAD+ to produce NADH, which will be used by the cell to produce ATP.
- In the final step of the breakdown of pyruvate, an acetyl group is transferred to Coenzyme A to produce acetyl CoA.

Key Terms

- **acetyl CoA**: a molecule that conveys the carbon atoms from glycolysis (pyruvate) to the citric acid cycle to be oxidized for energy production

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7.4: The Citric Acid Cycle

Learning Objectives

- List the steps of the Krebs (or citric acid) cycle

Citric Acid Cycle (Krebs Cycle)

Like the conversion of pyruvate to acetyl CoA, the citric acid cycle takes place in the matrix of the mitochondria. Almost all of the enzymes of the citric acid cycle are soluble, with the single exception of the enzyme succinate dehydrogenase, which is embedded in the inner membrane of the mitochondrion. Unlike glycolysis, the citric acid cycle is a closed loop: the last part of the pathway regenerates the compound used in the first step. The eight steps of the cycle are a series of redox, dehydration, hydration, and decarboxylation reactions that produce two carbon dioxide molecules, one GTP/ATP, and reduced forms of NADH and FADH2. This is considered an aerobic pathway because the NADH and FADH2 produced must transfer their electrons to the next pathway in the system, which will use oxygen. If this transfer does not occur, the oxidation steps of the citric acid cycle also do not occur. Note that the citric acid cycle produces very little ATP directly and does not directly consume oxygen.

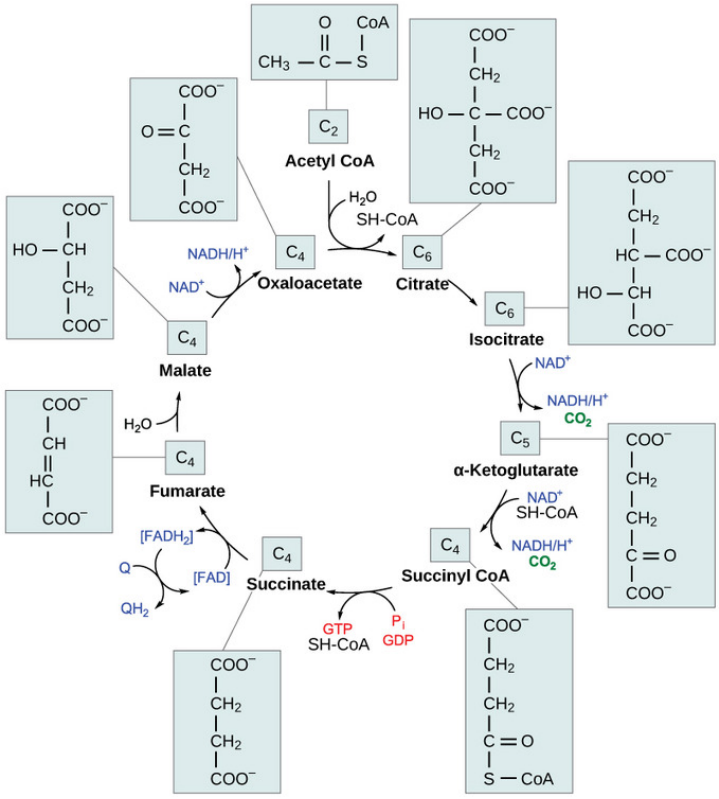


Figure **7.4.1**: The citric acid cycle: In the citric acid cycle, the acetyl group from acetyl CoA is attached to a four-carbon oxaloacetate molecule to form a six-carbon citrate molecule. Through a series of steps, citrate is oxidized, releasing two carbon dioxide molecules for each acetyl group fed into the cycle. In the process, three NAD+ molecules are reduced to NADH, one FAD molecule is reduced to FADH2, and one ATP or GTP (depending on the cell type) is produced (by substrate-level phosphorylation). Because the final product of the citric acid cycle is also the first reactant, the cycle runs continuously in the presence of sufficient reactants.

Steps in the Citric Acid Cycle

Step 1. The first step is a condensation step, combining the two-carbon acetyl group (from acetyl CoA) with a four-carbon oxaloacetate molecule to form a six-carbon molecule of citrate. CoA is bound to a sulfhydryl group (-SH) and diffuses away to eventually combine with another acetyl group. This step is irreversible because it is highly exergonic. The rate of this reaction is controlled by negative feedback and the amount of ATP available. If ATP levels increase, the rate of this reaction decreases. If ATP is in short supply, the rate increases.

Step 2. Citrate loses one water molecule and gains another as citrate is converted into its isomer, isocitrate.

Steps 3 and 4. In step three, isocitrate is oxidized, producing a five-carbon molecule, α-ketoglutarate, together with a molecule of $CO_2$and two electrons, which reduce NAD+ to NADH. This step is also regulated by negative feedback from ATP and NADH and by a positive effect of ADP. Steps three and four are both oxidation and decarboxylation steps, which release electrons that reduce NAD^+ to NADH and release carboxyl groups that form CO_2 molecules. α-Ketoglutarate is the product of step three, and a succinyl group is the product of step four. CoA binds the succinyl group to form succinyl CoA. The enzyme that catalyzes step four is regulated by feedback inhibition of ATP, succinyl CoA, and NADH.

Step 5. A phosphate group is substituted for coenzyme A, and a high- energy bond is formed. This energy is used in substrate-level phosphorylation (during the conversion of the succinyl group to succinate) to form either guanine triphosphate (GTP) or ATP. There are two forms of the enzyme, called isoenzymes, for this step, depending upon the type of animal tissue in which they are found. One form is found in tissues that use large amounts of ATP, such as heart and skeletal muscle. This form produces ATP. The second form of the enzyme is found in tissues that have a high number of anabolic pathways, such as liver. This form produces GTP. GTP is energetically equivalent to ATP; however, its use is more restricted. In particular, protein synthesis primarily uses GTP.

Step 6. Step six is a dehydration process that converts succinate into fumarate. Two hydrogen atoms are transferred to FAD, producing $FADH_2$. The energy contained in the electrons of these atoms is insufficient to reduce NAD^+ but adequate to reduce FAD. Unlike NADH, this carrier remains attached to the enzyme and transfers the electrons to the electron transport chain directly. This process is made possible by the localization of the enzyme catalyzing this step inside the inner membrane of the mitochondrion.

Step 7. Water is added to fumarate during step seven, and malate is produced. The last step in the citric acid cycle regenerates oxaloacetate by oxidizing malate. Another molecule of NADH is produced.

Products of the Citric Acid Cycle

Two carbon atoms come into the citric acid cycle from each acetyl group, representing four out of the six carbons of one glucose molecule. Two carbon dioxide molecules are released on each turn of the cycle; however, these do not necessarily contain the most recently-added carbon atoms. The two acetyl carbon atoms will eventually be released on later turns of the cycle; thus, all six carbon atoms from the original glucose molecule are eventually incorporated into carbon dioxide. Each turn of the cycle forms three NADH molecules and one $FADH_2$ molecule. These carriers will connect with the last portion of aerobic respiration to produce ATP molecules. One GTP or ATP is also made in each cycle. Several of the intermediate compounds in the citric acid cycle can be used in synthesizing non-essential amino acids; therefore, the cycle is amphibolic (both catabolic and anabolic).

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Key Points

- The four-carbon molecule, oxaloacetate, that began the cycle is regenerated after the eight steps of the citric acid cycle.
- The eight steps of the citric acid cycle are a series of redox, dehydration, hydration, and decarboxylation reactions.
- Each turn of the cycle forms one GTP or ATP as well as three NADH molecules and one FADH2 molecule, which will be used in further steps of cellular respiration to produce ATP for the cell.

Key Terms

- **citric acid cycle**: a series of chemical reactions used by all aerobic organisms to generate energy through the oxidization of acetate derived from carbohydrates, fats, and proteins into carbon dioxide
- **Krebs cycle**: a series of enzymatic reactions that occurs in all aerobic organisms; it involves the oxidative metabolism of acetyl units and serves as the main source of cellular energy
- **mitochondria**: in cell biology, a mitochondrion (plural mitochondria) is a membrane-enclosed organelle, often described as “cellular power plants” because they generate most of the ATP

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SECTION OVERVIEW

7.5: Electron Transport Chain and Chemiosmosis

7.5.1: Electron Transport Chain

7.5.2: Chemiosmosis and Oxidative Phosphorylation

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7.5.1: Electron Transport Chain

Learning Objectives

- Describe how electrons move through the electron transport chain

Oxidative phosphorylation is a highly efficient method of producing large amounts of ATP, the basic unit of energy for metabolic processes. During this process electrons are exchanged between molecules, which creates a chemical gradient that allows for the production of ATP. The most vital part of this process is the electron transport chain, which produces more ATP than any other part of cellular respiration.

Electron Transport Chain

The electron transport chain is the final component of aerobic respiration and is the only part of glucose metabolism that uses atmospheric oxygen. Electron transport is a series of redox reactions that resemble a relay race. Electrons are passed rapidly from one component to the next to the endpoint of the chain, where the electrons reduce molecular oxygen, producing water. This requirement for oxygen in the final stages of the chain can be seen in the overall equation for cellular respiration, which requires both glucose and oxygen.

A complex is a structure consisting of a central atom, molecule, or protein weakly connected to surrounding atoms, molecules, or proteins. The electron transport chain is an aggregation of four of these complexes (labeled I through IV), together with associated mobile electron carriers. The electron transport chain is present in multiple copies in the inner mitochondrial membrane of eukaryotes and the plasma membrane of prokaryotes.

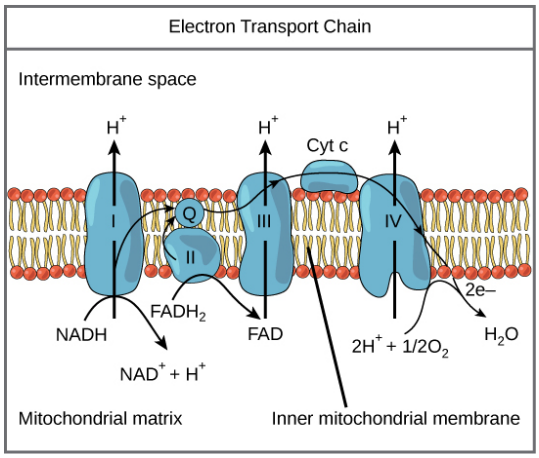


Figure **7.5.1.1**: The electron transport chain: The electron transport chain is a series of electron transporters embedded in the inner mitochondrial membrane that shuttles electrons from NADH and $FADH_2$ to molecular oxygen. In the process, protons are pumped from the mitochondrial matrix to the intermembrane space, and oxygen is reduced to form water.

Complex I

To start, two electrons are carried to the first complex aboard NADH. Complex I is composed of flavin mononucleotide (FMN) and an enzyme containing iron-sulfur (Fe-S). FMN, which is derived from vitamin B_2 (also called riboflavin), is one of several prosthetic groups or co-factors in the electron transport chain. A prosthetic group is a non-protein molecule required for the activity of a protein. Prosthetic groups can be organic or inorganic and are non-peptide molecules bound to a protein that facilitate its function.

Prosthetic groups include co-enzymes, which are the prosthetic groups of enzymes. The enzyme in complex I is NADH dehydrogenase, a very large protein containing 45 amino acid chains. Complex I can pump four hydrogen ions across the membrane from the matrix into the intermembrane space; it is in this way that the hydrogen ion gradient is established and maintained between the two compartments separated by the inner mitochondrial membrane.

Q and Complex II

Complex II directly receives $FADH_2$, which does not pass through complex I. The compound connecting the first and second complexes to the third is ubiquinone (Q). The Q molecule is lipid soluble and freely moves through the hydrophobic core of the membrane. Once it is reduced to QH_2, ubiquinone delivers its electrons to the next complex in the electron transport chain. Q receives the electrons derived from NADH from complex I and the electrons derived from $FADH_2$ from complex II, including succinate dehydrogenase. This enzyme and $FADH_2$ form a small complex that delivers electrons directly to the electron transport chain, bypassing the first complex. Since these electrons bypass, and thus do not energize, the proton pump in the first complex, fewer ATP molecules are made from the $FADH_2$ electrons. The number of ATP molecules ultimately obtained is directly proportional to the number of protons pumped across the inner mitochondrial membrane.

Complex III

The third complex is composed of cytochrome b, another Fe-S protein, Rieske center (2Fe-2S center), and cytochrome c proteins; this complex is also called cytochrome oxidoreductase. Cytochrome proteins have a prosthetic heme group. The heme molecule is similar to the heme in hemoglobin, but it carries electrons, not oxygen. As a result, the iron ion at its core is reduced and oxidized as it passes the electrons, fluctuating between different oxidation states: Fe^{2+} (reduced) and Fe^{3+} (oxidized). The heme molecules in the cytochromes have slightly different characteristics due to the effects of the different proteins binding them, which makes each complex. Complex III pumps protons through the membrane and passes its electrons to cytochrome c for transport to the fourth complex of proteins and enzymes. Cytochrome c is the acceptor of electrons from Q; however, whereas Q carries pairs of electrons, cytochrome c can accept only one at a time.

Complex IV

The fourth complex is composed of cytochrome proteins c, a, and a_3. This complex contains two heme groups (one in each of the cytochromes a and a_3) and three copper ions (a pair of Cu_A and one Cu_B in cytochrome a_3). The cytochromes hold an oxygen molecule very tightly between the iron and copper ions until the oxygen is completely reduced. The reduced oxygen then picks up two hydrogen ions from the surrounding medium to produce water (H_2O). The removal of the hydrogen ions from the system also contributes to the ion gradient used in the process of chemiosmosis.

Key Points

- Oxidative phosphorylation is the metabolic pathway in which electrons are transferred from electron donors to electron acceptors in redox reactions; this series of reactions releases energy which is used to form ATP.
- There are four protein complexes (labeled complex I-IV) in the electron transport chain, which are involved in moving electrons from NADH and $FADH_2$ to molecular oxygen.
- Complex I establishes the hydrogen ion gradient by pumping four hydrogen ions across the membrane from the matrix into the intermembrane space.
- Complex II receives $FADH_2$, which bypasses complex I, and delivers electrons directly to the electron transport chain.
- Ubiquinone (Q) accepts the electrons from both complex I and complex II and delivers them to complex III.
- Complex III pumps protons through the membrane and passes its electrons to cytochrome c for transport to the fourth complex of proteins and enzymes.
- Complex IV reduces oxygen; the reduced oxygen then picks up two hydrogen ions from the surrounding medium to make water.

Key Terms

- **prosthetic group**: The non-protein component of a conjugated protein.
- **complex**: A structure consisting of a central atom, molecule, or protein weakly connected to surrounding atoms, molecules, or proteins.
- **ubiquinone**: A lipid soluble substance that is a component of the electron transport chain and accepts electrons from complexes I and II.

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7.5.2: Chemiosmosis and Oxidative Phosphorylation

Learning Objectives

- Describe how the energy obtained from the electron transport chain powers chemiosmosis and discuss the role of hydrogen ions in the synthesis of ATP

During chemiosmosis, electron carriers like NADH and FADH donate electrons to the electron transport chain. The electrons cause conformation changes in the shapes of the proteins to pump H+ across a selectively permeable cell membrane. The uneven distribution of H^+ ions across the membrane establishes both concentration and electrical gradients (thus, an electrochemical gradient) owing to the hydrogen ions' positive charge and their aggregation on one side of the membrane.

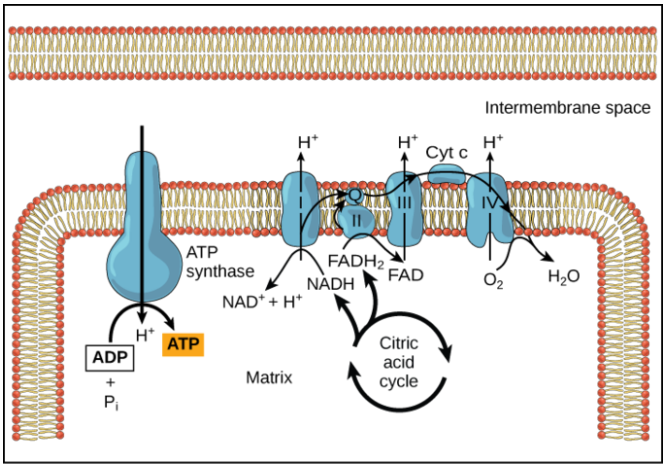


Figure 7.5.2.1: Chemiosmosis: In oxidative phosphorylation, the hydrogen ion gradient formed by the electron transport chain is used by ATP synthase to form ATP.

If the membrane were open to diffusion by the hydrogen ions, the ions would tend to spontaneously diffuse back across into the matrix, driven by their electrochemical gradient. However, many ions cannot diffuse through the nonpolar regions of phospholipid membranes without the aid of ion channels. Similarly, hydrogen ions in the matrix space can only pass through the inner mitochondrial membrane through a membrane protein called ATP synthase. This protein acts as a tiny generator turned by the force of the hydrogen ions diffusing through it, down their electrochemical gradient. The turning of this molecular machine harnesses the potential energy stored in the hydrogen ion gradient to add a phosphate to ADP, forming ATP.

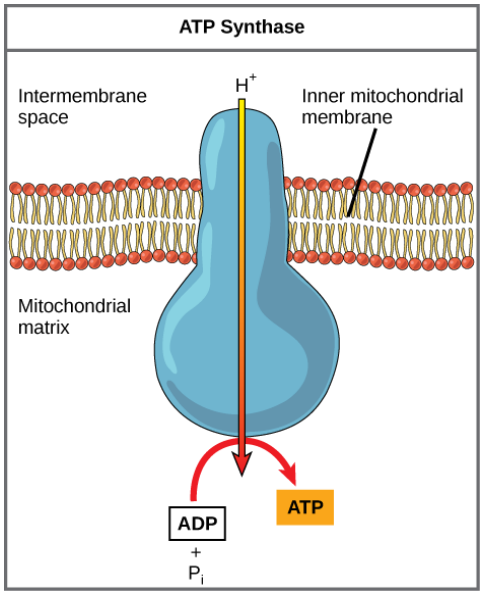


Figure **7.5.2.1**: ATP Synthase: ATP synthase is a complex, molecular machine that uses a proton (H+) gradient to form ATP from ADP and inorganic phosphate (Pi).

Chemiosmosis is used to generate 90 percent of the ATP made during aerobic glucose catabolism. The production of ATP using the process of chemiosmosis in mitochondria is called oxidative phosphorylation. It is also the method used in the light reactions of photosynthesis to harness the energy of sunlight in the process of photophosphorylation. The overall result of these reactions is the production of ATP from the energy of the electrons removed from hydrogen atoms. These atoms were originally part of a glucose molecule. At the end of the pathway, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen attract hydrogen ions (protons) from the surrounding medium and water is formed.

Key Points

- During chemiosmosis, the free energy from the series of reactions that make up the electron transport chain is used to pump hydrogen ions across the membrane, establishing an electrochemical gradient.
- Hydrogen ions in the matrix space can only pass through the inner mitochondrial membrane through a membrane protein called ATP synthase.
- As protons move through ATP synthase, ADP is turned into ATP.
- The production of ATP using the process of chemiosmosis in mitochondria is called oxidative phosphorylation.

Key Terms

- **ATP synthase**: An important enzyme that provides energy for the cell to use through the synthesis of adenosine triphosphate (ATP).
- **oxidative phosphorylation**: A metabolic pathway that uses energy released by the oxidation of nutrients to produce adenosine triphosphate (ATP).
- **chemiosmosis**: The movement of ions across a selectively permeable membrane, down their electrochemical gradient.

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7.6: ATP Energy Yield Energy Yield of Aerobic Respiration

ese atoms were originally part of a glucose molecule. At the end of the pathway, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen attract hydrogen ions (protons) from the surrounding medium and water is formed.

ATP Yield

The amount of energy (as ATP) gained from glucose catabolism varies across species and depends on other related cellular processes.

LEARNING OBJECTIVES

Describe the origins of variability in the amount of ATP that is produced per molecule of glucose consumed

KEY TAKEAWAYS

Key Points

- While glucose catabolism always produces energy, the amount of energy (in terms of ATP equivalents) produced can vary, especially across different species.
- The number of hydrogen ions the electron transport chain complexes can pump through the membrane varies between species.
- NAD^+ provides more ATP than FAD^+ in the electron transport chain and can lead to variance in ATP production.
- The use of intermediates from glucose catabolism in other biosynthetic pathways, such as amino acid synthesis, can lower the yield of ATP.

Key Terms

- **catabolism**: Destructive metabolism, usually including the release of energy and breakdown of materials.

ATP Yield

In a eukaryotic cell, the process of cellular respiration can metabolize one molecule of glucose into 30 to 32 ATP. The process of glycolysis only produces two ATP, while all the rest are produced during the electron transport chain. Clearly, the electron transport chain is vastly more efficient, but it can only be carried out in the presence of oxygen.

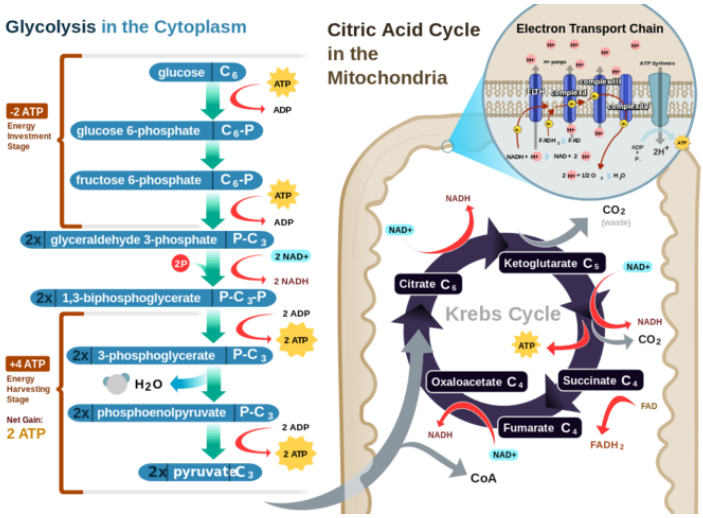


Figure 7.6.1: Cellular respiration in a eukaryotic cell: Glycolysis on the left portion of this illustration can be seen to yield 2 ATP molecules, while the Electron Transport Chain portion at the upper right will yield the remaining 30-32 ATP molecules under the presence of oxygen.

The number of ATP molecules generated via the catabolism of glucose can vary substantially. For example, the number of hydrogen ions the electron transport chain complexes can pump through the membrane varies between species. Another source of variance occurs during the shuttle of electrons across the membranes of the mitochondria. The NADH generated from glycolysis cannot easily enter mitochondria. Thus, electrons are picked up on the inside of mitochondria by either NAD^+ or FAD^+. These

FAD^+ molecules can transport fewer ions; consequently, fewer ATP molecules are generated when FAD^+ acts as a carrier. NAD^+ is used as the electron transporter in the liver, and FAD^+ acts in the brain.

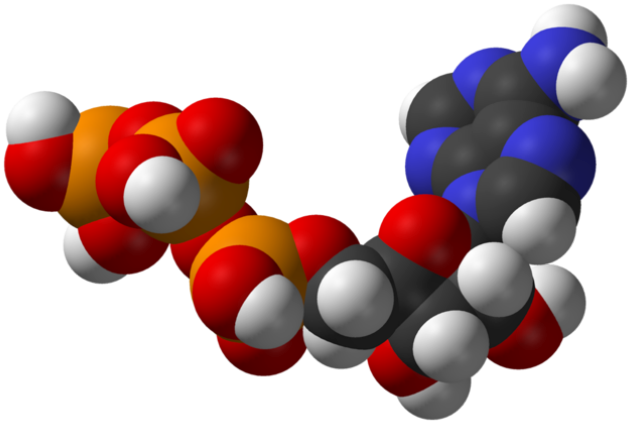


Figure **7.6.1**: Adenosine triphosphate: ATP is the main source of energy in many living organisms.

Another factor that affects the yield of ATP molecules generated from glucose is the fact that intermediate compounds in these pathways are used for other purposes. Glucose catabolism connects with the pathways that build or break down all other biochemical compounds in cells, but the result is not always ideal. For example, sugars other than glucose are fed into the glycolytic pathway for energy extraction. Moreover, the five-carbon sugars that form nucleic acids are made from intermediates in glycolysis. Certain nonessential amino acids can be made from intermediates of both glycolysis and the citric acid cycle. Lipids, such as cholesterol and triglycerides, are also made from intermediates in these pathways, and both amino acids and triglycerides are broken down for energy through these pathways. Overall, in living systems, these pathways of glucose catabolism extract about 34 percent of the energy contained in glucose.

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SECTION OVERVIEW

7.7: Regulation of Aerobic Respiration

7.7.1: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways

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7.7.1: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways

Skills to Develop

- Discuss the ways in which carbohydrate metabolic pathways, glycolysis, and the citric acid cycle interrelate with protein and lipid metabolic pathways
- Explain why metabolic pathways are not considered closed systems

You have learned about the catabolism of glucose, which provides energy to living cells. But living things consume more than glucose for food. How does a turkey sandwich end up as ATP in your cells? This happens because all of the catabolic pathways for carbohydrates, proteins, and lipids eventually connect into glycolysis and the citric acid cycle pathways (see Figure **7.7.1.2**). Metabolic pathways should be thought of as porous—that is, substances enter from other pathways, and intermediates leave for other pathways. These pathways are not closed systems. Many of the substrates, intermediates, and products in a particular pathway are reactants in other pathways.

Connections of Other Sugars to Glucose Metabolism

Glycogen, a polymer of glucose, is an energy storage molecule in animals. When there is adequate ATP present, excess glucose is shunted into glycogen for storage. Glycogen is made and stored in both liver and muscle. The glycogen will be hydrolyzed into glucose monomers (G-1-P) if blood sugar levels drop. The presence of glycogen as a source of glucose allows ATP to be produced for a longer period of time during exercise. Glycogen is broken down into G-1-P and converted into G-6-P in both muscle and liver cells, and this product enters the glycolytic pathway.

Sucrose is a disaccharide with a molecule of glucose and a molecule of fructose bonded together with a glycosidic linkage. Fructose is one of the three dietary monosaccharides, along with glucose and galactose (which is part of the milk sugar, the disaccharide lactose), which are absorbed directly into the bloodstream during digestion. The catabolism of both fructose and galactose produces the same number of ATP molecules as glucose.

Connections of Proteins to Glucose Metabolism

Proteins are hydrolyzed by a variety of enzymes in cells. Most of the time, the amino acids are recycled into the synthesis of new proteins. If there are excess amino acids, however, or if the body is in a state of starvation, some amino acids will be shunted into the pathways of glucose catabolism (Figure **7.7.1.1**). Each amino acid must have its amino group removed prior to entry into these pathways. The amino group is converted into ammonia. In mammals, the liver synthesizes urea from two ammonia molecules and a carbon dioxide molecule. Thus, urea is the principal waste product in mammals produced from the nitrogen originating in amino acids, and it leaves the body in urine.

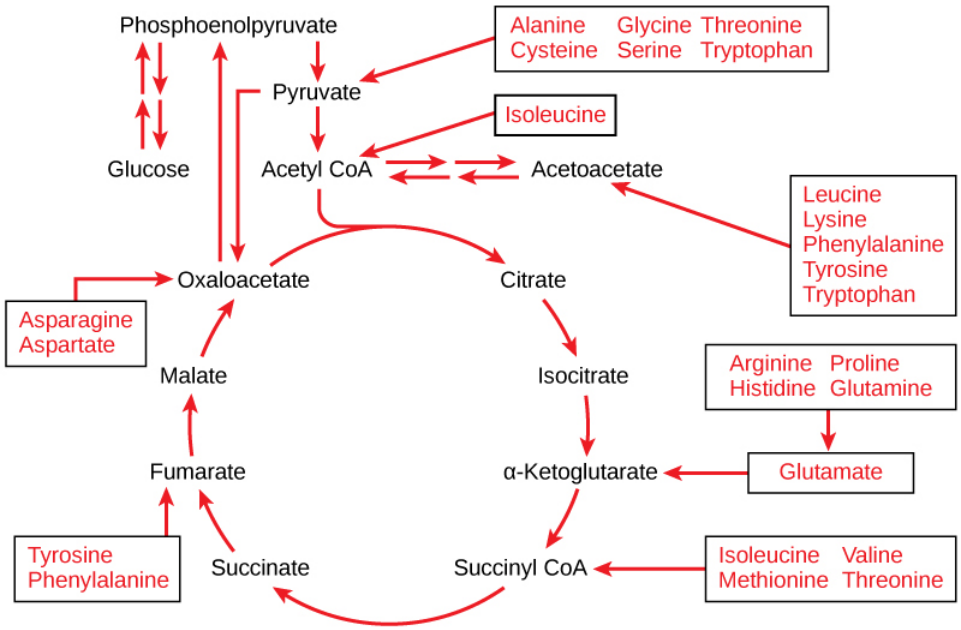


Figure **7.7.1.1**: The carbon skeletons of certain amino acids (indicated in boxes) derived from proteins can feed into the citric acid cycle. (credit: modification of work by Mikael Häggström)

Connections of Lipid and Glucose Metabolisms

The lipids that are connected to the glucose pathways are cholesterol and triglycerides. Cholesterol is a lipid that contributes to cell membrane flexibility and is a precursor of steroid hormones. The synthesis of cholesterol starts with acetyl groups and proceeds in only one direction. The process cannot be reversed.

Triglycerides are a form of long-term energy storage in animals. Triglycerides are made of glycerol and three fatty acids. Animals can make most of the fatty acids they need. Triglycerides can be both made and broken down through parts of the glucose catabolism pathways. Glycerol can be phosphorylated to glycerol-3-phosphate, which continues through glycolysis. Fatty acids are catabolized in a process called beta-oxidation that takes place in the matrix of the mitochondria and converts their fatty acid chains into two carbon units of acetyl groups. The acetyl groups are picked up by CoA to form acetyl CoA that proceeds into the citric acid cycle.

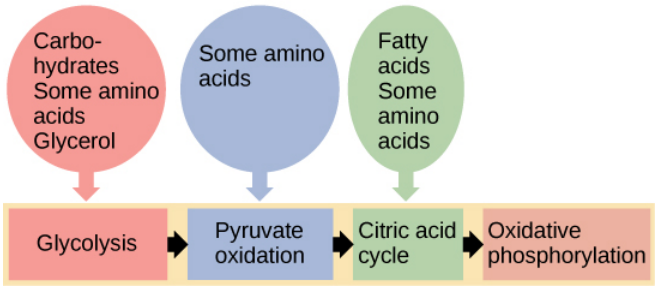


Figure **7.7.1.2**: Glycogen from the liver and muscles, hydrolyzed into glucose-1-phosphate, together with fats and proteins, can feed into the catabolic pathways for carbohydrates.

Evolution Connection: Pathways of Photosynthesis and Cellular Metabolism

The processes of photosynthesis and cellular metabolism consist of several very complex pathways. It is generally thought that the first cells arose in an aqueous environment—a “soup” of nutrients—probably on the surface of some porous clays. If these cells reproduced successfully and their numbers climbed steadily, it follows that the cells would begin to deplete the nutrients from the medium in which they lived as they shifted the nutrients into the components of their own bodies. This hypothetical situation would have resulted in natural selection favoring those organisms that could exist by using the nutrients that remained in their environment and by manipulating these nutrients into materials upon which they could survive. Selection would favor those organisms that could extract maximal value from the nutrients to which they had access.

An early form of photosynthesis developed that harnessed the sun's energy using water as a source of hydrogen atoms, but this pathway did not produce free oxygen (anoxygenic photosynthesis). (Early photosynthesis did not produce free oxygen because it did not use water as the source of hydrogen ions; instead, it used materials like hydrogen sulfide and consequently produced sulfur). It is thought that glycolysis developed at this time and could take advantage of the simple sugars being produced, but these reactions were unable to fully extract the energy stored in the carbohydrates. The development of glycolysis probably predated the evolution of photosynthesis, as it was well suited to extract energy from materials spontaneously accumulating in the "primeval soup." A later form of photosynthesis used water as a source of electrons and hydrogen, and generated free oxygen. Over time, the atmosphere became oxygenated, but not before the oxygen released oxidized metals in the ocean and created a "rust" layer in the sediment, permitting the dating of the rise of the first oxygenic photosynthesizers. Living things adapted to exploit this new atmosphere that allowed aerobic respiration as we know it to evolve. When the full process of oxygenic photosynthesis developed and the atmosphere became oxygenated, cells were finally able to use the oxygen expelled by photosynthesis to extract considerably more energy from the sugar molecules using the citric acid cycle and oxidative phosphorylation.

Summary

The breakdown and synthesis of carbohydrates, proteins, and lipids connect with the pathways of glucose catabolism. The simple sugars are galactose, fructose, glycogen, and pentose. These are catabolized during glycolysis. The amino acids from proteins connect with glucose catabolism through pyruvate, acetyl CoA, and components of the citric acid cycle. Cholesterol synthesis starts with acetyl groups, and the components of triglycerides come from glycerol-3-phosphate from glycolysis and acetyl groups produced in the mitochondria from pyruvate.

Contributors and Attributions

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7.8: Oxidation without O2

Skills to Develop

- Discuss the fundamental difference between anaerobic cellular respiration and fermentation
- Describe the type of fermentation that readily occurs in animal cells and the conditions that initiate that fermentation

In aerobic respiration, the final electron acceptor is an oxygen molecule, O_2. If aerobic respiration occurs, then ATP will be produced using the energy of high-energy electrons carried by NADH or $FADH_2$ to the electron transport chain. If aerobic respiration does not occur, NADH must be reoxidized to NAD^+ for reuse as an electron carrier for the glycolytic pathway to continue. How is this done? Some living systems use an organic molecule as the final electron acceptor. Processes that use an organic molecule to regenerate NAD^+ from NADH are collectively referred to as fermentation. In contrast, some living systems use an inorganic molecule as a final electron acceptor. Both methods are called anaerobic cellular respiration in which organisms convert energy for their use in the absence of oxygen.

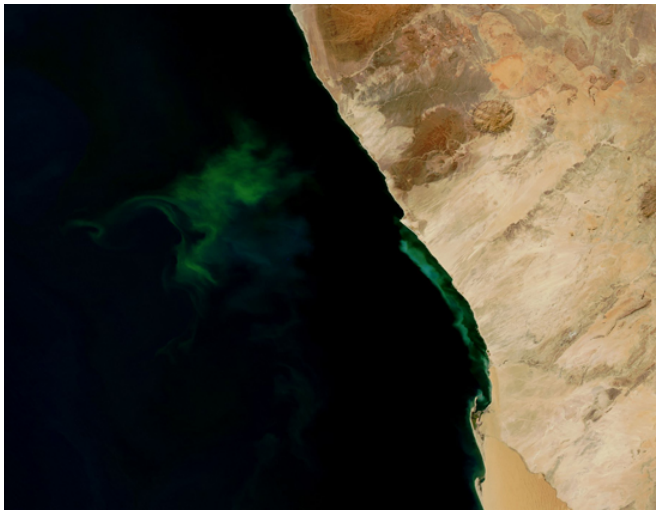
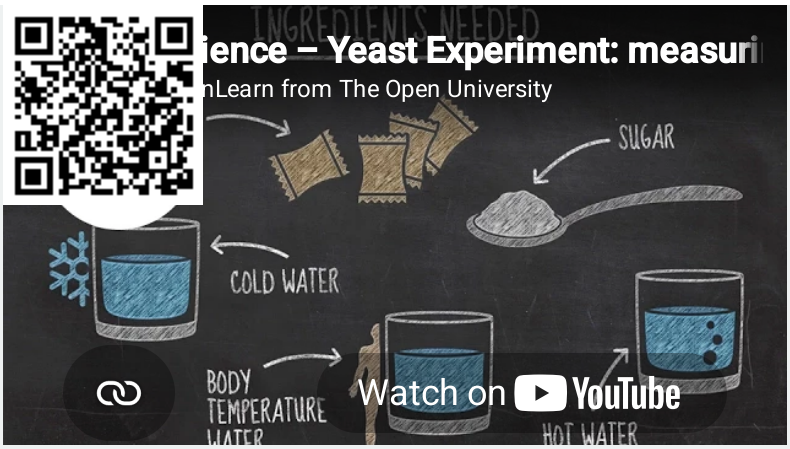


Figure 7.8.1: The green color seen in these coastal waters is from an eruption of hydrogen sulfide-producing bacteria. These anaerobic, sulfate-reducing bacteria release hydrogen sulfide gas as they decompose algae in the water. (credit: modification of work by NASA/Jeff Schmaltz, MODIS Land Rapid Response Team at NASA GSFC, Visible Earth Catalog of NASA images)

Anaerobic Cellular Respiration

Certain prokaryotes, including some species of bacteria and Archaea, use anaerobic respiration. For example, the group of Archaea called methanogens reduces carbon dioxide to methane to oxidize NADH. These microorganisms are found in soil and in the digestive tracts of ruminants, such as cows and sheep. Similarly, sulfate-reducing bacteria and Archaea, most of which are anaerobic (Figure 7.8.1), reduce sulfate to hydrogen sulfide to regenerate NAD^+ from NADH.

Link to Learning



Video 7.8.1: Watch this video to see anaerobic cellular respiration in action.

Lactic Acid Fermentation

The fermentation method used by animals and certain bacteria, like those in yogurt, is lactic acid fermentation (Figure 7.8.2). This type of fermentation is used routinely in mammalian red blood cells and in skeletal muscle that has an insufficient oxygen supply to allow aerobic respiration to continue (that is, in muscles used to the point of fatigue). In muscles, lactic acid accumulation must be removed by the blood circulation and the lactate brought to the liver for further metabolism. The chemical reactions of lactic acid fermentation are the following:

$$\text{Pyruvic acid} + \text{NADH} \leftrightarrow \text{lactic acid} + \text{NAD}^+$$

The enzyme used in this reaction is lactate dehydrogenase (LDH). The reaction can proceed in either direction, but the reaction from left to right is inhibited by acidic conditions. Such lactic acid accumulation was once believed to cause muscle stiffness, fatigue, and soreness, although more recent research disputes this hypothesis. Once the lactic acid has been removed from the muscle and circulated to the liver, it can be reconverted into pyruvic acid and further catabolized for energy.

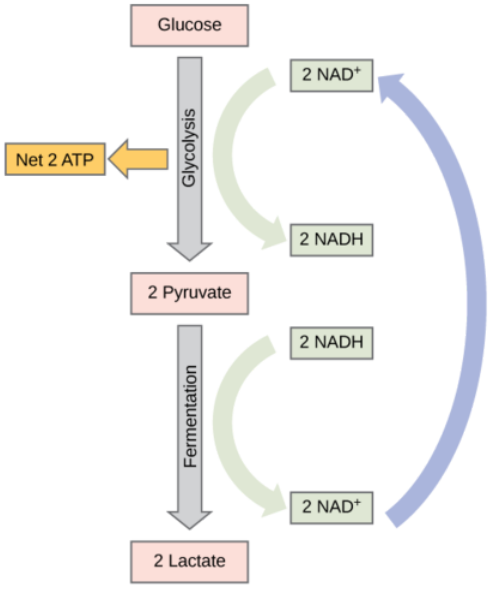


Figure 7.8.2: Lactic acid fermentation is common in muscle cells that have run out of oxygen.

Exercise 7.8.1

Tremetol, a metabolic poison found in the white snake root plant, prevents the metabolism of lactate. When cows eat this plant, it is concentrated in the milk they produce. Humans who consume the milk become ill. Symptoms of this disease, which include vomiting, abdominal pain, and tremors, become worse after exercise. Why do you think this is the case?

Answer

The illness is caused by lactate accumulation. Lactate levels rise after exercise, making the symptoms worse. Milk sickness is rare today, but was common in the Midwestern United States in the early 1800s.

Alcohol Fermentation

Another familiar fermentation process is alcohol fermentation (Figure **7.8.3**) that produces ethanol, an alcohol. The first chemical reaction of alcohol fermentation is the following (CO_2 does not participate in the second reaction):

$$\text{Pyruvic acid} \rightarrow CO_2 + \text{acetaldehyde} + NADH \rightarrow \text{ethanol} + NAD^+$$

The first reaction is catalyzed by pyruvate decarboxylase, a cytoplasmic enzyme, with a coenzyme of thiamine pyrophosphate (TPP, derived from vitamin B_1 and also called thiamine). A carboxyl group is removed from pyruvic acid, releasing carbon dioxide as a gas. The loss of carbon dioxide reduces the size of the molecule by one carbon, making acetaldehyde. The second reaction is catalyzed by alcohol dehydrogenase to oxidize NADH to NAD^+ and reduce acetaldehyde to ethanol. The fermentation of pyruvic acid by yeast produces the ethanol found in alcoholic beverages. Ethanol tolerance of yeast is variable, ranging from about 5 percent to 21 percent, depending on the yeast strain and environmental conditions.



Figure **7.8.3**: Fermentation of grape juice into wine produces CO_2 as a byproduct. Fermentation tanks have valves so that the pressure inside the tanks created by the carbon dioxide produced can be released.

Other Types of Fermentation

Other fermentation methods occur in bacteria. Many prokaryotes are facultatively anaerobic. This means that they can switch between aerobic respiration and fermentation, depending on the availability of oxygen. Certain prokaryotes, like *Clostridia*, are obligate anaerobes. Obligate anaerobes live and grow in the absence of molecular oxygen. Oxygen is a poison to these microorganisms and kills them on exposure. It should be noted that all forms of fermentation, except lactic acid fermentation, produce gas. The production of particular types of gas is used as an indicator of the fermentation of specific carbohydrates, which plays a role in the laboratory identification of the bacteria. Various methods of fermentation are used by assorted organisms to ensure an adequate supply of NAD^+ for the sixth step in glycolysis. Without these pathways, that step would not occur and no ATP would be harvested from the breakdown of glucose.

Summary

If NADH cannot be oxidized through aerobic respiration, another electron acceptor is used. Most organisms will use some form of fermentation to accomplish the regeneration of NAD^+, ensuring the continuation of glycolysis. The regeneration of NAD^+ in fermentation is not accompanied by ATP production; therefore, the potential of NADH to produce ATP using an electron transport chain is not utilized.

anaerobic cellular respiration

process in which organisms convert energy for their use in the absence of oxygen

fermentation

process of regenerating NAD^+ with either an inorganic or organic compound serving as the final electron acceptor, occurs in the absence; occurs in the absence of oxygen

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SECTION OVERVIEW

7.9: Catabolism of Proteins and Fats

7.9.1: Connecting Proteins to Glucose Metabolism

7.9.2: Connecting Lipids to Glucose Metabolism

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7.9.1: Connecting Proteins to Glucose Metabolism

Learning Objectives

- Describe the role played by proteins in glucose metabolism

Metabolic pathways should be thought of as porous; that is, substances enter from other pathways and intermediates leave for other pathways. These pathways are not closed systems. Many of the substrates, intermediates, and products in a particular pathway are reactants in other pathways. Proteins are a good example of this phenomenon. They can be broken down into their constituent amino acids and used at various steps of the pathway of glucose catabolism.

Proteins are hydrolyzed by a variety of enzymes in cells. Most of the time, the amino acids are recycled into the synthesis of new proteins or are used as precursors in the synthesis of other important biological molecules, such as hormones, nucleotides, or neurotransmitters. However, if there are excess amino acids, or if the body is in a state of starvation, some amino acids will be shunted into the pathways of glucose catabolism.

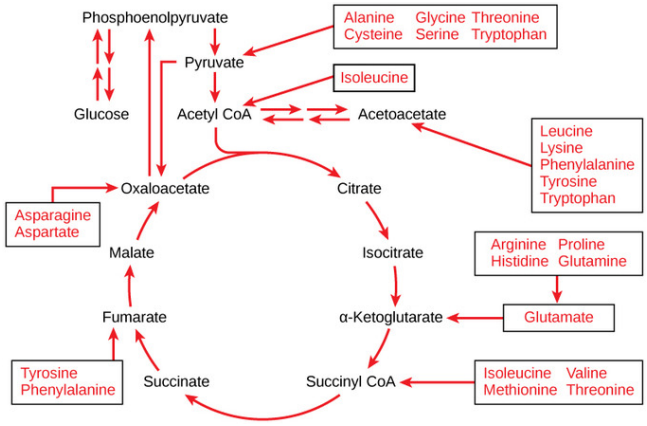


Figure **7.9.1.1**: Connection of Amino Acids to Glucose Metabolism Pathways: The carbon skeletons of certain amino acids (indicated in boxes) are derived from proteins and can feed into pyruvate, acetyl CoA, and the citric acid cycle.

Each amino acid must have its amino group removed (deamination) prior to the carbon chain's entry into these pathways. When the amino group is removed from an amino acid, it is converted into ammonia through the urea cycle. The remaining atoms of the amino acid result in a keto acid: a carbon chain with one ketone and one carboxylic acid group. In mammals, the liver synthesizes urea from two ammonia molecules and a carbon dioxide molecule. Thus, urea is the principal waste product in mammals produced from the nitrogen originating in amino acids; it leaves the body in urine. The keto acid can then enter the citric acid cycle.

When deaminated, amino acids can enter the pathways of glucose metabolism as pyruvate, acetyl CoA, or several components of the citric acid cycle. For example, deaminated asparagine and aspartate are converted into oxaloacetate and enter glucose catabolism in the citric acid cycle. Deaminated amino acids can also be converted into another intermediate molecule before entering the pathways. Several amino acids can enter glucose catabolism at multiple locations.

Key Points

- Amino acids must be deaminated before entering any of the pathways of glucose catabolism: the amino group is converted to ammonia, which is used by the liver in the synthesis of urea.
- Deaminated amino acids can be converted into pyruvate, acetyl CoA, or some components of the citric acid cycle to enter the pathways of glucose catabolism.
- Several amino acids can enter the glucose catabolism pathways at multiple locations.

Key Terms

- **catabolism**: Destructive metabolism, usually including the release of energy and breakdown of materials.
- **keto acid**: Any carboxylic acid that also contains a ketone group.
- **deamination**: The removal of an amino group from a compound.

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7.9.2: Connecting Lipids to Glucose Metabolism

Learning Objectives

- Explain the connection of lipids to glucose metabolism

Like sugars and amino acids, the catabolic pathways of lipids are also connected to the glucose catabolism pathways. The lipids that are connected to the glucose pathways are cholesterol and triglycerides.

Cholesterol

Cholesterol contributes to cell membrane flexibility and is a precursor to steroid hormones. The synthesis of cholesterol starts with acetyl groups, which are transferred from acetyl CoA, and proceeds in only one direction; the process cannot be reversed. Thus, synthesis of cholesterol requires an intermediate of glucose metabolism.

Triglycerides

Triglycerides, a form of long-term energy storage in animals, are made of glycerol and three fatty acids. Animals can make most of the fatty acids they need. Triglycerides can be both made and broken down through parts of the glucose catabolism pathways. Glycerol can be phosphorylated to glycerol-3-phosphate, which continues through glycolysis.

Fatty acids are catabolized in a process called beta-oxidation that takes place in the matrix of the mitochondria and converts their fatty acid chains into two carbon units of acetyl groups, while producing NADH and $FADH_2$. The acetyl groups are picked up by CoA to form acetyl CoA that proceeds into the citric acid cycle as it combines with oxaloacetate. The NADH and $FADH_2$ are then used by the electron transport chain.

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Key Points

- Many types of lipids exist, but cholesterol and triglycerides are the lipids that enter the pathways of glucose catabolism.
- Through the process of phosphorylation, glycerol can be converted to glycerol-3-phosphate during the glycolytic pathway.
- When fatty acids are broken down into acetyl groups through beta-oxidation, the acetyl groups are used by CoA to form acetyl-CoA, which enters the citric acid cycle to produce ATP.
- Beta-oxidation produces $FADH_2$ and NADH, which are used by the electron transport chain for ATP production.

Key Terms

- **beta-oxidation**: A process that takes place in the matrix of the mitochondria and catabolizes fatty acids by converting them to acetyl groups while producing NADH and FADH2.
- **lipid**: A group of organic compounds including fats, oils, waxes, sterols, and triglycerides; characterized by being insoluble in water; account for most of the fat present in the human body.

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7.10: Evolution of Metabolism

Many models have been proposed to describe the mechanisms by which novel metabolic pathways evolve. These include the sequential addition of novel enzymes to a short ancestral pathway, the duplication and then divergence of entire pathways as well as the recruitment of pre-existing enzymes and their assembly into a novel reaction pathway. [1] The relative importance of these mechanisms is unclear, but genomic studies have shown that enzymes in a pathway are likely to have a shared ancestry, suggesting that many pathways have evolved in a step-by-step fashion with novel functions created from pre-existing steps in the pathway. [2] An alternative model comes from studies that trace the evolution of proteins' structures in metabolic networks, this has suggested that enzymes are pervasively recruited, borrowing enzymes to perform similar functions in different metabolic pathways (evident in the MANET database).[3] These recruitment processes result in an evolutionary enzymatic mosaic. [4]. A third possibility is that some parts of metabolism might exist as "modules" that can be reused in different pathways and perform similar functions on different molecules.[5].

As well as the evolution of new metabolic pathways, evolution can also cause the loss of metabolic functions. For example, in some parasites metabolic processes that are not essential for survival are lost and preformed amino acids, nucleotides and carbohydrates may instead be scavenged from the host [6]. Similar reduced metabolic capabilities are seen in endosymbiotic organisms. [7]

A striking feature of metabolism is the similarity of the basic metabolic pathways among vastly different species[8]. For example, the set of carboxylic acids that are best known as the intermediates in the citric acid cycle are present in all known organisms, being found in species as diverse as the unicellular bacterium *Escherichia coli* and huge multicellular organisms like elephants.[9]. These similarities in metabolic pathways are likely due to their early appearance in evolutionary history, and their retention is likely due to their efficacy.[10,11]. In various diseases, such as type II diabetes, metabolic syndrome, and cancer, normal metabolism is disrupted.[12]. The metabolism of cancer cells is also different from the metabolism of normal cells, and these differences can be used to find targets for therapeutic intervention in cancer.[13]

Excerpted from Wikipedia: Metabolism https://en.wikipedia.org/wiki/Metabolism Accessed 14. November 2023

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CHAPTER OVERVIEW

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SECTION OVERVIEW

8.1: Overview of Photosynthesis

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8.1.1: The Purpose and Process of Photosynthesis

Learning Objectives

- Describe the process of photosynthesis

The Importance of Photosynthesis

The processes of all organisms—from bacteria to humans—require energy. To get this energy, many organisms access stored energy by eating food. Carnivores eat other animals and herbivores eat plants. But where does the stored energy in food originate? All of this energy can be traced back to the process of photosynthesis and light energy from the sun.

Photosynthesis is essential to all life on earth. It is the only biological process that captures energy from outer space (sunlight) and converts it into chemical energy in the form of G3P (
Glyceraldehyde 3-phosphate) which in turn can be made into sugars and other molecular compounds. Plants use these compounds in all of their metabolic processes; plants do not need to consume other organisms for food because they build all the molecules they need. Unlike plants, animals need to consume other organisms to consume the molecules they need for their metabolic processes.

The Process of Photosynthesis

During photosynthesis, molecules in leaves capture sunlight and energize electrons, which are then stored in the covalent bonds of carbohydrate molecules. That energy within those covalent bonds will be released when they are broken during cell respiration. How long lasting and stable are those covalent bonds? The energy extracted today by the burning of coal and petroleum products represents sunlight energy captured and stored by photosynthesis almost 200 million years ago.

Plants, algae, and a group of bacteria called cyanobacteria are the only organisms capable of performing photosynthesis. Because they use light to manufacture their own food, they are called photoautotrophs (“self-feeders using light”). Other organisms, such as animals, fungi, and most other bacteria, are termed heterotrophs (“other feeders”) because they must rely on the sugars produced by photosynthetic organisms for their energy needs. A third very interesting group of bacteria synthesize sugars, not by using sunlight’s energy, but by extracting energy from inorganic chemical compounds; hence, they are referred to as chemoautotrophs.

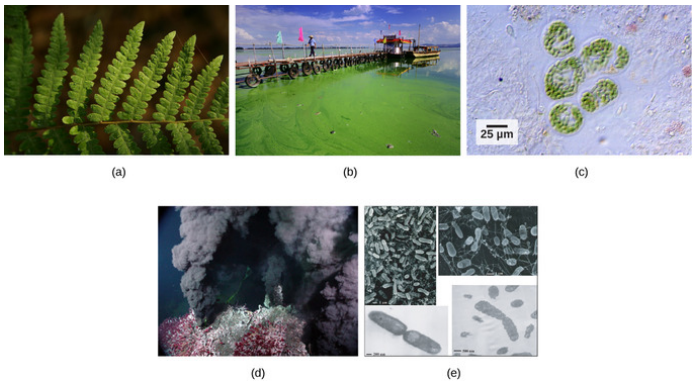


Figure **8.1.1.1**: Photosynthetic and Chemosynthetic Organisms: Photoautotrophs, including (a) plants, (b) algae, and (c) cyanobacteria, synthesize their organic compounds via photosynthesis using sunlight as an energy source. Cyanobacteria and planktonic algae can grow over enormous areas in water, at times completely covering the surface. In a (d) deep sea vent, chemoautotrophs, such as these (e) thermophilic bacteria, capture energy from inorganic compounds to produce organic compounds. The ecosystem surrounding the vents has a diverse array of animals, such as tubeworms, crustaceans, and octopuses that derive energy from the bacteria.

The importance of photosynthesis is not just that it can capture sunlight’s energy. A lizard sunning itself on a cold day can use the sun’s energy to warm up. Photosynthesis is vital because it evolved as a way to store the energy in solar radiation (the “photo-” part) as high-energy electrons in the carbon-carbon bonds of carbohydrate molecules (the “-synthesis” part). Those carbohydrates are the energy source that heterotrophs use to power the synthesis of ATP via respiration. Therefore, photosynthesis powers 99

percent of Earth’s ecosystems. When a top predator, such as a wolf, preys on a deer, the wolf is at the end of an energy path that went from nuclear reactions on the surface of the sun, to light, to photosynthesis, to vegetation, to deer, and finally to wolf.

Key Points

- Photosynthesis evolved as a way to store the energy in solar radiation as high-energy electrons in carbohydrate molecules.
- Plants, algae, and cyanobacteria, known as photoautotrophs, are the only organisms capable of performing photosynthesis.
- Heterotrophs, unable to produce their own food, rely on the carbohydrates produced by photosynthetic organisms for their energy needs.

Key Terms

- **photosynthesis**: the process by which plants and other photoautotrophs generate carbohydrates and oxygen from carbon dioxide, water, and light energy in chloroplasts
- **photoautotroph**: an organism that can synthesize its own food by using light as a source of energy
- **chemoautotroph**: a simple organism, such as a protozoan, that derives its energy from chemical processes rather than photosynthesis

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8.1.2: Main Structures and Summary of Photosynthesis

Learning Objectives

- Describe the main structures involved in photosynthesis and recall the chemical equation that summarizes the process of photosynthesis

Overview of Photosynthesis

Photosynthesis is a multi-step process that requires sunlight, carbon dioxide, and water as substrates. It produces oxygen and glyceraldehyde-3-phosphate (G3P or GA3P), simple carbohydrate molecules that are high in energy and can subsequently be converted into glucose, sucrose, or other sugar molecules. These sugar molecules contain covalent bonds that store energy. Organisms break down these molecules to release energy for use in cellular work.

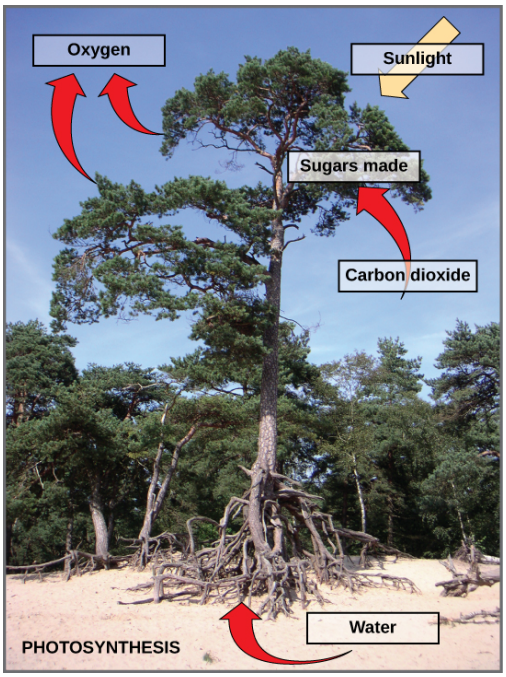


Figure **8.1.2.1**: Photosynthesis: Photosynthesis uses solar energy, carbon dioxide, and water to produce energy-storing carbohydrates. Oxygen is generated as a waste product of photosynthesis.

The energy from sunlight drives the reaction of carbon dioxide and water molecules to produce sugar and oxygen, as seen in the chemical equation for photosynthesis. Though the equation looks simple, it is carried out through many complex steps. Before learning the details of how photoautotrophs convert light energy into chemical energy, it is important to become familiar with the structures involved.

Photosynthesis Equation							
Carbon dioxide	+	Water	SUNLIGHT →	Sugar	+	Oxygen	
$6CO_2$		$6H_2O$		$C_6H_{12}O_6$		$6O_2$	

Figure **8.1.2.1**: Chemical equation for photosynthesis: The basic equation for photosynthesis is deceptively simple. In reality, the process includes many steps involving intermediate reactants and products. Glucose, the primary energy source in cells, is made from two three-carbon GA3P molecules.

Photosynthesis and the Leaf

In plants, photosynthesis generally takes place in leaves, which consist of several layers of cells. The process of photosynthesis occurs in a middle layer called the mesophyll. The gas exchange of carbon dioxide and oxygen occurs through small, regulated

openings called stomata (singular: stoma), which also play a role in the plant's regulation of water balance. The stomata are typically located on the underside of the leaf, which minimizes water loss. Each stoma is flanked by guard cells that regulate the opening and closing of the stomata by swelling or shrinking in response to osmotic changes.

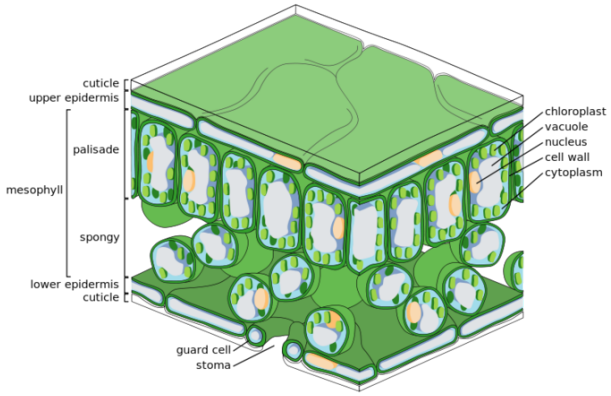


Figure **8.1.2.1**: Structure of a leaf (cross-section): Photosynthesis takes place in the mesophyll. The palisade layer contains most of the chloroplast and principal region in which photosynthesis is carried out. The airy spongy layer is the region of storage and gas exchange. The stomata regulate carbon dioxide and water balance.

Photosynthesis within the Chloroplast

In all autotrophic eukaryotes, photosynthesis takes place inside an organelle called a chloroplast. For plants, chloroplast-containing cells exist in the mesophyll. Chloroplasts have a double membrane envelope composed of an outer membrane and an inner membrane. Within the double membrane are stacked, disc-shaped structures called thylakoids.

Embedded in the thylakoid membrane is chlorophyll, a pigment that absorbs certain portions of the visible spectrum and captures energy from sunlight. Chlorophyll gives plants their green color and is responsible for the initial interaction between light and plant material, as well as numerous proteins that make up the electron transport chain. The thylakoid membrane encloses an internal space called the thylakoid lumen. A stack of thylakoids is called a granum, and the liquid-filled space surrounding the granum is the stroma or "bed."

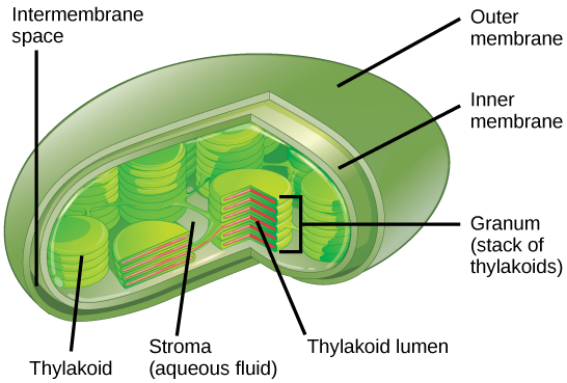


Figure **8.1.2.1**: Structure of the Chloroplast: Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. Stacks of thylakoids called grana form a third membrane layer.

Key Points

- The chemical equation for photosynthesis is $6CO2+6H2O \rightarrow C6H12O6+6O2$.$6CO2+6H2O \rightarrow C6H12O6+6O2$.
- In plants, the process of photosynthesis takes place in the mesophyll of the leaves, inside the chloroplasts.
- Chloroplasts contain disc-shaped structures called thylakoids, which contain the pigment chlorophyll.
- Chlorophyll absorbs certain portions of the visible spectrum and captures energy from sunlight.

Key Terms

- **chloroplast**: An organelle found in the cells of green plants and photosynthetic algae where photosynthesis takes place.
- **mesophyll**: A layer of cells that comprises most of the interior of the leaf between the upper and lower layers of epidermis.

- **stoma**: A pore in the leaf and stem epidermis that is used for gaseous exchange.

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8.1.3: The Two Parts of Photosynthesis

Learning Objectives

- Distinguish between the two parts of photosynthesis

Light-Dependent Reactions

Just as the name implies, light-dependent reactions require sunlight. In the light-dependent reactions, energy from sunlight is absorbed by chlorophyll and converted into stored chemical energy, in the form of the electron carrier molecule NADPH (nicotinamide adenine dinucleotide phosphate) and the energy currency molecule ATP (adenosine triphosphate). The light-dependent reactions take place in the thylakoid membranes in the granum (stack of thylakoids), within the chloroplast.

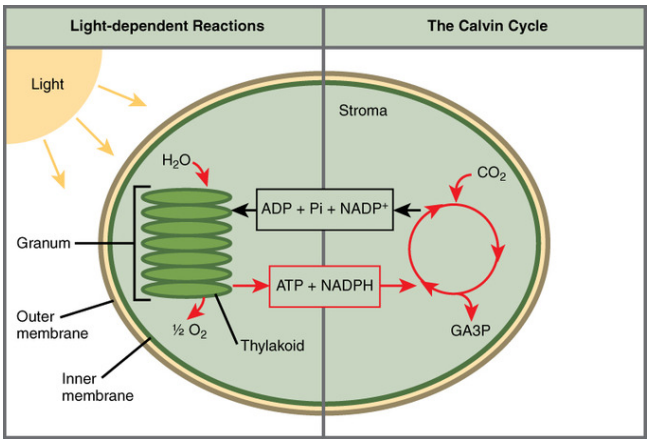


Figure **8.1.3.1**: The two stages of photosynthesis: Photosynthesis takes place in two stages: light-dependent reactions and the Calvin cycle (light-independent reactions). Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. The Calvin cycle, which takes place in the stroma, uses energy derived from these compounds to make GA3P from CO2.

Photosystems

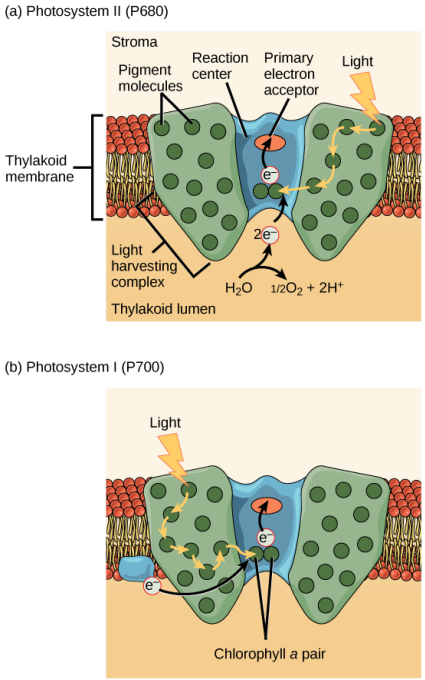


Figure **8.1.3.1**: Photosystems I & II: As explained above, the photosystems manipulate electrons with energy harvested from light.

The process that converts light energy into chemical energy takes place in a multi-protein complex called a photosystem. Two types of photosystems are embedded in the thylakoid membrane: photosystem II (PSII) and photosystem I (PSI). Each photosystem plays a key role in capturing the energy from sunlight by exciting electrons. These energized electrons are transported by “energy carrier” molecules, which power the light-independent reactions.

Photosystems consist of a light-harvesting complex and a reaction center. Pigments in the light-harvesting complex pass light energy to two special chlorophyll *a* molecules in the reaction center. The light excites an electron from the chlorophyll *a* pair, which passes to the primary electron acceptor. The excited electron must then be replaced. In photosystem II, the electron comes from the splitting of water, which releases oxygen as a waste product. In photosystem I, the electron comes from the chloroplast electron transport chain.

The two photosystems oxidize different sources of the low-energy electron supply, deliver their energized electrons to different places, and respond to different wavelengths of light.

Light-Independent Reactions

In the light-independent reactions or Calvin cycle, the energized electrons from the light-dependent reactions provide the energy to form carbohydrates from carbon dioxide molecules. The light-independent reactions are sometimes called the Calvin cycle because of the cyclical nature of the process.

Although the light-independent reactions do not use light as a reactant (and as a result can take place at day or night), they require the products of the light-dependent reactions to function. The light-independent molecules depend on the energy carrier molecules, ATP and NADPH, to drive the construction of new carbohydrate molecules. After the energy is transferred, the energy carrier molecules return to the light-dependent reactions to obtain more energized electrons. In addition, several enzymes of the light-independent reactions are activated by light.

Photosynthesis takes place in two sequential stages:

1. The light-dependent reactions;
2. The light-independent reactions, or Calvin Cycle.

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Key Points

- In light-dependent reactions, the energy from sunlight is absorbed by chlorophyll and converted into chemical energy in the form of electron carrier molecules like ATP and NADPH.
- Light energy is harnessed in Photosystems I and II, both of which are present in the thylakoid membranes of chloroplasts.
- In light-independent reactions (the Calvin cycle), carbohydrate molecules are assembled from carbon dioxide using the chemical energy harvested during the light-dependent reactions.

Key Terms

- **photosystem**: Either of two biochemical systems active in chloroplasts that are part of photosynthesis.

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8.2: Photosynthesis - Dicovering the Secrets

This chapter talks about various scientists and their path towards discovering photosynthesis.

van Helmont

Perhaps the first experiment designed to explore the nature of photosynthesis was that reported by the Dutch physician van Helmont in 1648. Some years earlier, van Helmont had placed in a large pot exactly 200 pounds (91 kg) of soil that had been thoroughly dried in an oven. Then he moistened the soil with rain water and planted a 5-pound (2.3 kg) willow shoot in it. He then placed the pot in the ground and covered its rim with a perforated iron plate. The perforations allowed water and air to reach the soil but lessened the chance that dirt or other debris would be blown into the pot from the outside.

For five years, van Helmont kept his plant watered with rain water or distilled water. At the end of that time, he carefully removed the young tree and found that it had gained 164 pound, 3 ounces (74.5 kg). (This figure did not include the weight of the leaves that had been shed during the previous four autumns.) He then redried the soil and found that it weighed only 2 ounces (57 g) less that the original 200 pounds (91 kg). Faced with these experimental facts, van Helmont theorized that the increase in weight of the willow arose from the water alone. He did not consider the possibility that gases in the air might be involved.

Joseph Priestley

The first evidence that gases participate in photosynthesis was reported by Joseph Priestley in 1772. He knew that if a burning candle is placed in a sealed chamber, the candle soon goes out. If a mouse is then placed in the chamber, it soon suffocates because the process of combustion has used up all the oxygen in the air — the gas on which animal respiration depends. However, Priestley discovered that if a plant is placed in an atmosphere lacking oxygen, it soon replenishes the oxygen, and a mouse can survive in the resulting mixture. Priestley thought (erroneously) that it was simply the growth of the plant that accounted for this.

Ingen-Housz

It was another Dutch physician, Ingen-Housz, who discovered in 1778 that the effect observed by Priestley occurred only when the plant was illuminated. A plant kept in the dark in a sealed chamber consumes oxygen just as a mouse (or candle) does.

Ingen-Housz also demonstrated that only green parts of plants liberated oxygen during photosynthesis. Nongreen plant structure, such as woody stems, roots, flowers, and fruits actually consume oxygen in the process of respiration. We now know that this is because photosynthesis can go on only in the presence of the green pigment chlorophyll.

Jean Senebier

The growth of plants is accompanied by an increase in their carbon content. A Swiss minister, Jean Senebier, discovered that the source of this carbon is carbon dioxide and that the release of oxygen during photosynthesis accompanies the uptake of carbon dioxide. Senebier concluded (erroneously as it turned out) that in photosynthesis carbon dioxide is decomposed, with the carbon becoming incorporated in the organic matter of the plant and the oxygen being released.

$$CO_2 + H_2O \rightarrow (CH_2O) + O_2$$

(The parentheses around the CH_2O signify that no specific molecule is being indicated but, instead, the ratio of atoms in some carbohydrate, e.g., glucose, $C_6H_{12}O_6$.) The equation also indicates that the ratio of carbon dioxide consumed to oxygen release is 1:1, a finding that was carefully demonstrated in the years following Senebier's work. Using glucose as the carbohydrate product, we can write the equation for photosynthesis as

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$$

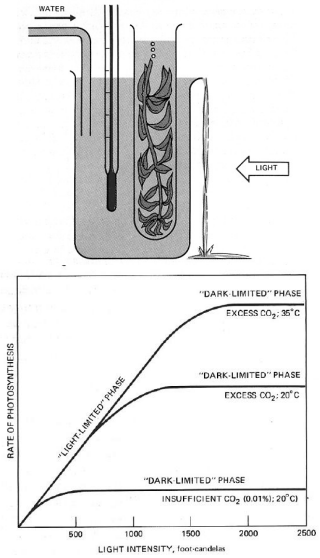


Figure **8.2.1**: (left) Elodea experiment by Blackman (right) Blackman experiment graphic interpretation

The above equation shows the relationship between the substances used in and produced by the process. It tells us nothing about the intermediate steps. That photosynthesis does involve at least two quite distinct processes became apparent from the experiments of the British plant physiologist F. F. Blackman. His results can easily be duplicated by using the setup in Figure 4.9.1. The green water plant *Elodea* (available wherever aquarium supplies are sold) is the test organism. When a sprig is placed upside down in a dilute solution of $NaHCO_3$ (which serves as a source of CO_2) and illuminated with a flood lamp, oxygen bubbles are soon given off from the cut portion of the stem. One then counts the number of bubbles given off in a fixed interval of time at each of several light intensities. Plotting these data produces a graph like the one in Figure 4.9.2.

Since the rate of photosynthesis does not continue to increase indefinitely with increased illumination, Blackman concluded that at least two distinct processes are involved: one, a reaction that requires light and the other, a reaction that does not. This latter is called a "dark" reaction although it **can** go on in the light. Blackman theorized that at moderate light intensities, the "light" reaction limits or "paces" the entire process. In other words, at these intensities the dark reaction is capable of handling all the intermediate substances produced by the light reaction. With increasing light intensities, however, a point is eventually reached when the dark reaction is working at maximum capacity. Any further illumination is ineffective, and the process reaches a steady rate.

This interpretation is strengthened by repeating the experiment as a somewhat higher temperature. Most chemical reactions proceed more rapidly at higher temperatures (up to a point). At 35°C, the rate of photosynthesis does not level off until greater light intensities are present. This suggest that the dark reaction is now working faster. The fact that at low light intensities the rate of photosynthesis is no greater at 35°C than at 20°C also supports the idea that it is a light reaction that is limiting the process in this range. Light reactions depend, not on temperature, but simply on the intensity of illumination.

The increased rate of photosynthesis with increased temperature does not occur if the supply of CO_2 is limited. As the figure shows, the overall rate of photosynthesis reaches a steady value at lower light intensities if the amount of CO_2 available is limited. Thus CO_2 concentration must be added as a third factor regulating the rate at which photosynthesis occurs. As a practical matter, however, the concentration available to terrestrial plants is simply that found in the atmosphere: 0.035%.

Van Niel

It was the American microbiologist Van Niel who first glimpsed the role that light plays in photosynthesis. He studied photosynthesis in purple sulfur bacteria. These microorganisms synthesize glucose from CO_2 as do green plants, and they need light to do so. Water, however, is not the starting material. Instead they use hydrogen sulfide (H_2S). Furthermore, no oxygen is liberated during this photosynthesis but rather elemental sulfur. Van Niel reasoned that the action of light caused a decomposition of H_2S into hydrogen and sulfur atoms. Then, in a series of dark reactions, the hydrogen atoms were used to reduce CO_2 to carbohydrate:

$$CO_2 + 2\,H_2S \longrightarrow (CH_2O) + H_2O + 2\,S \tag{8.2.1}$$

Van Niel envisioned a parallel to the process of photosynthesis as it occurs in green plants. There the energy of light causes water to break up into hydrogen and oxygen. The hydrogen atoms are then used to reduce CO_2 in a series of dark reactions:

$$CO_2 + 2\,H_2O \longrightarrow (CH_2O) + H_2O + O_2 \tag{8.2.2}$$

If this theory is correct, then it follows that all of the oxygen released during photosynthesis comes from water just as all the sulfur produced by the purple sulfur bacteria comes from H_2S. This conclusion directly contradicts Senebier's theory that the oxygen liberated in photosynthesis comes from the carbon dioxide. If Van Niel's theory is correct, then the equation for photosynthesis would have to be rewritten:

$$6\,CO_2 + 12\,H_2O \longrightarrow C_6H_{12}O_6 + 6\,H_2O + 6\,O_2 \tag{8.2.3}$$

In science, a theory should be testable. By deduction, one can make a prediction of how a particular experiment will come out if the theory is sound. In this case, the crucial experiments needed to test the two theories had to await the time when the growth of atomic research made it possible to produce isotopes other than those found naturally or in greater concentrations than are found naturally.

Samuel Ruben

In air, water and other natural materials containing oxygen, 99.76% of the oxygen atoms are ^{16}O and only 0.20% of them are the heavier isotope ^{18}O. In 1941, Samuel Ruben and his coworkers at the University of California were able to prepare specially "labeled" water in which the 0.85% of the molecules contained ^{18}O atoms. When this water was supplied to a suspension of photosynthesizing algae, the proportion of ^{18}O in the oxygen gas that was evolved was 0.85%, the same as that of the water supplied, and not simply the 0.20% found in all natural samples of oxygen (and its compounds like CO_2).

		% ^{18}O FOUND IN		
EXPERIMENT		H_2O	CO_2	O_2
1.	START	0.85	0.20	—
	FINISH	0.85	0.61*	0.86
2.	START	0.20	0.68	—
	FINISH	0.20	0.57	0.20

* A non-biochemical exchange of oxygen atoms between the water and the bicarbonate ions used as a source of CO_2 explains the uptake of the isotope by CO_2 in the first experiment.

These results clearly demonstrated that Senebier's interpretation was in error. If all the oxygen liberated during photosynthesis comes from the carbon dioxide, we would expect the oxygen evolved in Ruben's experiment to contain simply the 0.20% found naturally. If, on the other hand, both the carbon dioxide and the water contribute to the oxygen released, we would expect its isotopic composition to have been some intermediate figure. In fact, the isotopic composition of the evolved oxygen was the same as that of the water used.

Ruben and his colleagues also prepared a source of carbon dioxide that was enriched in ^{18}O atoms. When algae carried out photosynthesis using this material and **natural** water, the oxygen that was given off was not enriched in ^{18}O. It contained simply the 0.20% ^{18}O found in the natural water used. The heavy atoms presumably became incorporated in the other two products (carbohydrate and by-product water).

These experiments lent great support to Van Niel's idea that one function of light in photosynthesis was the separation of the hydrogen and oxygen atoms of water molecules. But there remained to work out just how the hydrogen atoms were made available to the dark reactions.

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SECTION OVERVIEW

8.3: Pigments

8.3.1: Introduction to Light Energy

8.3.2: Absorption of Light

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8.3.1: Introduction to Light Energy

Learning Objectives

- Explain the difference between short and long wavelengths.

What Is Light Energy?

The sun emits an enormous amount of electromagnetic radiation (solar or light energy). Humans can see only a fraction of this energy, which is referred to as “visible light.” The manner in which solar energy travels is described as waves. Scientists can determine the amount of energy of a wave by measuring its wavelength, the distance between consecutive points of a wave, such as from crest to crest or from trough to trough.

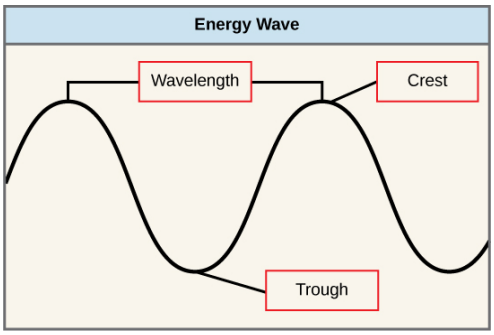


Figure **8.3.1.1**: Wavelengths: The wavelength of a single wave is the distance between two consecutive points of similar position (two crests or two troughs) along the wave.

Visible light constitutes only one of many types of electromagnetic radiation emitted from the sun and other stars. The electromagnetic spectrum is the range of all possible frequencies of radiation. The electromagnetic spectrum shows several types of electromagnetic radiation originating from the sun, including X-rays and ultraviolet (UV) rays. The higher-energy waves can penetrate tissues and damage cells and DNA, which explains why both X-rays and UV rays can be harmful to living organisms. Scientists differentiate the various types of radiant energy from the sun within the electromagnetic spectrum.The difference between wavelengths relates to the amount of energy carried by them.

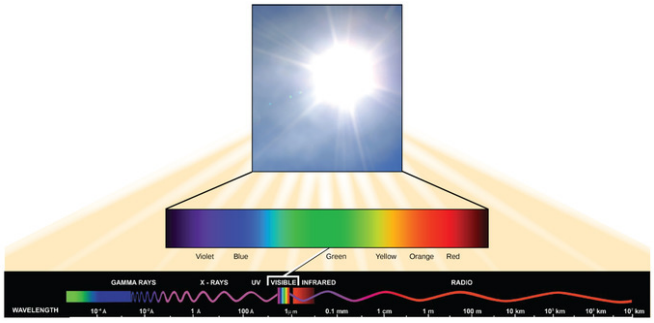


Figure **8.3.1.1**: The Electromagnetic Spectrum: The sun emits energy in the form of electromagnetic radiation. This radiation exists at different wavelengths, each of which has its own characteristic energy. All electromagnetic radiation, including visible light, is characterized by its wavelength.

Each type of electromagnetic radiation travels at a particular wavelength. The longer the wavelength, the less energy is carried. Short, tight waves carry the most energy. This may seem illogical, but think of it in terms of a person moving a heavy rope. It takes little effort by a person to move a rope in long, wide waves. To make a rope move in short, tight waves, a person would need to apply significantly more energy.

Key Points

- The amount of energy of a wave can be determined by measuring its wavelength, the distance between consecutive points of a wave.

- Visible light is a type of radiant energy within the electromagnetic spectrum; other types of electromagnetic radiation include UV, infrared, gamma, and radio rays as well as X-rays.
- The difference between wavelengths relates to the amount of energy carried by them; short, tight waves carry more energy than long, wide waves.

Key Terms

- **electromagnetic spectrum**: the entire range of wavelengths of all known radiations consisting of oscillating electric and magnetic fields, including gamma rays, visible light, infrared, radio waves, and X-rays
- **wavelength**: the length of a single cycle of a wave, as measured by the distance between one peak or trough of a wave and the next; it corresponds to the velocity of the wave divided by its frequency
- **visible light**: the part of the electromagnetic spectrum, between infrared and ultraviolet, that is visible to the human eye

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8.3.2: Absorption of Light

Learning Objectives

- Differentiate between chlorophyll and carotenoids.

Absorption of Light

Light energy initiates the process of photosynthesis when pigments absorb the light. Organic pigments have a narrow range of energy levels that they can absorb. Energy levels lower than those represented by red light are insufficient to raise an orbital electron to an excited, or quantum, state. Energy levels higher than those in blue light will physically tear the molecules apart, a process called bleaching. For example, retinal pigments can only "see" (absorb) 700 nm to 400 nm light; this is visible light. For the same reasons, plant pigment molecules absorb only light in the wavelength range of 700 nm to 400 nm; plant physiologists refer to this range for plants as photosynthetically-active radiation.

The visible light seen by humans as the color white light actually exists in a rainbow of colors in the electromagnetic spectrum, with violet and blue having shorter wavelengths and, thus, higher energy. At the other end of the spectrum, toward red, the wavelengths are longer and have lower energy.

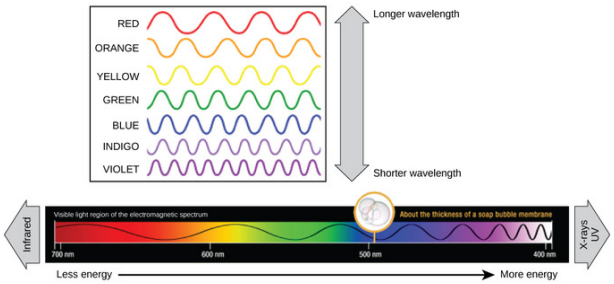


Figure 8.3.2.1: Visible Light: The colors of visible light do not carry the same amount of energy. Violet has the shortest wavelength and, therefore, carries the most energy, whereas red has the longest wavelength and carries the least amount of energy.

Understanding Pigments

Different kinds of pigments exist, each of which has evolved to absorb only certain wavelengths or colors of visible light. Pigments reflect or transmit the wavelengths they cannot absorb, making them appear in the corresponding color.

Chlorophylls and carotenoids are the two major classes of photosynthetic pigments found in plants and algae; each class has multiple types of pigment molecules. There are five major chlorophylls: *a*, *b*, *c* and *d*, along with a related molecule found in prokaryotes called bacteriochlorophyll.

With dozens of different forms, carotenoids are a much larger group of pigments. The carotenoids found in fruit, such as the red of tomato (lycopene), the yellow of corn seeds (zeaxanthin), or the orange of an orange peel (β-carotene), are used to attract seed-dispersing organisms. In photosynthesis, carotenoids function as photosynthetic pigments that are very efficient molecules for the disposal of excess energy. When a leaf is exposed to full sun, the light-dependent reactions are required to process an enormous amount of energy; if that energy is not handled properly, it can do significant damage. Therefore, many carotenoids are stored in the thylakoid membrane to absorb excess energy and safely release that energy as heat.

Each type of pigment can be identified by the specific pattern of wavelengths it absorbs from visible light, which is the absorption spectrum. Chlorophyll *a* absorbs light in the blue-violet region, while chlorophyll *b* absorbs red-blue light. Neither *a* or *b* absorb green light; because green is reflected or transmitted, chlorophyll appears green. Carotenoids absorb light in the blue-green and violet region and reflect the longer yellow, red, and orange wavelengths.

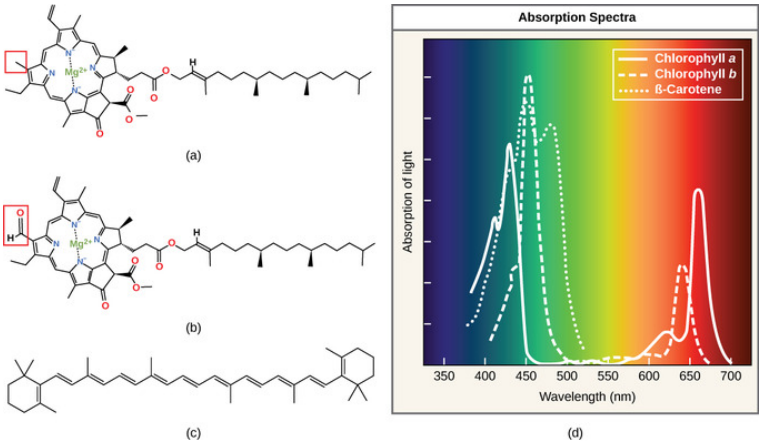


Figure **8.3.2.1**: Chlorophyll a and b: (a) Chlorophyll *a*, (b) chlorophyll *b*, and (c) β-carotene are hydrophobic organic pigments found in the thylakoid membrane. Chlorophyll *a* and *b*, which are identical except for the part indicated in the red box, are responsible for the green color of leaves. β-carotene is responsible for the orange color in carrots. Each pigment has (d) a unique absorbance spectrum.

Many photosynthetic organisms have a mixture of pigments. In this way organisms can absorb energy from a wider range of wavelengths. Not all photosynthetic organisms have full access to sunlight. Some organisms grow underwater where light intensity and quality decrease and change with depth. Other organisms grow in competition for light. Plants on the rainforest floor must be able to absorb any light that comes through because the taller trees absorb most of the sunlight and scatter the remaining solar radiation

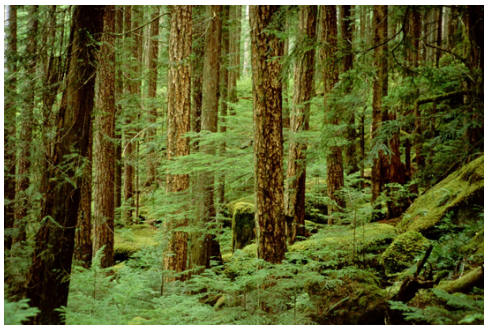


Figure **8.3.2.1**: Pigments in Plants: Plants that commonly grow in the shade have adapted to low levels of light by changing the relative concentrations of their chlorophyll pigments.

When studying a photosynthetic organism, scientists can determine the types of pigments present by using a spectrophotometer. These instruments can differentiate which wavelengths of light a substance can absorb. Spectrophotometers measure transmitted light and compute its absorption. By extracting pigments from leaves and placing these samples into a spectrophotometer, scientists can identify which wavelengths of light an organism can absorb.

Key Points

- Plant pigment molecules absorb only light in the wavelength range of 700 nm to 400 nm; this range is referred to as photosynthetically-active radiation.
- Violet and blue have the shortest wavelengths and the most energy, whereas red has the longest wavelengths and carries the least amount of energy.
- Pigments reflect or transmit the wavelengths they cannot absorb, making them appear in the corresponding color.
- Chorophylls and carotenoids are the major pigments in plants; while there are dozens of carotenoids, there are only five important chorophylls: *a*, *b*, *c*, *d*, and bacteriochlorophyll.
- Chlorophyll *a* absorbs light in the blue-violet region, chlorophyll *b* absorbs red-blue light, and both *a* and *b* reflect green light (which is why chlorophyll appears green).
- Carotenoids absorb light in the blue-green and violet region and reflect the longer yellow, red, and orange wavelengths; these pigments also dispose excess energy out of the cell.

Key Terms

- **chlorophyll**: Any of a group of green pigments that are found in the chloroplasts of plants and in other photosynthetic organisms such as cyanobacteria.
- **carotenoid**: Any of a class of yellow to red plant pigments including the carotenes and xanthophylls.
- **spectrophotometer**: An instrument used to measure the intensity of electromagnetic radiation at different wavelengths.

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SECTION OVERVIEW

8.4: Photosystem Organization

8.4.1: The Light-Dependent Reactions of Photosynthesis

8.4.2: Processes of the Light-Dependent Reactions

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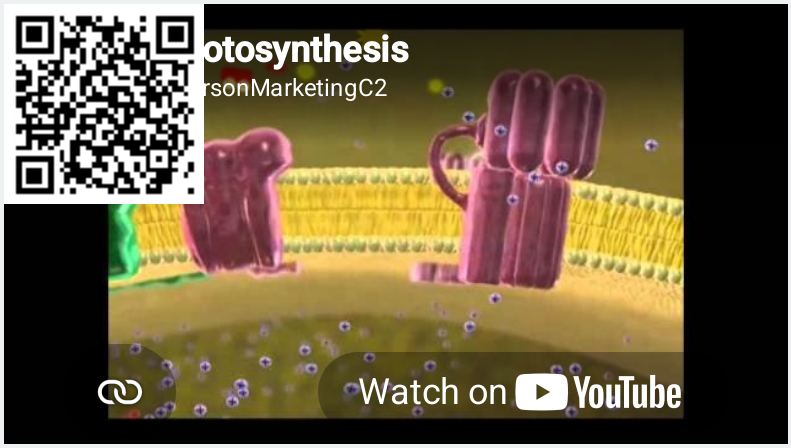
8.4.1: The Light-Dependent Reactions of Photosynthesis

How can light be used to make food? It is easy to think of light as something that exists and allows living organisms, such as humans, to see, but light is a form of energy. Like all energy, light can travel, change form, and be harnessed to do work. In the case of photosynthesis, light energy is transformed into chemical energy, which autotrophs use to build carbohydrate molecules. However, autotrophs only use a specific component of sunlight (Figure **8.4.1.1**).



Figure 8.4.1.1: Autotrophs can capture light energy from the sun, converting it into chemical energy used to build food molecules. (credit: modification of work by Gerry Atwell, U.S. Fish and Wildlife Service)

CONCEPT IN ACTION



Watch the process of photosynthesis within a leaf in this video.

What Is Light Energy?

The sun emits an enormous amount of electromagnetic radiation (solar energy). Humans can see only a fraction of this energy, which is referred to as “visible light.” The manner in which solar energy travels can be described and measured as waves. Scientists can determine the amount of energy of a wave by measuring its wavelength, the distance between two consecutive, similar points in a series of waves, such as from crest to crest or trough to trough (Figure 8.4.1.2).

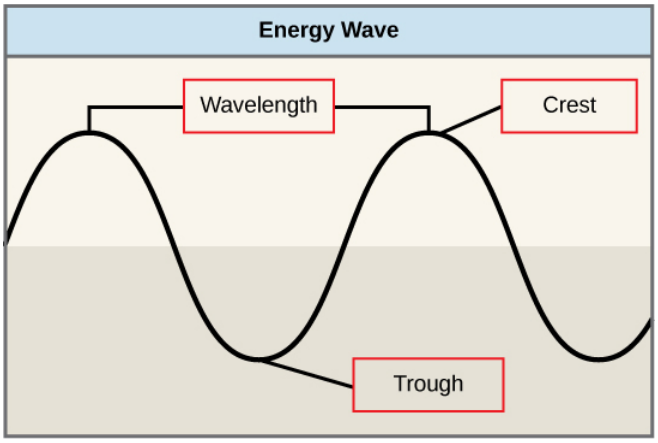


Figure 8.4.1.2: The wavelength of a single wave is the distance between two consecutive points along the wave.

Visible light constitutes only one of many types of electromagnetic radiation emitted from the sun. The electromagnetic spectrum is the range of all possible wavelengths of radiation (Figure 8.4.1.3). Each wavelength corresponds to a different amount of energy carried.

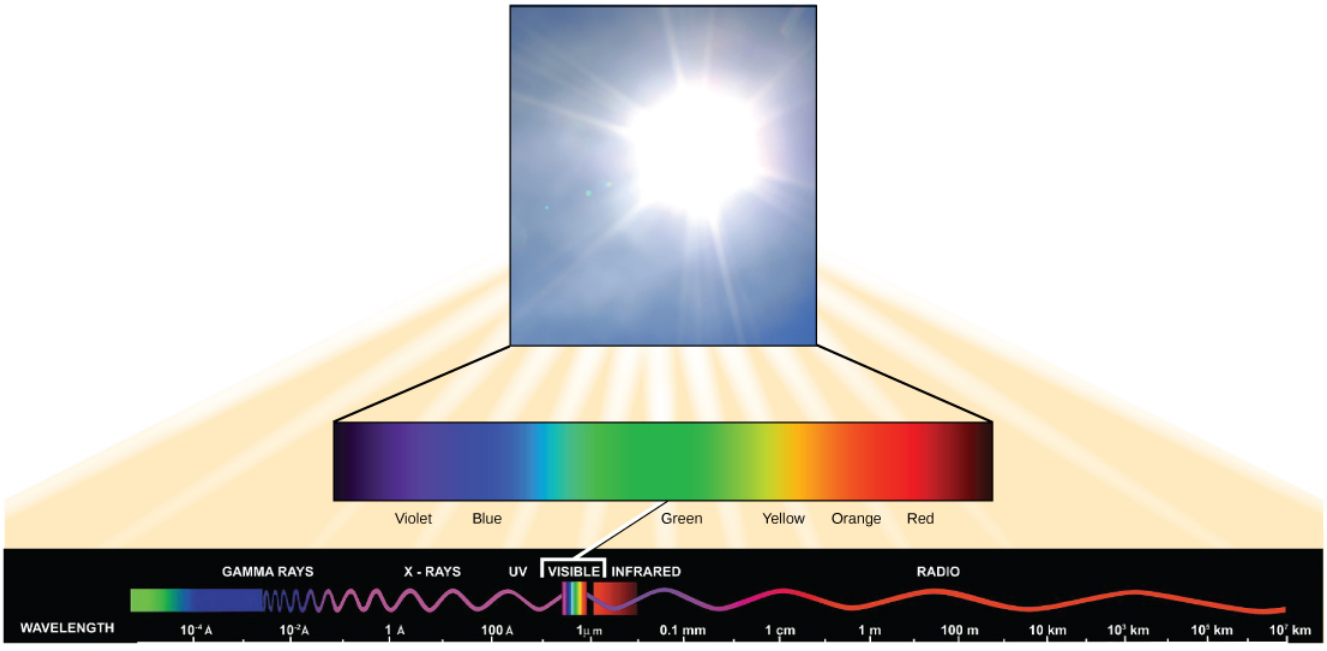


Figure 8.4.1.3: The sun emits energy in the form of electromagnetic radiation. This radiation exists in different wavelengths, each of which has its own characteristic energy. Visible light is one type of energy emitted from the sun.

Each type of electromagnetic radiation has a characteristic range of wavelengths. The longer the wavelength (or the more stretched out it appears), the less energy is carried. Short, tight waves carry the most energy. This may seem illogical, but think of it in terms of a piece of moving rope. It takes little effort by a person to move a rope in long, wide waves. To make a rope move in short, tight waves, a person would need to apply significantly more energy.

The sun emits (Figure 8.4.1.3) a broad range of electromagnetic radiation, including X-rays and ultraviolet (UV) rays. The higher-energy waves are dangerous to living things; for example, X-rays and UV rays can be harmful to humans.

Absorption of Light

Light energy enters the process of photosynthesis when pigments absorb the light. In plants, pigment molecules absorb only visible light for photosynthesis. The visible light seen by humans as white light actually exists in a rainbow of colors. Certain objects, such as a prism or a drop of water, disperse white light to reveal these colors to the human eye. The visible light portion of the electromagnetic spectrum is perceived by the human eye as a rainbow of colors, with violet and blue having shorter wavelengths and, therefore, higher energy. At the other end of the spectrum toward red, the wavelengths are longer and have lower energy.

Understanding Pigments

Different kinds of pigments exist, and each absorbs only certain wavelengths (colors) of visible light. Pigments reflect the color of the wavelengths that they cannot absorb.

All photosynthetic organisms contain a pigment called chlorophyll *a*, which humans see as the common green color associated with plants. Chlorophyll *a* absorbs wavelengths from either end of the visible spectrum (blue and red), but not from green. Because green is reflected, chlorophyll appears green.

Other pigment types include chlorophyll *b* (which absorbs blue and red-orange light) and the carotenoids. Each type of pigment can be identified by the specific pattern of wavelengths it absorbs from visible light, which is its absorption spectrum.

Many photosynthetic organisms have a mixture of pigments; between them, the organism can absorb energy from a wider range of visible-light wavelengths. Not all photosynthetic organisms have full access to sunlight. Some organisms grow underwater where light intensity decreases with depth, and certain wavelengths are absorbed by the water. Other organisms grow in competition for light. Plants on the rainforest floor must be able to absorb any bit of light that comes through, because the taller trees block most of the sunlight (Figure 8.4.1.4).

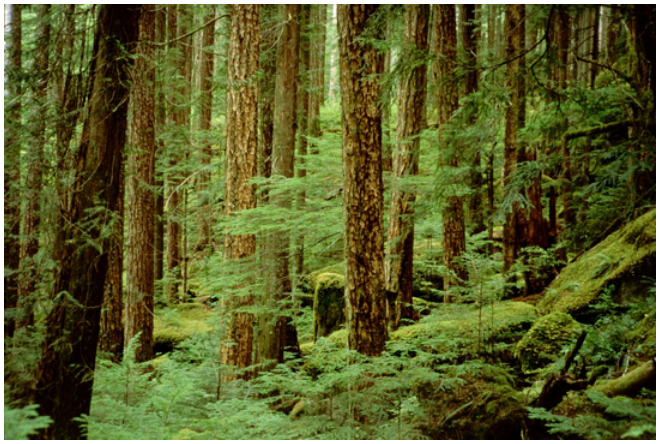


Figure 8.4.1.4: Plants that commonly grow in the shade benefit from having a variety of light-absorbing pigments. Each pigment can absorb different wavelengths of light, which allows the plant to absorb any light that passes through the taller trees. (credit: Jason Hollinger)

How Light-Dependent Reactions Work

The overall purpose of the light-dependent reactions is to convert light energy into chemical energy. This chemical energy will be used by the Calvin cycle to fuel the assembly of sugar molecules.

The light-dependent reactions begin in a grouping of pigment molecules and proteins called a photosystem. Photosystems exist in the membranes of thylakoids. A pigment molecule in the photosystem absorbs one photon, a quantity or “packet” of light energy, at a time.

A photon of light energy travels until it reaches a molecule of chlorophyll. The photon causes an electron in the chlorophyll to become “excited.” The energy given to the electron allows it to break free from an atom of the chlorophyll molecule. Chlorophyll is therefore said to “donate” an electron (Figure 8.4.1.5).

To replace the electron in the chlorophyll, a molecule of water is split. This splitting releases an electron and results in the formation of oxygen (O_2) and hydrogen ions (H^+) in the thylakoid space. Technically, each breaking of a water molecule releases a

pair of electrons, and therefore can replace two donated electrons.

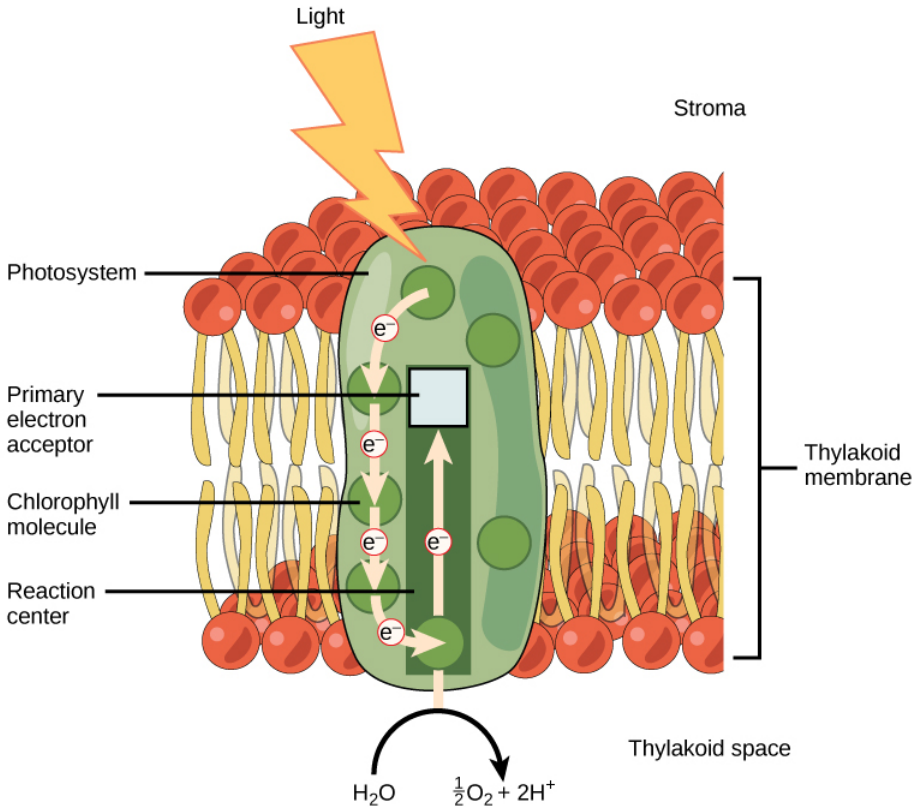


Figure 8.4.1.5: Light energy is absorbed by a chlorophyll molecule and is passed along a pathway to other chlorophyll molecules. The energy culminates in a molecule of chlorophyll found in the reaction center. The energy "excites" one of its electrons enough to leave the molecule and be transferred to a nearby primary electron acceptor. A molecule of water splits to release an electron, which is needed to replace the one donated. Oxygen and hydrogen ions are also formed from the splitting of water.

The replacing of the electron enables chlorophyll to respond to another photon. The oxygen molecules produced as byproducts find their way to the surrounding environment. The hydrogen ions play critical roles in the remainder of the light-dependent reactions.

Keep in mind that the purpose of the light-dependent reactions is to convert solar energy into chemical carriers that will be used in the Calvin cycle. In eukaryotes and some prokaryotes, two photosystems exist. The first is called photosystem II, which was named for the order of its discovery rather than for the order of the function.

After the photon hits, photosystem II transfers the free electron to the first in a series of proteins inside the thylakoid membrane called the electron transport chain. As the electron passes along these proteins, energy from the electron fuels membrane pumps that actively move hydrogen ions against their concentration gradient from the stroma into the thylakoid space. This is quite analogous to the process that occurs in the mitochondrion in which an electron transport chain pumps hydrogen ions from the mitochondrial stroma across the inner membrane and into the intermembrane space, creating an electrochemical gradient. After the energy is used, the electron is accepted by a pigment molecule in the next photosystem, which is called photosystem I (Figure 8.4.1.6).

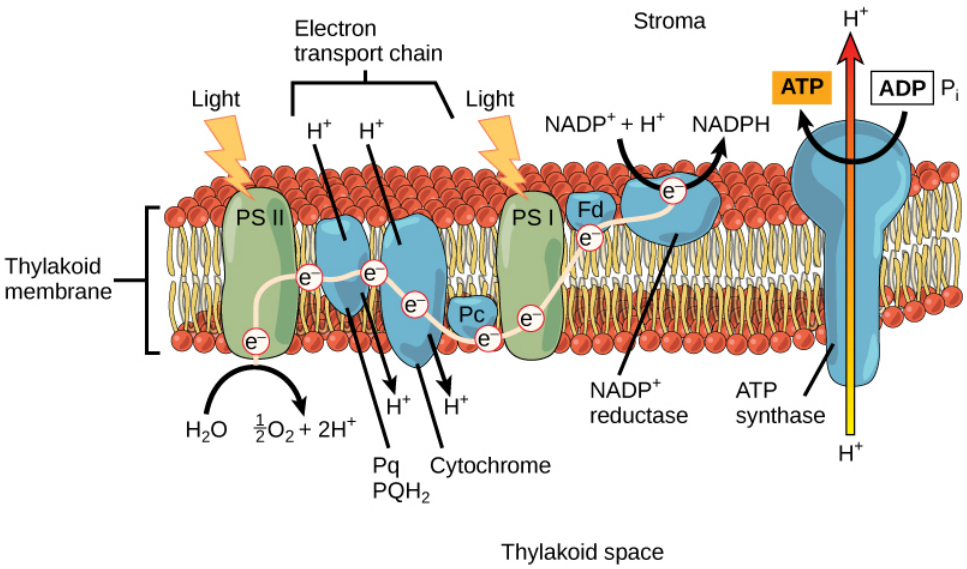


Figure 8.4.1.6: From photosystem II, the electron travels along a series of proteins. This electron transport system uses the energy from the electron to pump hydrogen ions into the interior of the thylakoid. A pigment molecule in photosystem I accepts the electron.

Generating an Energy Carrier: ATP

In the light-dependent reactions, energy absorbed by sunlight is stored by two types of energy-carrier molecules: ATP and NADPH. The energy that these molecules carry is stored in a bond that holds a single atom to the molecule. For ATP, it is a phosphate atom, and for NADPH, it is a hydrogen atom. Recall that NADH was a similar molecule that carried energy in the mitochondrion from the citric acid cycle to the electron transport chain. When these molecules release energy into the Calvin cycle, they each lose atoms to become the lower-energy molecules ADP and $NADP^+$.

The buildup of hydrogen ions in the thylakoid space forms an electrochemical gradient because of the difference in the concentration of protons (H^+) and the difference in the charge across the membrane that they create. This potential energy is harvested and stored as chemical energy in ATP through chemiosmosis, the movement of hydrogen ions down their electrochemical gradient through the transmembrane enzyme ATP synthase, just as in the mitochondrion.

The hydrogen ions are allowed to pass through the thylakoid membrane through an embedded protein complex called ATP synthase. This same protein generated ATP from ADP in the mitochondrion. The energy generated by the hydrogen ion stream allows ATP synthase to attach a third phosphate to ADP, which forms a molecule of ATP in a process called photophosphorylation. The flow of hydrogen ions through ATP synthase is called chemiosmosis, because the ions move from an area of high to low concentration through a semi-permeable structure.

Generating Another Energy Carrier: NADPH

The remaining function of the light-dependent reaction is to generate the other energy-carrier molecule, NADPH. As the electron from the electron transport chain arrives at photosystem I, it is re-energized with another photon captured by chlorophyll. The energy from this electron drives the formation of NADPH from $NADP^+$ and a hydrogen ion (H^+). Now that the solar energy is stored in energy carriers, it can be used to make a sugar molecule.

Summary

In the first part of photosynthesis, the light-dependent reaction, pigment molecules absorb energy from sunlight. The most common and abundant pigment is chlorophyll *a*. A photon strikes photosystem II to initiate photosynthesis. Energy travels through the electron transport chain, which pumps hydrogen ions into the thylakoid space. This forms an electrochemical gradient. The ions flow through ATP synthase from the thylakoid space into the stroma in a process called chemiosmosis to form molecules of ATP, which are used for the formation of sugar molecules in the second stage of photosynthesis. Photosystem I absorbs a second photon, which results in the formation of an NADPH molecule, another energy carrier for the Calvin cycle reactions.

Glossary

absorption spectrum
: the specific pattern of absorption for a substance that absorbs electromagnetic radiation

chlorophyll *a*
: the form of chlorophyll that absorbs violet-blue and red light

chlorophyll *b*
: the form of chlorophyll that absorbs blue and red-orange light

electromagnetic spectrum
: the range of all possible frequencies of radiation

photon
: a distinct quantity or “packet” of light energy

photosystem
: a group of proteins, chlorophyll, and other pigments that are used in the light-dependent reactions of photosynthesis to absorb light energy and convert it into chemical energy

wavelength
: the distance between consecutive points of a wave

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8.4.2: Processes of the Light-Dependent Reactions

Learning Objectives

- Describe how light energy is converted into ATP and NADPH.

How Light-Dependent Reactions Work

The overall function of light-dependent reactions, the first stage of photosynthesis, is to convert solar energy into chemical energy in the form of NADPH and ATP, which are used in light-independent reactions and fuel the assembly of sugar molecules. Protein complexes and pigment molecules work together to produce NADPH and ATP.

Producing Chemical Energy

Light energy is converted into chemical energy in a multiprotein complex called a photosystem. Two types of photosystems, photosystem I (PSI) and photosystem II (PSII), are found in the thylakoid membrane inside the chloroplast. Each photosystem consists of multiple antenna proteins that contain a mixture of 300–400 chlorophyll *a* and *b* molecules, as well as other pigments like carotenoids. Cytochrome b6f complex and ATP synthase are also major protein complexes in the thylakoid membrane that work with the photosystems to create ATP and NADPH.

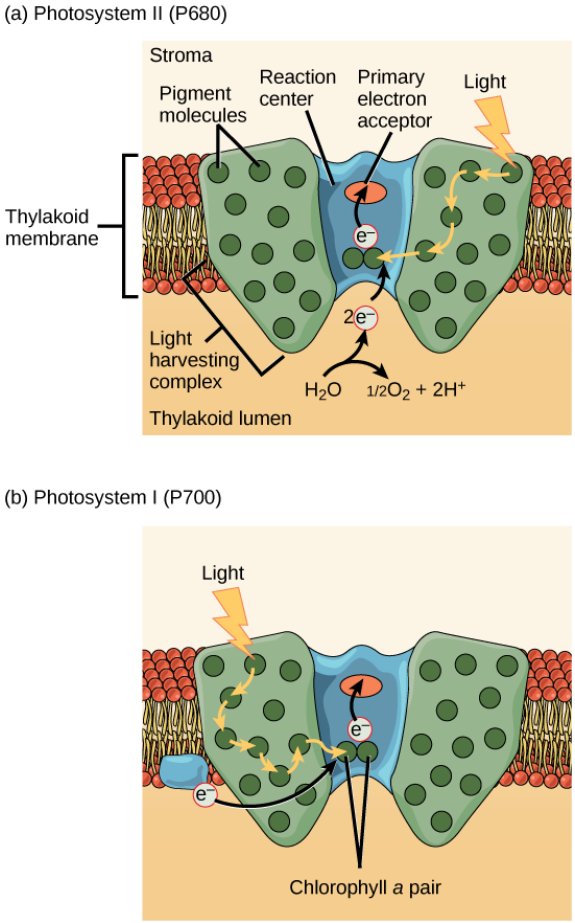


Figure **8.4.2.1**: Photosystems I & II: A photosystem consists of a light-harvesting complex and a reaction center. Pigments in the light-harvesting complex pass light energy to two special chlorophyll a molecules in the reaction center. The light excites an electron from the chlorophyll a pair, which passes to the primary electron acceptor. The excited electron must then be replaced. In (a) photosystem II, the electron comes from the splitting of water, which releases oxygen as a waste product. In (b) photosystem I, the electron comes from the chloroplast electron transport chain.

The two photosystems absorb light energy through proteins containing pigments, such as chlorophyll. The light-dependent reactions begin in photosystem II. In PSII, energy from sunlight is used to split water, which releases two electrons, two hydrogen

atoms, and one oxygen atom. When a chlorophyll *a* molecule within the reaction center of PSII absorbs a photon, the electron in this molecule attains a higher energy level. Because this state of an electron is very unstable, the electron is transferred to another molecule creating a chain of redox reactions called an electron transport chain (ETC). The electron flow goes from PSII to cytochrome b6f to PSI; as electrons move between these two photosystems, they lose energy. Because the electrons have lost energy prior to their arrival at PSI, they must be re-energized by PSI. Therefore, another photon is absorbed by the PSI antenna. That energy is transmitted to the PSI reaction center. This reaction center, known as P700, is oxidized and sends a high-energy electron to reduce NADP+ to NADPH. This process illustrates oxygenic photosynthesis, wherein the first electron donor is water and oxygen is created as a waste product.

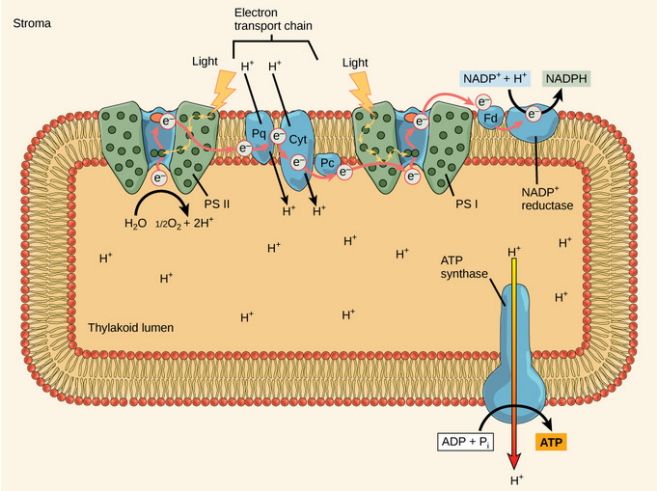


Figure **8.4.2.1**: Photosystem II: In the photosystem II (PSII) reaction center, energy from sunlight is used to extract electrons from water. The electrons travel through the chloroplast electron transport chain to photosystem I (PSI), which reduces NADP+ to NADPH. The electron transport chain moves protons across the thylakoid membrane into the lumen. At the same time, splitting of water adds protons to the lumen while reduction of NADPH removes protons from the stroma. The net result is a low pH in the thylakoid lumen and a high pH in the stroma. ATP synthase uses this electrochemical gradient to make ATP.

Cytochrome b6f and ATP synthase work together to create ATP. This process, called photophosphorylation, occurs in two different ways. In non-cyclic photophosphorylation, cytochrome b6f uses the energy of electrons from PSII to pump hydrogen ions from the lumen (an area of high concentration) to the stroma (an area of low concentration). The energy released by the hydrogen ion stream allows ATP synthase to attach a third phosphate group to ADP, which forms ATP. This flow of hydrogen ions through ATP synthase is called chemiosmosis because the ions move from an area of high to an area of low concentration through a semi-permeable structure. In cyclic photophosphorylation, cytochrome b6f uses the energy of electrons from both PSII and PSI to create more ATP and to stop the production of NADPH. Cyclic phosphorylation is important to maintain the right proportions of NADPH and ATP, which will carry out light-independent reactions later on.

The net-reaction of all light-dependent reactions in oxygenic photosynthesis is: $2H_2O + 2NADP+ + 3ADP + 3Pi \rightarrow O_2 + 2NADPH + 3ATP$

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Key Points

- Light energy splits water and extracts electrons in photosystem II (PSII); then electrons are moved from PSII to cytochrome b6f to photosystem I (PSI) and reduce in energy.
- Electrons are re-energized in PSI and those high energy electrons reduce $NADP^+$ to NADPH.
- In non-cyclic photophosphorylation, cytochrome b6f uses the energy of electrons from PSII to pump hydrogen ions from the lumen to the stroma; this energy allows ATP synthase to attach a third phosphate group to ADP, which forms ATP.
- In cyclic photophosphorylation, cytochrome b6f uses the energy of electrons from both PSII and PSI to create more ATP and to stop the production of NADPH, maintaining the right proportions of NADPH and ATP.

Key Terms

- **photosystem**: Either of two biochemical systems, active in chloroplasts, that are part of photosynthesis.
- **photophosphorylation**: The addition of a phosphate (PO43-) group to a protein or other organic molecule by photosynthesis.
- **chemiosmosis**: The movement of ions across a selectively permeable membrane, down their electrochemical gradient.

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SECTION OVERVIEW

8.5: Carbon Fixation- The Calvin Cycle

After the energy from the sun is converted and packaged into ATP and NADPH, the cell has the fuel needed to build food in the form of carbohydrate molecules. The carbohydrate molecules made will have a backbone of carbon atoms. Where does the carbon come from? The carbon atoms used to build carbohydrate molecules come from carbon dioxide, the gas that animals exhale with each breath. The Calvin cycle is the term used for the reactions of photosynthesis that use the energy stored by the light-dependent reactions to form glucose and other carbohydrate molecules.

The Interworkings of the Calvin Cycle

In plants, carbon dioxide (CO_2) enters the chloroplast through the stomata and diffuses into the stroma of the chloroplast—the site of the Calvin cycle reactions where sugar is synthesized. The reactions are named after the scientist who discovered them, and reference the fact that the reactions function as a cycle. Others call it the Calvin-Benson cycle to include the name of another scientist involved in its discovery (Figure 8.5.1).

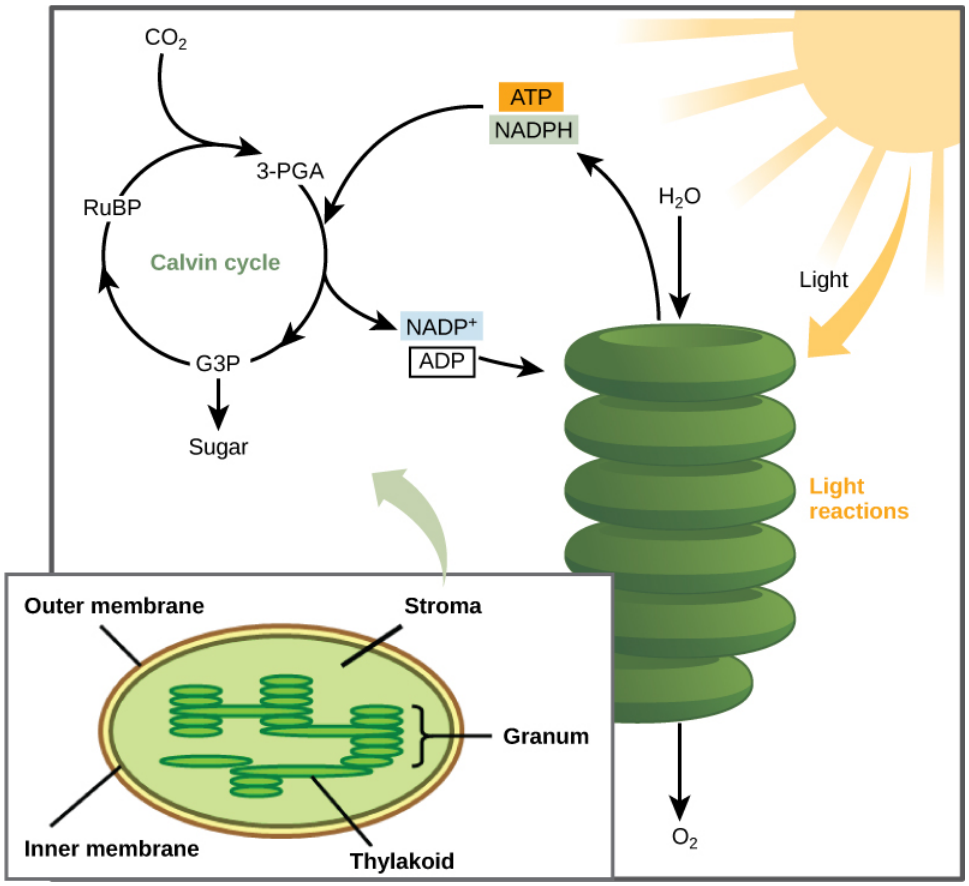


Figure 8.5.1: Light-dependent reactions harness energy from the sun to produce ATP and NADPH. These energy-carrying molecules travel into the stroma where the Calvin cycle reactions take place.

The Calvin cycle reactions (Figure 8.5.2) can be organized into three basic stages: fixation, reduction, and regeneration. In the stroma, in addition to CO_2, two other chemicals are present to initiate the Calvin cycle: an enzyme abbreviated RuBisCO, and the molecule ribulose bisphosphate (RuBP). RuBP has five atoms of carbon and a phosphate group on each end.

RuBisCO catalyzes a reaction between CO_2 and RuBP, which forms a six-carbon compound that is immediately converted into two three-carbon compounds. This process is called carbon fixation, because CO_2 is "fixed" from its inorganic form into organic molecules.

ATP and NADPH use their stored energy to convert the three-carbon compound, 3-PGA, into another three-carbon compound called G3P. This type of reaction is called a reduction reaction, because it involves the gain of electrons. A reduction is the gain of an electron by an atom or molecule. The molecules of ADP and NAD^+, resulting from the reduction reaction, return to the light-dependent reactions to be re-energized.

One of the G3P molecules leaves the Calvin cycle to contribute to the formation of the carbohydrate molecule, which is commonly glucose ($C_6H_{12}O_6$). Because the carbohydrate molecule has six carbon atoms, it takes six turns of the Calvin cycle to make one carbohydrate molecule (one for each carbon dioxide molecule fixed). The remaining G3P molecules regenerate RuBP, which enables the system to prepare for the carbon-fixation step. ATP is also used in the regeneration of RuBP.

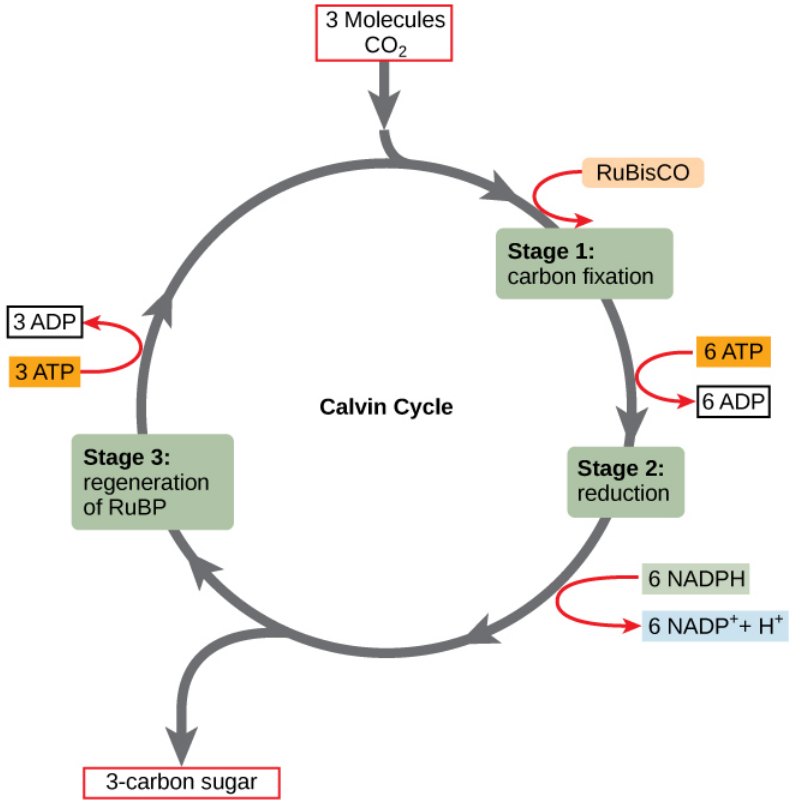


Figure 8.5.2: The Calvin cycle has three stages. In stage 1, the enzyme RuBisCO incorporates carbon dioxide into an organic molecule. In stage 2, the organic molecule is reduced. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue.

In summary, it takes six turns of the Calvin cycle to fix six carbon atoms from CO_2. These six turns require energy input from 12 ATP molecules and 12 NADPH molecules in the reduction step and 6 ATP molecules in the regeneration step.

CONCEPT IN ACTION

The following is a link to an animation of the Calvin cycle. Click Stage 1, Stage 2, and then Stage 3 to see G3P and ATP regenerate to form RuBP.

EVOLUTION IN ACTION: Photosynthesis

The shared evolutionary history of all photosynthetic organisms is conspicuous, as the basic process has changed little over eras of time. Even between the giant tropical leaves in the rainforest and tiny cyanobacteria, the process and components of photosynthesis that use water as an electron donor remain largely the same. Photosystems function to absorb light and use electron transport chains to convert energy. The Calvin cycle reactions assemble carbohydrate molecules with this energy.

However, as with all biochemical pathways, a variety of conditions leads to varied adaptations that affect the basic pattern. Photosynthesis in dry-climate plants (Figure 8.5.3) has evolved with adaptations that conserve water. In the harsh dry heat, every drop of water and precious energy must be used to survive. Two adaptations have evolved in such plants. In one form, a

more efficient use of CO_2 allows plants to photosynthesize even when CO_2 is in short supply, as when the stomata are closed on hot days. The other adaptation performs preliminary reactions of the Calvin cycle at night, because opening the stomata at this time conserves water due to cooler temperatures. In addition, this adaptation has allowed plants to carry out low levels of photosynthesis without opening stomata at all, an extreme mechanism to face extremely dry periods.



Figure 8.5.3: Living in the harsh conditions of the desert has led plants like this cactus to evolve variations in reactions outside the Calvin cycle. These variations increase efficiency and help conserve water and energy. (credit: Piotr Wojtkowski)

Photosynthesis in Prokaryotes

The two parts of photosynthesis—the light-dependent reactions and the Calvin cycle—have been described, as they take place in chloroplasts. However, prokaryotes, such as cyanobacteria, lack membrane-bound organelles. Prokaryotic photosynthetic autotrophic organisms have infoldings of the plasma membrane for chlorophyll attachment and photosynthesis (Figure 8.5.4). It is here that organisms like cyanobacteria can carry out photosynthesis.

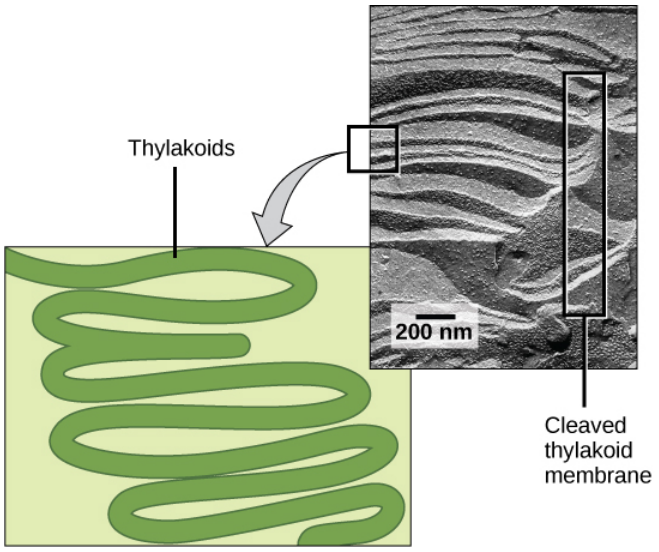


Figure 8.5.4: A photosynthetic prokaryote has infolded regions of the plasma membrane that function like thylakoids. Although these are not contained in an organelle, such as a chloroplast, all of the necessary components are present to carry out photosynthesis. (credit: scale-bar data from Matt Russell)

The Energy Cycle

Living things access energy by breaking down carbohydrate molecules. However, if plants make carbohydrate molecules, why would they need to break them down? Carbohydrates are storage molecules for energy in all living things. Although energy can be stored in molecules like ATP, carbohydrates are much more stable and efficient reservoirs for chemical energy. Photosynthetic organisms also carry out the reactions of respiration to harvest the energy that they have stored in carbohydrates, for example, plants have mitochondria in addition to chloroplasts.

You may have noticed that the overall reaction for photosynthesis:

$$6\,CO_2 + 6\,H_2O \longrightarrow C_6H_{12}O_6 + 6\,O_2$$

is the reverse of the overall reaction for cellular respiration:

$$6\,O_2 + C_6H_{12}O_6 \longrightarrow 6\,CO_2 + 6\,H_2O$$

Photosynthesis produces oxygen as a byproduct, and respiration produces carbon dioxide as a byproduct.

In nature, there is no such thing as waste. Every single atom of matter is conserved, recycling indefinitely. Substances change form or move from one type of molecule to another, but never disappear (Figure 8.5.5).

CO_2 is no more a form of waste produced by respiration than oxygen is a waste product of photosynthesis. Both are byproducts of reactions that move on to other reactions. Photosynthesis absorbs energy to build carbohydrates in chloroplasts, and aerobic cellular respiration releases energy by using oxygen to break down carbohydrates. Both organelles use electron transport chains to generate the energy necessary to drive other reactions. Photosynthesis and cellular respiration function in a biological cycle, allowing organisms to access life-sustaining energy that originates millions of miles away in a star.

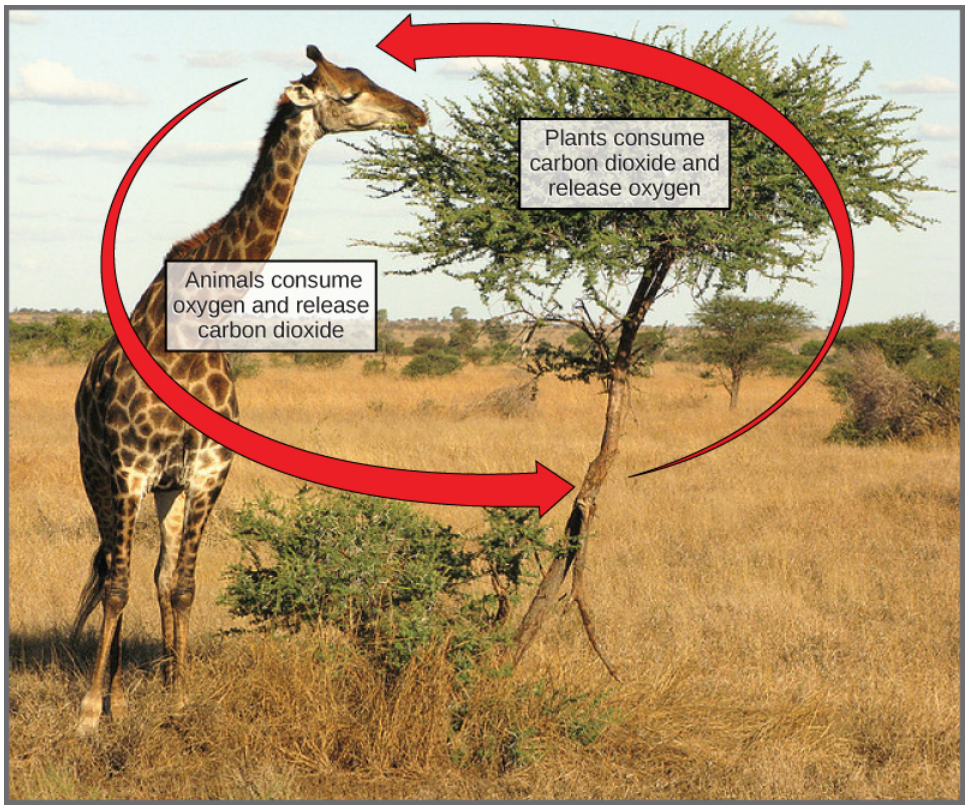


Figure 8.5.5: In the carbon cycle, the reactions of photosynthesis and cellular respiration share reciprocal reactants and products. (credit: modification of work by Stuart Bassil)

Summary

Using the energy carriers formed in the first stage of photosynthesis, the Calvin cycle reactions fix CO_2 from the environment to build carbohydrate molecules. An enzyme, RuBisCO, catalyzes the fixation reaction, by combining CO_2 with RuBP. The resulting six-carbon compound is broken down into two three-carbon compounds, and the energy in ATP and NADPH is used to convert these molecules into G3P. One of the three-carbon molecules of G3P leaves the cycle to become a part of a carbohydrate molecule. The remaining G3P molecules stay in the cycle to be formed back into RuBP, which is ready to react with more CO_2. Photosynthesis forms a balanced energy cycle with the process of cellular respiration. Plants are capable of both photosynthesis and cellular respiration, since they contain both chloroplasts and mitochondria.

Glossary

Calvin cycle
: the reactions of photosynthesis that use the energy stored by the light-dependent reactions to form glucose and other carbohydrate molecules

carbon fixation
: the process of converting inorganic CO_2 gas into organic compounds

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8.5.1: The Calvin Cycle

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8.5.1: The Calvin Cycle

Learning Objectives

- Describe the Calvin Cycle

The Calvin Cycle

In plants, carbon dioxide (CO_2) enters the leaves through stomata, where it diffuses over short distances through intercellular spaces until it reaches the mesophyll cells. Once in the mesophyll cells, CO_2 diffuses into the stroma of the chloroplast, the site of light-independent reactions of photosynthesis. These reactions actually have several names associated with them. Other names for light-independent reactions include the Calvin cycle, the Calvin-Benson cycle, and dark reactions. The most outdated name is dark reactions, which can be misleading because it implies incorrectly that the reaction only occurs at night or is independent of light, which is why most scientists and instructors no longer use it.

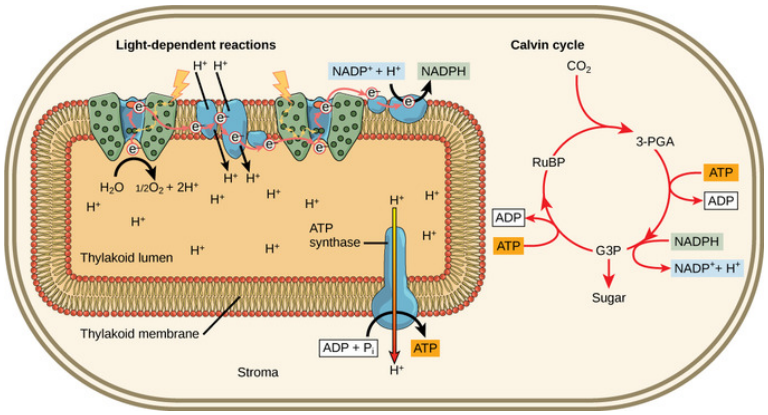


Figure 8.5.1.1: Light Reactions: Light-dependent reactions harness energy from the sun to produce chemical bonds, ATP, and NADPH. These energy-carrying molecules are made in the stroma where the Calvin cycle takes place. The Calvin cycle is not totally independent of light since it relies on ATP and NADH, which are products of the light-dependent reactions.

The light-independent reactions of the Calvin cycle can be organized into three basic stages: fixation, reduction, and regeneration.

Stage 1: Fixation

In the stroma, in addition to CO_2,two other components are present to initiate the light-independent reactions: an enzyme called ribulose bisphosphate carboxylase (RuBisCO) and three molecules of ribulose bisphosphate (RuBP). RuBP has five atoms of carbon, flanked by two phosphates. RuBisCO catalyzes a reaction between CO_2 and RuBP. For each CO_2 molecule that reacts with one RuBP, two molecules of 3-phosphoglyceric acid (3-PGA) form. 3-PGA has three carbons and one phosphate. Each turn of the cycle involves only one RuBP and one carbon dioxide and forms two molecules of 3-PGA. The number of carbon atoms remains the same, as the atoms move to form new bonds during the reactions (3 atoms from $3CO_2$ + 15 atoms from 3RuBP = 18 atoms in 3 atoms of 3-PGA). This process is called carbon fixation because CO_2 is “fixed” from an inorganic form into organic molecules.

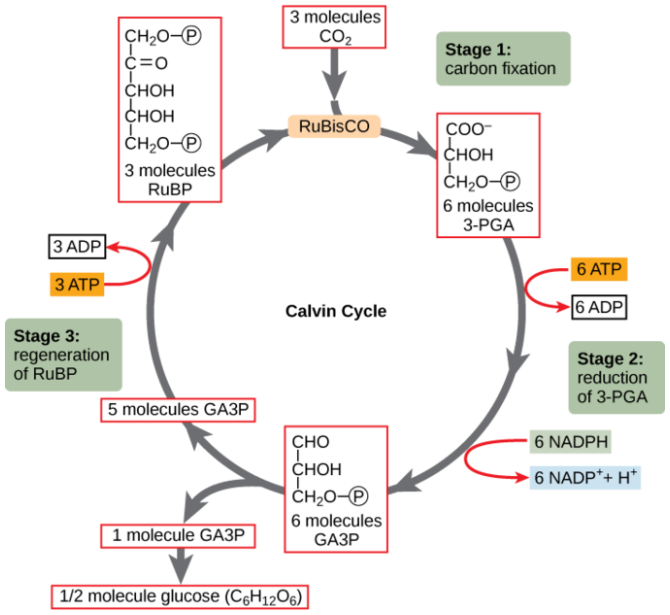


Figure **8.5.1.1**: The Calvin Cycle: The Calvin cycle has three stages. In stage 1, the enzyme RuBisCO incorporates carbon dioxide into an organic molecule, 3-PGA. In stage 2, the organic molecule is reduced using electrons supplied by NADPH. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue. Only one carbon dioxide molecule is incorporated at a time, so the cycle must be completed three times to produce a single three-carbon GA3P molecule, and six times to produce a six-carbon glucose molecule.

Stage 2: Reduction

ATP and NADPH are used to convert the six molecules of 3-PGA into six molecules of a chemical called glyceraldehyde 3-phosphate (G3P). This is a reduction reaction because it involves the gain of electrons by 3-PGA. Recall that a reduction is the gain of an electron by an atom or molecule. Six molecules of both ATP and NADPH are used. For ATP, energy is released with the loss of the terminal phosphate atom, converting it to ADP; for NADPH, both energy and a hydrogen atom are lost, converting it into $NADP^+$. Both of these molecules return to the nearby light-dependent reactions to be reused and reenergized.

Stage 3: Regeneration

At this point, only one of the G3P molecules leaves the Calvin cycle and is sent to the cytoplasm to contribute to the formation of other compounds needed by the plant. Because the G3P exported from the chloroplast has three carbon atoms, it takes three “turns” of the Calvin cycle to fix enough net carbon to export one G3P. But each turn makes two G3Ps, thus three turns make six G3Ps. One is exported while the remaining five G3P molecules remain in the cycle and are used to regenerate RuBP, which enables the system to prepare for more CO_2 to be fixed. Three more molecules of ATP are used in these regeneration reactions.

Key Points

- The Calvin cycle refers to the light-independent reactions in photosynthesis that take place in three key steps.
- Although the Calvin Cycle is not directly dependent on light, it is indirectly dependent on light since the necessary energy carriers (ATP and NADPH) are products of light-dependent reactions.
- In fixation, the first stage of the Calvin cycle, light-independent reactions are initiated; CO2 is fixed from an inorganic to an organic molecule.
- In the second stage, ATP and NADPH are used to reduce 3-PGA into G3P; then ATP and NADPH are converted to ADP and $NADP^+$, respectively.
- In the last stage of the Calvin Cycle, RuBP is regenerated, which enables the system to prepare for more CO_2 to be fixed.

Key Terms

- **light-independent reaction**: chemical reactions during photosynthesis that convert carbon dioxide and other compounds into glucose, taking place in the stroma

- **rubisco**: (ribulose bisphosphate carboxylase) a plant enzyme which catalyzes the fixing of atmospheric carbon dioxide during photosynthesis by catalyzing the reaction between carbon dioxide and RuBP
- **ribulose bisphosphate**: an organic substance that is involved in photosynthesis, reacts with carbon dioxide to form 3-PGA

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SECTION OVERVIEW

8.6: Photorespiration

8.6.1: CAM and C4 Photosynthesis

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8.6.1: CAM and C4 Photosynthesis

Learning Objectives

- Compare C4 and CAM photosynthesis

Photosynthesis in desert plants has evolved adaptations that conserve water. In harsh, dry heat, every drop of water must be used to survive. Because stomata must open to allow for the uptake of CO_2, water escapes from the leaf during active photosynthesis. Desert plants have evolved processes to conserve water and deal with harsh conditions. A more efficient use of CO_2 allows plants to adapt to living with less water.

Some plants such as cacti can prepare materials for photosynthesis during the night by a temporary carbon fixation and storage process, because opening the stomata at this time conserves water due to cooler temperatures. In addition, cacti have evolved the ability to carry out low levels of photosynthesis without opening stomata at all, a mechanism for surviving extremely dry periods.



Figure 8.6.1.1: Cactus: The harsh conditions of the desert have led plants like these cacti to evolve variations of the light-independent reactions of photosynthesis. These variations increase the efficiency of water usage, helping to conserve water and energy.

CAM Photosynthesis

Xerophytes, such as cacti and most succulents, also use
phosphoenolpyruvate (PEP) carboxylase to capture carbon dioxide in a process called crassulacean acid metabolism (CAM). In contrast to C_4 metabolism, which *physically* separates the CO_2 fixation to PEP from the Calvin cycle, CAM *temporally* separates these two processes.

CAM plants have a different leaf anatomy from C_3 plants, and fix the CO_2 at night, when their stomata are open. CAM plants store the CO_2 mostly in the form of malic acid via carboxylation of phosphoenolpyruvate to oxaloacetate, which is then reduced to malate. Decarboxylation of malate during the day releases CO_2 inside the leaves, thus allowing carbon fixation to 3-phosphoglycerate by RuBisCO. Sixteen thousand species of plants use CAM.

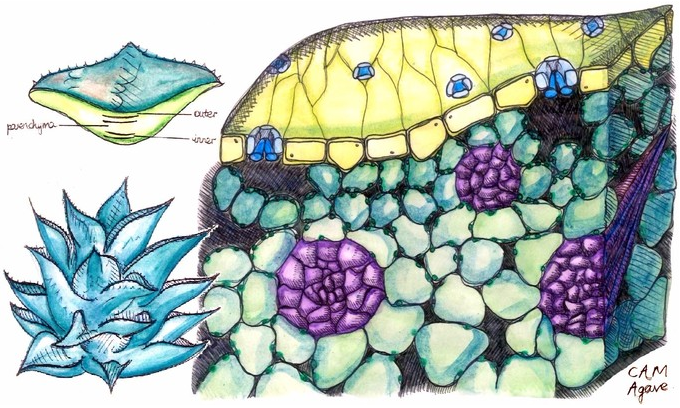
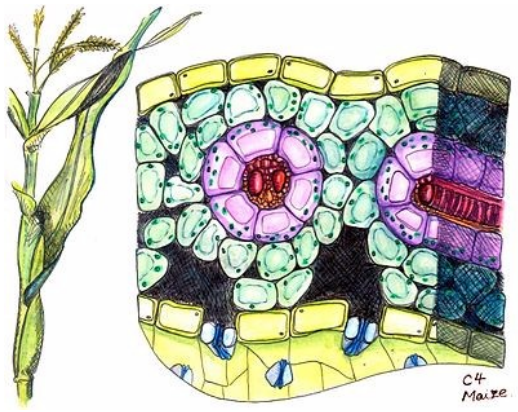


Figure **8.6.1.1**: Cross section of agave, a CAM plant: Cross section of a CAM (crassulacean acid metabolism) plant, specifically of an agave leaf. Vascular bundles shown. Drawing based on microscopic images courtesy of Cambridge University Plant Sciences Department.

C_4 Carbon Fixation

The C4 pathway bears resemblance to CAM; both act to concentrate CO_2 around RuBisCO, thereby increasing its efficiency. CAM concentrates it temporally, providing CO_2 during the day and not at night, when respiration is the dominant reaction.

C_4 plants, in contrast, concentrate CO_2 spatially, with a RuBisCO reaction centre in a "bundle sheath cell" that is inundated with CO_2. Due to the inactivity required by the CAM mechanism, C_4 carbon fixation has a greater efficiency in terms of PGA synthesis.



Cross section of maize, a C_4 plant

Cross section of a C4 plant, specifically of a maize leaf. Drawing based on microscopic images courtesy of Cambridge University Plant Sciences Department.

C_4 plants can produce more sugar than C_3 plants in conditions of high light and temperature. Many important crop plants are C_4 plants, including maize, sorghum, sugarcane, and millet. Plants that do not use PEP-carboxylase in carbon fixation are called C3 plants because the primary carboxylation reaction, catalyzed by RuBisCO, produces the three-carbon 3-phosphoglyceric acids directly in the Calvin-Benson cycle. Over 90% of plants use C_3 carbon fixation, compared to 3% that use C_4 carbon fixation; however, the evolution of C_4 in over 60 plant lineages makes it a striking example of convergent evolution.

Key Points

- The process of photosynthesis in desert plants has evolved mechanisms to conserve water.
- Plants that use crassulacean acid metabolism (CAM) photosynthesis fix CO_2 at night, when their stomata are open.
- Plants that use C4 carbon fixation concentrate carbon dioxide spatially, using "bundle sheath cells" which are inundated with CO_2.

Key Terms

- **crassulacean acid metabolism**: A carbon fixation pathway that evolved in some plants as an adaptation to arid conditions, in which the stomata in the leaves remain shut during the day to reduce evapotranspiration, but open at night to collect carbon dioxide (CO2).
- **C4 carbon fixation**: A form of photosynthesis in which plants concentrate CO2 spatially, with a RuBisCO reaction centre in a “bundle sheath cell” that is inundated with CO2

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CHAPTER OVERVIEW

9: Cell Communication

9.1: Overview of Cell Communication

9.1.1: Methods of Intracellular Signaling

9.2: Types of Receptors

9.3: Intracellular Receptors

9.3.1: Nuclear Hormone Receptors

9.4: Signal Transduction Through Receptor Kinases

9.4.1: Receptor Tyrosine Kinases (RTKs)

9.5: Signal Transduction Through G Protein Coupled Receptors

9.5.1: G-protein Coupled Receptors (GPCRs)

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SECTION OVERVIEW

9.1: Overview of Cell Communication

Skills to Develop

- Describe four types of signaling found in multicellular organisms
- Compare internal receptors with cell-surface receptors
- Recognize the relationship between a ligand’s structure and its mechanism of action

There are two kinds of communication in the world of living cells. Communication between cells is called intercellular signaling, and communication within a cell is called intracellular signaling. An easy way to remember the distinction is by understanding the Latin origin of the prefixes: inter- means "between" (for example, intersecting lines are those that cross each other) and intra- means "inside" (like intravenous).

Chemical signals are released by signaling cells in the form of small, usually volatile or soluble molecules called ligands. A ligand is a molecule that binds another specific molecule, in some cases, delivering a signal in the process. Ligands can thus be thought of as signaling molecules. Ligands interact with proteins in target cells, which are cells that are affected by chemical signals; these proteins are also called receptors. Ligands and receptors exist in several varieties; however, a specific ligand will have a specific receptor that typically binds only that ligand.

Forms of Signaling

There are four categories of chemical signaling found in multicellular organisms: paracrine signaling, endocrine signaling, autocrine signaling, and direct signaling across gap junctions (Figure **9.1.1**). The main difference between the different categories of signaling is the distance that the signal travels through the organism to reach the target cell. Not all cells are affected by the same signals.

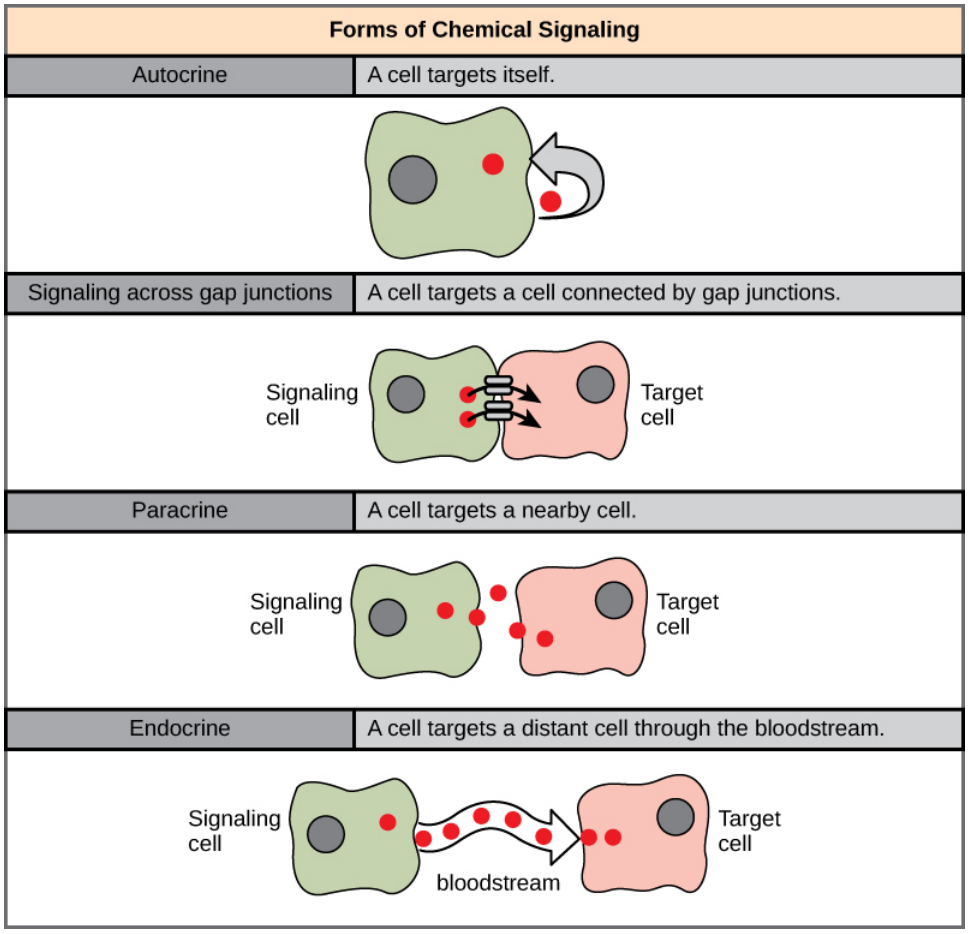


Figure 9.1.1: In chemical signaling, a cell may target itself (autocrine signaling), a cell connected by gap junctions, a nearby cell (paracrine signaling), or a distant cell (endocrine signaling). Paracrine signaling acts on nearby cells, endocrine signaling uses the circulatory system to transport ligands, and autocrine signaling acts on the signaling cell. Signaling via gap junctions involves signaling molecules moving directly between adjacent cells.

Paracrine Signaling

Signals that act locally between cells that are close together are called *paracrine signals*. Paracrine signals move by diffusion through the extracellular matrix. These types of signals usually elicit quick responses that last only a short amount of time. In order to keep the response localized, paracrine ligand molecules are normally quickly degraded by enzymes or removed by neighboring cells. Removing the signals will reestablish the concentration gradient for the signal, allowing them to quickly diffuse through the intracellular space if released again.

One example of paracrine signaling is the transfer of signals across synapses between nerve cells. A nerve cell consists of a cell body, several short, branched extensions called dendrites that receive stimuli, and a long extension called an axon, which transmits signals to other nerve cells or muscle cells. The junction between nerve cells where signal transmission occurs is called a synapse. A synaptic signal is a chemical signal that travels between nerve cells. Signals within the nerve cells are propagated by fast-moving electrical impulses. When these impulses reach the end of the axon, the signal continues on to a dendrite of the next cell by the release of chemical ligands called neurotransmitters by the presynaptic cell (the cell emitting the signal). The neurotransmitters are transported across the very small distances between nerve cells, which are called chemical synapses (Figure 9.1.2). The small distance between nerve cells allows the signal to travel quickly; this enables an immediate response, such as, Take your hand off the stove!

When the neurotransmitter binds the receptor on the surface of the postsynaptic cell, the electrochemical potential of the target cell changes, and the next electrical impulse is launched. The neurotransmitters that are released into the chemical synapse are degraded quickly or get reabsorbed by the presynaptic cell so that the recipient nerve cell can recover quickly and be prepared to respond rapidly to the next synaptic signal.

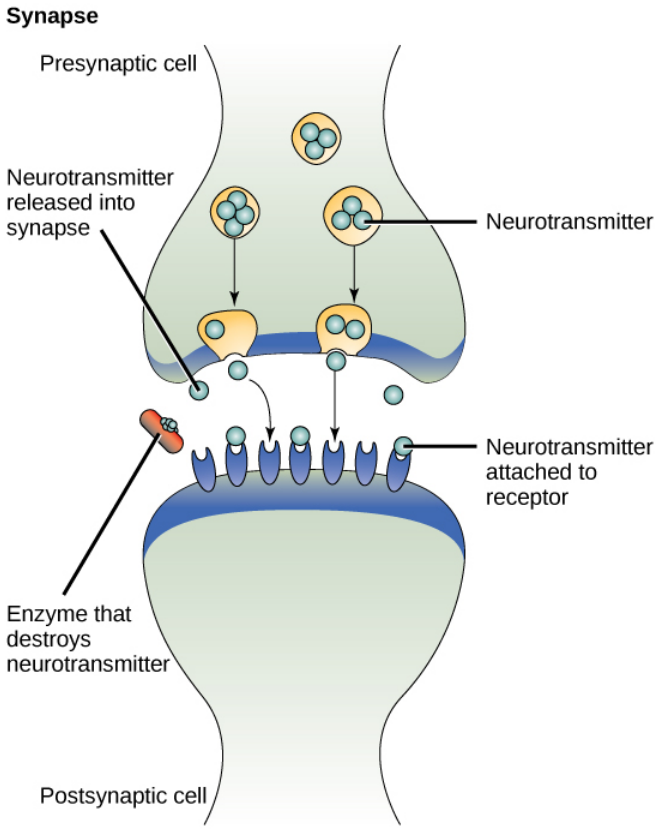


Figure **9.1.2**: The distance between the presynaptic cell and the postsynaptic cell—called the synaptic gap—is very small and allows for rapid diffusion of the neurotransmitter. Enzymes in the synapatic cleft degrade some types of neurotransmitters to terminate the signal.

Endocrine Signaling

Signals from distant cells are called endocrine signals, and they originate from endocrine cells. (In the body, many endocrine cells are located in endocrine glands, such as the thyroid gland, the hypothalamus, and the pituitary gland.) These types of signals usually produce a slower response but have a longer-lasting effect. The ligands released in endocrine signaling are called hormones, signaling molecules that are produced in one part of the body but affect other body regions some distance away.

Hormones travel the large distances between endocrine cells and their target cells via the bloodstream, which is a relatively slow way to move throughout the body. Because of their form of transport, hormones get diluted and are present in low concentrations when they act on their target cells. This is different from paracrine signaling, in which local concentrations of ligands can be very high.

Autocrine Signaling

Autocrine signals are produced by signaling cells that can also bind to the ligand that is released. This means the signaling cell and the target cell can be the same or a similar cell (the prefix *auto-* means self, a reminder that the signaling cell sends a signal to itself). This type of signaling often occurs during the early development of an organism to ensure that cells develop into the correct tissues and take on the proper function. Autocrine signaling also regulates pain sensation and inflammatory responses. Further, if a cell is infected with a virus, the cell can signal itself to undergo programmed cell death, killing the virus in the process. In some cases, neighboring cells of the same type are also influenced by the released ligand. In embryological development, this process of stimulating a group of neighboring cells may help to direct the differentiation of identical cells into the same cell type, thus ensuring the proper developmental outcome.

Direct Signaling Across Gap Junctions

Gap junctions in animals and plasmodesmata in plants are connections between the plasma membranes of neighboring cells. These water-filled channels allow small signaling molecules, called intracellular mediators, to diffuse between the two cells. Small

molecules, such as calcium ions (Ca^{2+}), are able to move between cells, but large molecules like proteins and DNA cannot fit through the channels. The specificity of the channels ensures that the cells remain independent but can quickly and easily transmit signals. The transfer of signaling molecules communicates the current state of the cell that is directly next to the target cell; this allows a group of cells to coordinate their response to a signal that only one of them may have received. In plants, plasmodesmata are ubiquitous, making the entire plant into a giant, communication network.

Types of Receptors

Receptors are protein molecules in the target cell or on its surface that bind ligand. There are two types of receptors, internal receptors and cell-surface receptors.

Internal receptors

Internal receptors, also known as intracellular or cytoplasmic receptors, are found in the cytoplasm of the cell and respond to hydrophobic ligand molecules that are able to travel across the plasma membrane. Once inside the cell, many of these molecules bind to proteins that act as regulators of mRNA synthesis (transcription) to mediate gene expression. Gene expression is the cellular process of transforming the information in a cell's DNA into a sequence of amino acids, which ultimately forms a protein. When the ligand binds to the internal receptor, a conformational change is triggered that exposes a DNA-binding site on the protein. The ligand-receptor complex moves into the nucleus, then binds to specific regulatory regions of the chromosomal DNA and promotes the initiation of transcription (Figure **9.1.3**). Transcription is the process of copying the information in a cells DNA into a special form of RNA called messenger RNA (mRNA); the cell uses information in the mRNA (which moves out into the cytoplasm and associates with ribosomes) to link specific amino acids in the correct order, producing a protein. Internal receptors can directly influence gene expression without having to pass the signal on to other receptors or messengers.

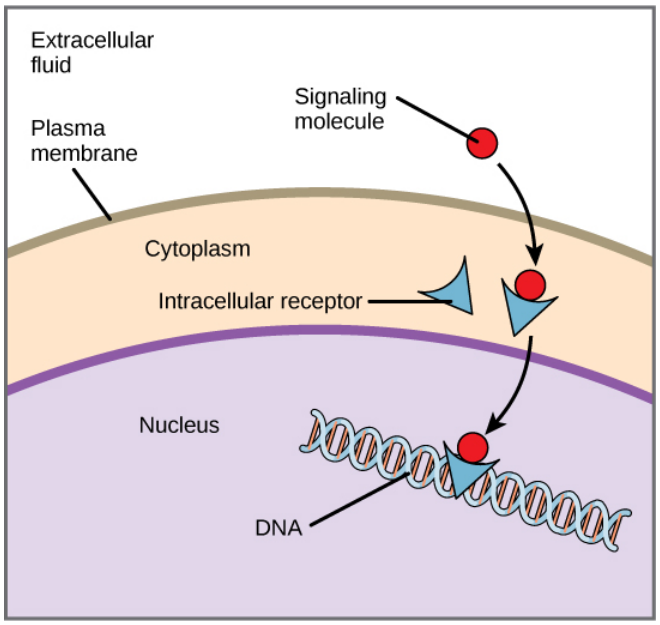


Figure **9.1.3**: Hydrophobic signaling molecules typically diffuse across the plasma membrane and interact with intracellular receptors in the cytoplasm. Many intracellular receptors are transcription factors that interact with DNA in the nucleus and regulate gene expression.

Cell-Surface Receptors

Cell-surface receptors, also known as transmembrane receptors, are cell surface, membrane-anchored (integral) proteins that bind to external ligand molecules. This type of receptor spans the plasma membrane and performs signal transduction, in which an extracellular signal is converted into an intercellular signal. Ligands that interact with cell-surface receptors do not have to enter the cell that they affect. Cell-surface receptors are also called cell-specific proteins or markers because they are specific to individual cell types.

Because cell-surface receptor proteins are fundamental to normal cell functioning, it should come as no surprise that a malfunction in any one of these proteins could have severe consequences. Errors in the protein structures of certain receptor molecules have

been shown to play a role in hypertension (high blood pressure), asthma, heart disease, and cancer.

Each cell-surface receptor has three main components: an external ligand-binding domain, a hydrophobic membrane-spanning region, and an intracellular domain inside the cell. The ligand-binding domain is also called the extracellular domain. The size and extent of each of these domains vary widely, depending on the type of receptor.

Evolution Connection: How Viruses Recognize a Host

Unlike living cells, many viruses do not have a plasma membrane or any of the structures necessary to sustain life. Some viruses are simply composed of an inert protein shell containing DNA or RNA. To reproduce, viruses must invade a living cell, which serves as a host, and then take over the hosts cellular apparatus. But how does a virus recognize its host?

Viruses often bind to cell-surface receptors on the host cell. For example, the virus that causes human influenza (flu) binds specifically to receptors on membranes of cells of the respiratory system. Chemical differences in the cell-surface receptors among hosts mean that a virus that infects a specific species (for example, humans) cannot infect another species (for example, chickens).

However, viruses have very small amounts of DNA or RNA compared to humans, and, as a result, viral reproduction can occur rapidly. Viral reproduction invariably produces errors that can lead to changes in newly produced viruses; these changes mean that the viral proteins that interact with cell-surface receptors may evolve in such a way that they can bind to receptors in a new host. Such changes happen randomly and quite often in the reproductive cycle of a virus, but the changes only matter if a virus with new binding properties comes into contact with a suitable host. In the case of influenza, this situation can occur in settings where animals and people are in close contact, such as poultry and swine farms.[1] Once a virus jumps to a new host, it can spread quickly. Scientists watch newly appearing viruses (called emerging viruses) closely in the hope that such monitoring can reduce the likelihood of global viral epidemics.

Cell-surface receptors are involved in most of the signaling in multicellular organisms. There are three general categories of cell-surface receptors: ion channel-linked receptors, G-protein-linked receptors, and enzyme-linked receptors.

Ion channel-linked receptors bind a ligand and open a channel through the membrane that allows specific ions to pass through. To form a channel, this type of cell-surface receptor has an extensive membrane-spanning region. In order to interact with the phospholipid fatty acid tails that form the center of the plasma membrane, many of the amino acids in the membrane-spanning region are hydrophobic in nature. Conversely, the amino acids that line the inside of the channel are hydrophilic to allow for the passage of water or ions. When a ligand binds to the extracellular region of the channel, there is a conformational change in the proteins structure that allows ions such as sodium, calcium, magnesium, and hydrogen to pass through (Figure **9.1.4**).

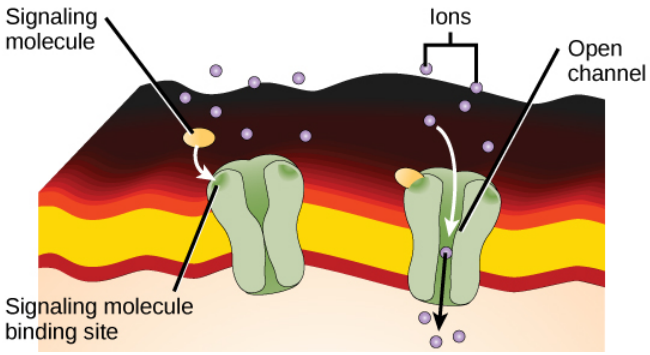


Figure **9.1.4**: Gated ion channels form a pore through the plasma membrane that opens when the signaling molecule binds. The open pore then allows ions to flow into or out of the cell.

G-protein-linked receptors bind a ligand and activate a membrane protein called a G-protein. The activated G-protein then interacts with either an ion channel or an enzyme in the membrane (Figure **9.1.5**). All G-protein-linked receptors have seven transmembrane domains, but each receptor has its own specific extracellular domain and G-protein-binding site.

Cell signaling using G-protein-linked receptors occurs as a cyclic series of events. Before the ligand binds, the inactive G-protein can bind to a newly revealed site on the receptor specific for its binding. Once the G-protein binds to the receptor, the resultant shape change activates the G-protein, which releases GDP and picks up GTP. The subunits of the G-protein then split into the α

subunit and the $\beta\gamma$ subunit. One or both of these G-protein fragments may be able to activate other proteins as a result. After awhile, the GTP on the active α subunit of the G-protein is hydrolyzed to GDP and the $\beta\gamma$ subunit is deactivated. The subunits reassociate to form the inactive G-protein and the cycle begins anew.

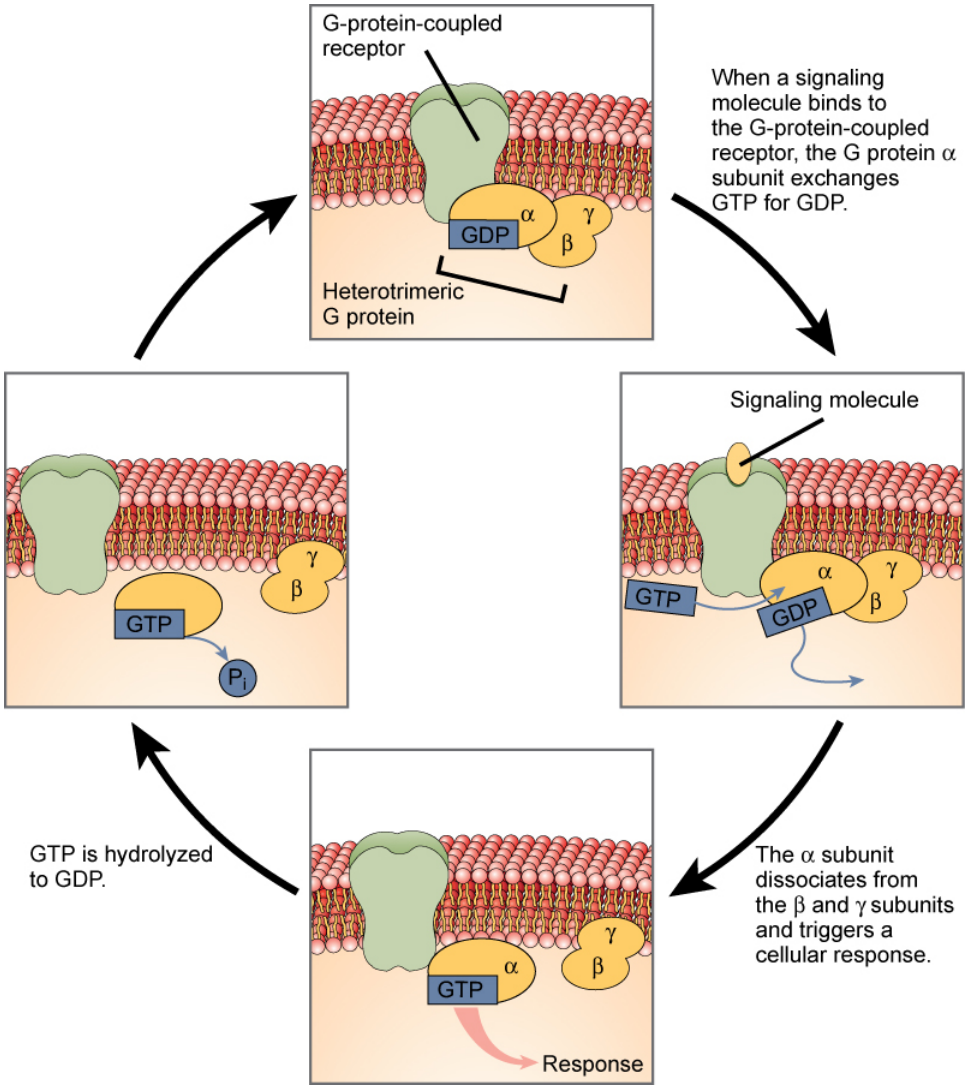
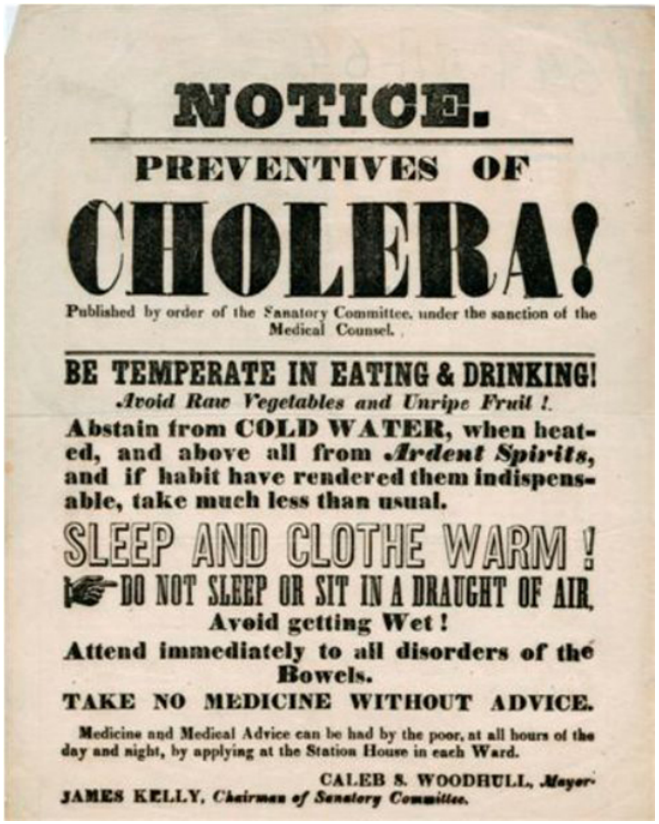


Figure **9.1.5**: Heterotrimeric G proteins have three subunits: α, β, and γ. When a signaling molecule binds to a G-protein-coupled receptor in the plasma membrane, a GDP molecule associated with the α subunit is exchanged for GTP. The β and γ subunits dissociate from the α subunit, and a cellular response is triggered either by the α subunit or the dissociated $\beta\gamma$ pair. Hydrolysis of GTP to GDP terminates the signal.

G-protein-linked receptors have been extensively studied and much has been learned about their roles in maintaining health. Bacteria that are pathogenic to humans can release poisons that interrupt specific G-protein-linked receptor function, leading to illnesses such as pertussis, botulism, and cholera. In cholera (Figure **9.1.6**), for example, the water-borne bacterium *Vibrio cholerae* produces a toxin, choleragen, that binds to cells lining the small intestine. The toxin then enters these intestinal cells, where it modifies a G-protein that controls the opening of a chloride channel and causes it to remain continuously active, resulting in large losses of fluids from the body and potentially fatal dehydration as a result.



NOTICE.

PREVENTIVES OF

CHOLERA!

Published by order of the Sanatory Committee, under the sanction of the Medical Counsel.

BE TEMPERATE IN EATING & DRINKING!

Avoid Raw Vegetables and Unripe Fruit !.

Abstain from COLD WATER, when heated, and above all from *Ardent Spirits*, and if habit have rendered them indispensable, take much less than usual.

SLEEP AND CLOTHE WARM !

DO NOT SLEEP OR SIT IN A DRAUGHT OF AIR.

Avoid getting Wet !

Attend immediately to all disorders of the Bowels.

TAKE NO MEDICINE WITHOUT ADVICE.

Medicine and Medical Advice can be had by the poor, at all hours of the day and night, by applying at the Station House in each Ward.

CALEB S. WOODHULL, *Mayor.*

JAMES KELLY, *Chairman of Sanatory Committee.*

Figure **9.1.6**: Transmitted primarily through contaminated drinking water, cholera is a major cause of death in the developing world and in areas where natural disasters interrupt the availability of clean water. The cholera bacterium, *Vibrio cholerae*, creates a toxin that modifies G-protein-mediated cell signaling pathways in the intestines. Modern sanitation eliminates the threat of cholera outbreaks, such as the one that swept through New York City in 1866. This poster from that era shows how, at that time, the way that the disease was transmitted was not understood. (credit: New York City Sanitary Commission)

Enzyme-linked receptors are cell-surface receptors with intracellular domains that are associated with an enzyme. In some cases, the intracellular domain of the receptor itself is an enzyme. Other enzyme-linked receptors have a small intracellular domain that interacts directly with an enzyme. The enzyme-linked receptors normally have large extracellular and intracellular domains, but the membrane-spanning region consists of a single alpha-helical region of the peptide strand. When a ligand binds to the extracellular domain, a signal is transferred through the membrane, activating the enzyme. Activation of the enzyme sets off a chain of events within the cell that eventually leads to a response. One example of this type of enzyme-linked receptor is the tyrosine kinase receptor (Figure **9.1.7**). A kinase is an enzyme that transfers phosphate groups from ATP to another protein. The tyrosine kinase receptor transfers phosphate groups to tyrosine molecules (tyrosine residues). First, signaling molecules bind to the extracellular domain of two nearby tyrosine kinase receptors. The two neighboring receptors then bond together, or dimerize. Phosphates are then added to tyrosine residues on the intracellular domain of the receptors (phosphorylation). The phosphorylated residues can then transmit the signal to the next messenger within the cytoplasm.

Art Connection

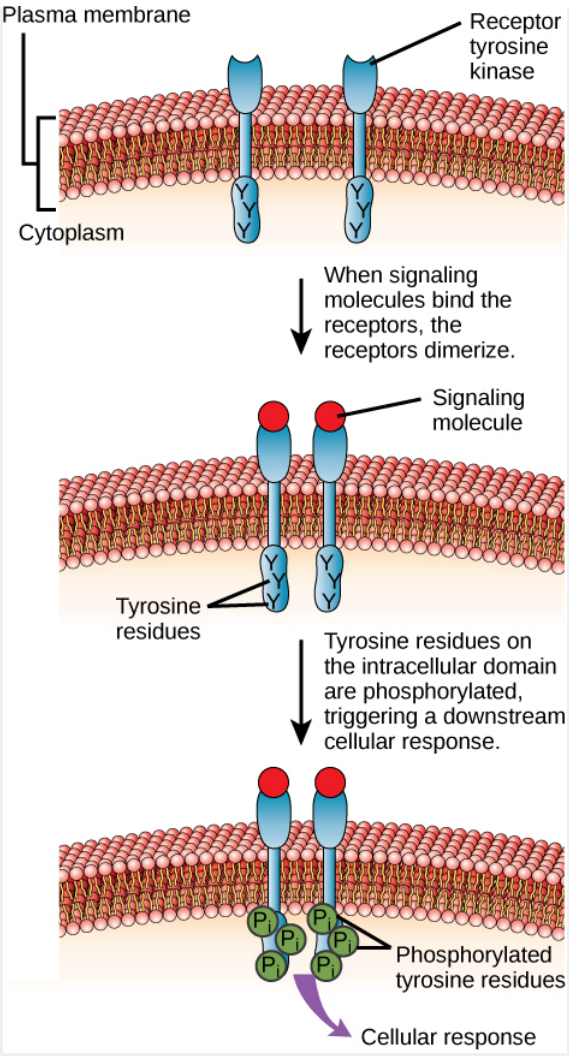


Figure **9.1.7**: A receptor tyrosine kinase is an enzyme-linked receptor with a single transmembrane region, and extracellular and intracellular domains. Binding of a signaling molecule to the extracellular domain causes the receptor to dimerize. Tyrosine residues on the intracellular domain are then autophosphorylated, triggering a downstream cellular response. The signal is terminated by a phosphatase that removes the phosphates from the phosphotyrosine residues.

HER2 is a receptor tyrosine kinase. In 30 percent of human breast cancers, HER2 is permanently activated, resulting in unregulated cell division. Lapatinib, a drug used to treat breast cancer, inhibits HER2 receptor tyrosine kinase autophosphorylation (the process by which the receptor adds phosphates onto itself), thus reducing tumor growth by 50 percent. Besides autophosphorylation, which of the following steps would be inhibited by Lapatinib?

A. Signaling molecule binding, dimerization, and the downstream cellular response
B. Dimerization, and the downstream cellular response
C. The downstream cellular response
D. Phosphatase activity, dimerization, and the downsteam cellular response

Signaling Molecules

Produced by signaling cells and the subsequent binding to receptors in target cells, ligands act as chemical signals that travel to the target cells to coordinate responses. The types of molecules that serve as ligands are incredibly varied and range from small proteins to small ions like calcium (Ca^{2+}).

Small Hydrophobic Ligands

Small hydrophobic ligands can directly diffuse through the plasma membrane and interact with internal receptors. Important members of this class of ligands are the steroid hormones. Steroids are lipids that have a hydrocarbon skeleton with four fused rings; different steroids have different functional groups attached to the carbon skeleton. Steroid hormones include the female sex hormone, estradiol, which is a type of estrogen; the male sex hormone, testosterone; and cholesterol, which is an important structural component of biological membranes and a precursor of steroid hormones (Figure **9.1.8**). Other hydrophobic hormones include thyroid hormones and vitamin D. In order to be soluble in blood, hydrophobic ligands must bind to carrier proteins while they are being transported through the bloodstream.

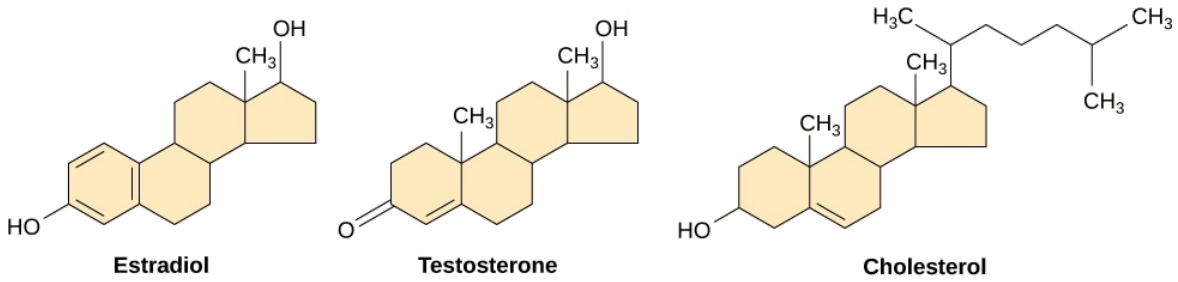


Figure **9.1.8**: Steroid hormones have similar chemical structures to their precursor, cholesterol. Because these molecules are small and hydrophobic, they can diffuse directly across the plasma membrane into the cell, where they interact with internal receptors.

Water-Soluble Ligands

Water-soluble ligands are polar and therefore cannot pass through the plasma membrane unaided; sometimes, they are too large to pass through the membrane at all. Instead, most water-soluble ligands bind to the extracellular domain of cell-surface receptors. This group of ligands is quite diverse and includes small molecules, peptides, and proteins.

Other Ligands

Nitric oxide (NO) is a gas that also acts as a ligand. It is able to diffuse directly across the plasma membrane, and one of its roles is to interact with receptors in smooth muscle and induce relaxation of the tissue. NO has a very short half-life and therefore only functions over short distances. Nitroglycerin, a treatment for heart disease, acts by triggering the release of NO, which causes blood vessels to dilate (expand), thus restoring blood flow to the heart. NO has become better known recently because the pathway that it affects is targeted by prescription medications for erectile dysfunction, such as Viagra (erection involves dilated blood vessels).

Summary

Cells communicate by both inter- and intracellular signaling. Signaling cells secrete ligands that bind to target cells and initiate a chain of events within the target cell. The four categories of signaling in multicellular organisms are paracrine signaling, endocrine signaling, autocrine signaling, and direct signaling across gap junctions. Paracrine signaling takes place over short distances. Endocrine signals are carried long distances through the bloodstream by hormones, and autocrine signals are received by the same cell that sent the signal or other nearby cells of the same kind. Gap junctions allow small molecules, including signaling molecules, to flow between neighboring cells.

Internal receptors are found in the cell cytoplasm. Here, they bind ligand molecules that cross the plasma membrane; these receptor-ligand complexes move to the nucleus and interact directly with cellular DNA. Cell-surface receptors transmit a signal from outside the cell to the cytoplasm. Ion channel-linked receptors, when bound to their ligands, form a pore through the plasma membrane through which certain ions can pass. G-protein-linked receptors interact with a G-protein on the cytoplasmic side of the plasma membrane, promoting the exchange of bound GDP for GTP and interacting with other enzymes or ion channels to transmit a signal. Enzyme-linked receptors transmit a signal from outside the cell to an intracellular domain of a membrane-bound enzyme. Ligand binding causes activation of the enzyme. Small hydrophobic ligands (like steroids) are able to penetrate the plasma membrane and bind to internal receptors. Water-soluble hydrophilic ligands are unable to pass through the membrane; instead, they bind to cell-surface receptors, which transmit the signal to the inside of the cell.

Art Connections

Figure 9.1.7: HER2 is a receptor tyrosine kinase. In 30 percent of human breast cancers, HER2 is permanently activated, resulting in unregulated cell division. Lapatinib, a drug used to treat breast cancer, inhibits HER2 receptor tyrosine kinase autophosphorylation (the process by which the receptor adds phosphates onto itself), thus reducing tumor growth by 50 percent. Besides autophosphorylation, which of the following steps would be inhibited by Lapatinib?

A. Signaling molecule binding, dimerization, and the downstream cellular response.
B. Dimerization, and the downstream cellular response.
C. The downstream cellular response.
D. Phosphatase activity, dimerization, and the downsteam cellular response.

Answer

C. The downstream cellular response would be inhibited.

Footnotes

1. 1 A. B. Sigalov, The School of Nature. IV. Learning from Viruses, *Self/Nonself* 1, no. 4 (2010): 282-298. Y. Cao, X. Koh, L. Dong, X. Du, A. Wu, X. Ding, H. Deng, Y. Shu, J. Chen, T. Jiang, Rapid Estimation of Binding Activity of Influenza Virus Hemagglutinin to Human and Avian Receptors, *PLoS One* 6, no. 4 (2011): e18664.

Glossary

autocrine signal
signal that is sent and received by the same or similar nearby cells

cell-surface receptor
cell-surface protein that transmits a signal from the exterior of the cell to the interior, even though the ligand does not enter the cell

chemical synapse
small space between axon terminals and dendrites of nerve cells where neurotransmitters function

endocrine cell
cell that releases ligands involved in endocrine signaling (hormones)

endocrine signal
long-distance signal that is delivered by ligands (hormones) traveling through an organisms circulatory system from the signaling cell to the target cell

enzyme-linked receptor
cell-surface receptor with intracellular domains that are associated with membrane-bound enzymes

extracellular domain
region of a cell-surface receptor that is located on the cell surface

G-protein-linked receptor
cell-surface receptor that activates membrane-bound G-proteins to transmit a signal from the receptor to nearby membrane components

intercellular signaling
communication between cells

internal receptor

(also, intracellular receptor) receptor protein that is located in the cytosol of a cell and binds to ligands that pass through the plasma membrane

intracellular mediator
(also, second messenger) small molecule that transmits signals within a cell

intracellular signaling
communication within cells

ion channel-linked receptor
cell-surface receptor that forms a plasma membrane channel, which opens when a ligand binds to the extracellular domain (ligand-gated channels)

ligand
molecule produced by a signaling cell that binds with a specific receptor, delivering a signal in the process

neurotransmitter
chemical ligand that carries a signal from one nerve cell to the next

paracrine signal
signal between nearby cells that is delivered by ligands traveling in the liquid medium in the space between the cells

receptor
protein in or on a target cell that bind to ligands

signaling cell
cell that releases signal molecules that allow communication with another cell

synaptic signal
chemical signal (neurotransmitter) that travels between nerve cells

target cell
cell that has a receptor for a signal or ligand from a signaling cell

9.1.1: Methods of Intracellular Signaling

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9.1.1: Methods of Intracellular Signaling

Learning Objectives

- Explain how the binding of a ligand initiates signal transduction throughout a cell

The induction of a signaling pathway depends on the modification of a cellular component by an enzyme. There are numerous enzymatic modifications that can occur which are recognized in turn by the next component downstream.

One of the most common chemical modifications that occurs in signaling pathways is the addition of a phosphate group (PO_4^{-3}) to a molecule such as a protein in a process called phosphorylation. The phosphate can be added to a nucleotide such as GMP to form GDP or GTP. Phosphates are also often added to serine, threonine, and tyrosine residues of proteins where they replace the hydroxyl group of the amino acid. The transfer of the phosphate is catalyzed by an enzyme called a kinase. Various kinases are named for the substrate they phosphorylate. Phosphorylation of serine and threonine residues often activates enzymes. Phosphorylation of tyrosine residues can either affect the activity of an enzyme or create a binding site that interacts with downstream components in the signaling cascade. Phosphorylation may activate or inactivate enzymes; the reversal of phosphorylation, dephosphorylation by a phosphatase, will reverse the effect.

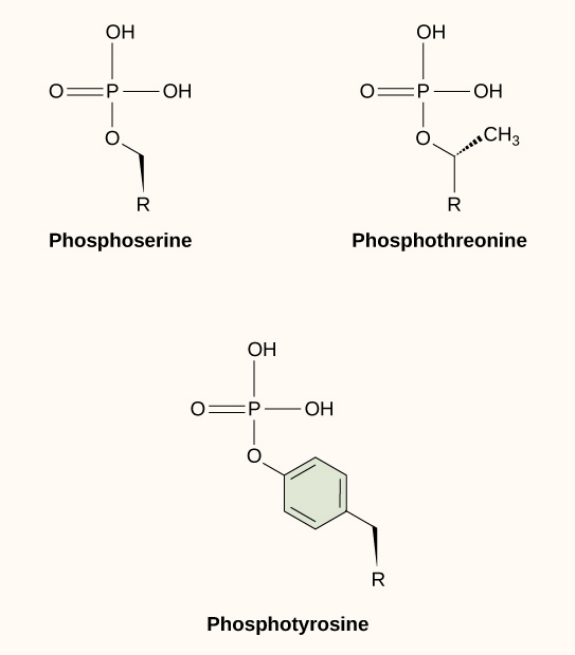


Figure 9.1.1.1: Example of phosphorylation: In protein phosphorylation, a phosphate group (PO4-3) is added to residues of the amino acids serine, threonine, and tyrosine.

The activation of second messengers is also a common event after the induction of a signaling pathway. They are small molecules that propagate a signal after it has been initiated by the binding of the signaling molecule to the receptor. These molecules help to spread a signal through the cytoplasm by altering the behavior of certain cellular proteins.

Calcium ion is a widely-used second messenger. The free concentration of calcium ions (Ca^{2+}) within a cell is very low because ion pumps in the plasma membrane continuously use adenosine-5′-triphosphate (ATP) to remove it. For signaling purposes, Ca^{2+} is stored in cytoplasmic vesicles, such as the endoplasmic reticulum, or accessed from outside the cell. When signaling occurs, ligand-gated calcium ion channels allow the higher levels of Ca^{2+} that are present outside the cell (or in intracellular storage compartments) to flow into the cytoplasm, which raises the concentration of cytoplasmic Ca^{2+}. The response to the increase in Ca^{2+} varies, depending on the cell type involved. For example, in the β-cells of the pancreas, Ca^{2+} signaling leads to the release of insulin, whereas in muscle cells, an increase in Ca^{2+} leads to muscle contractions.

Another second messenger utilized in many different cell types is cyclic AMP (cAMP). Cyclic AMP is synthesized by the enzyme adenylyl cyclase from ATP. The main role of cAMP in cells is to bind to and activate an enzyme called cAMP-dependent kinase

(A-kinase). A-kinase regulates many vital metabolic pathways. It phosphorylates serine and threonine residues of its target proteins, activating them in the process. A-kinase is found in many different types of cells; the target proteins in each kind of cell are different. Differences give rise to the variation of the responses to cAMP in different cells.

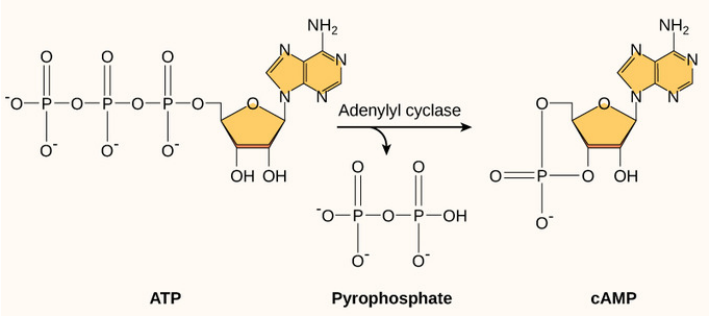


Figure 9.1.1.1: Example of cAMP as a second messenger: This diagram shows the mechanism for the formation of cyclic AMP (cAMP). cAMP serves as a second messenger to activate or inactivate proteins within the cell. Termination of the signal occurs when an enzyme called phosphodiesterase converts cAMP into AMP.

Present in small concentrations in the plasma membrane, inositol phospholipids are lipids that can also be converted into second messengers. Because these molecules are membrane components, they are located near membrane-bound receptors and can easily interact with them. Phosphatidylinositol (PI) is the main phospholipid that plays a role in cellular signaling. Enzymes known as kinases phosphorylate PI to form PI-phosphate (PIP) and PI-bisphosphate (PIP_2).

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Key Points

- Phosphorylation, the addition of a phosphate group to a molecule such as a protein, is one of the most common chemical modifications that occurs in signaling pathways.
- The activation of second messengers, small molecules that propagate a signal, is a common event after the induction of a signaling pathway.
- Calcium ion, cyclic AMP, and inositol phospholipids are examples of widely-used second messengers.

Key Terms

- **second messenger**: any substance used to transmit a signal within a cell, especially one which triggers a cascade of events by activating cellular components
- **phosphorylation**: the addition of a phosphate group to a compound; often catalyzed by enzymes

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9.2: Types of Receptors

Learning Objectives

- Compare internal receptors with cell-surface receptors

Types of Receptors

Receptors are protein molecules in the target cell or on its surface that bind ligands. There are two types of receptors: internal receptors and cell-surface receptors.

Internal receptors

Internal receptors, also known as intracellular or cytoplasmic receptors, are found in the cytoplasm of the cell and respond to hydrophobic ligand molecules that are able to travel across the plasma membrane. Once inside the cell, many of these molecules bind to proteins that act as regulators of mRNA synthesis to mediate gene expression. Gene expression is the cellular process of transforming the information in a cell's DNA into a sequence of amino acids that ultimately forms a protein. When the ligand binds to the internal receptor, a conformational change exposes a DNA-binding site on the protein. The ligand-receptor complex moves into the nucleus, binds to specific regulatory regions of the chromosomal DNA, and promotes the initiation of transcription. Internal receptors can directly influence gene expression without having to pass the signal on to other receptors or messengers.

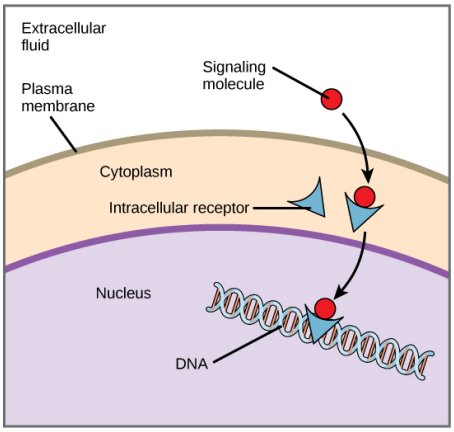


Figure **9.2.1**: Intracellular Receptors: Hydrophobic signaling molecules typically diffuse across the plasma membrane and interact with intracellular receptors in the cytoplasm. Many intracellular receptors are transcription factors that interact with DNA in the nucleus and regulate gene expression.

Cell-Surface Receptors

Cell-surface receptors, also known as transmembrane receptors, are cell surface, membrane-anchored, or integral proteins that bind to external ligand molecules. This type of receptor spans the plasma membrane and performs signal transduction, converting an extracellular signal into an intracellular signal. Ligands that interact with cell-surface receptors do not have to enter the cell that they affect. Cell-surface receptors are also called cell-specific proteins or markers because they are specific to individual cell types.

Each cell-surface receptor has three main components: an external ligand-binding domain (extracellular domain), a hydrophobic membrane-spanning region, and an intracellular domain inside the cell. The size and extent of each of these domains vary widely, depending on the type of receptor.

Cell-surface receptors are involved in most of the signaling in multicellular organisms. There are three general categories of cell-surface receptors: ion channel-linked receptors, G-protein-linked receptors, and enzyme-linked receptors.

Ion Channel-Linked Receptors

Ion channel-linked receptors bind a ligand and open a channel through the membrane that allows specific ions to pass through. To form a channel, this type of cell-surface receptor has an extensive membrane-spanning region. In order to interact with the phospholipid fatty acid tails that form the center of the plasma membrane, many of the amino acids in the membrane-spanning

region are hydrophobic in nature. Conversely, the amino acids that line the inside of the channel are hydrophilic to allow for the passage of water or ions. When a ligand binds to the extracellular region of the channel, there is a conformational change in the protein's structure that allows ions such as sodium, calcium, magnesium, and hydrogen to pass through.

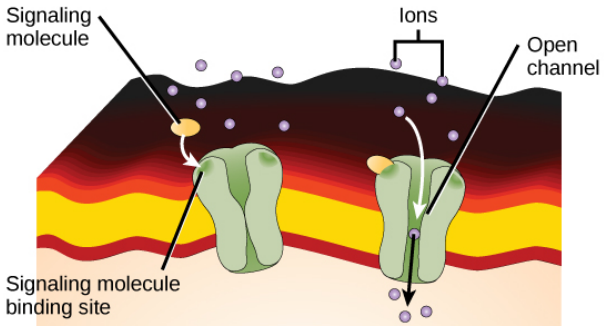


Figure **9.2.1**: Gated-Ion Channels: Gated ion channels form a pore through the plasma membrane that opens when the signaling molecule binds. The open pore then allows ions to flow into or out of the cell.

G-Protein Linked Receptors

G-protein-linked receptors bind a ligand and activate a membrane protein called a G-protein. The activated G-protein then interacts with either an ion channel or an enzyme in the membrane. All G-protein-linked receptors have seven transmembrane domains, but each receptor has its own specific extracellular domain and G-protein-binding site.

Cell signaling using G-protein-linked receptors occurs as a cyclic series of events. Before the ligand binds, the inactive G-protein can bind to a newly-revealed site on the receptor specific for its binding. Once the G-protein binds to the receptor, the resultant shape change activates the G-protein, which releases GDP and picks up GTP. The subunits of the G-protein then split into the α subunit and the β subunit. One or both of these G-protein fragments may be able to activate other proteins as a result. Later, the GTP on the active α subunit of the G-protein is hydrolyzed to GDP and the β subunit is deactivated. The subunits reassociate to form the inactive G-protein, and the cycle starts over.

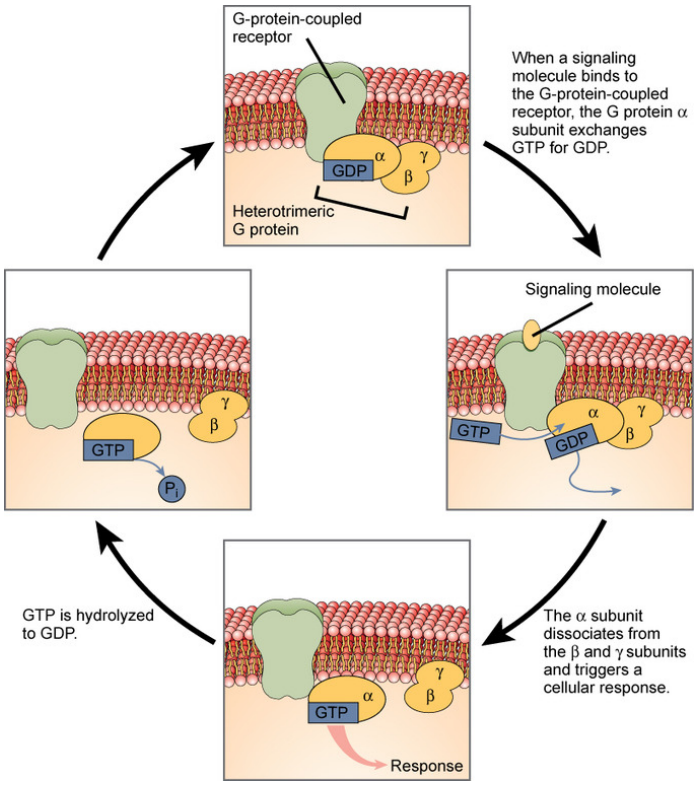


Figure **9.2.1**: G-proteins: Heterotrimeric G proteins have three subunits: α, β, and γ. When a signaling molecule binds to a G-protein-coupled receptor in the plasma membrane, a GDP molecule associated with the α subunit is exchanged for GTP. The β and γ subunits dissociate from the α subunit, and a cellular response is triggered either by the α subunit or the dissociated β pair. Hydrolysis of GTP to GDP terminates the signal.

Enzyme-Linked Receptors

Enzyme-linked receptors are cell-surface receptors with intracellular domains that are associated with an enzyme. In some cases, the intracellular domain of the receptor itself is an enzyme or the enzyme-linked receptor has an intracellular domain that interacts directly with an enzyme. The enzyme-linked receptors normally have large extracellular and intracellular domains, but the membrane-spanning region consists of a single alpha-helical region of the peptide strand. When a ligand binds to the extracellular domain, a signal is transferred through the membrane and activates the enzyme, which sets off a chain of events within the cell that eventually leads to a response. An example of this type of enzyme-linked receptor is the tyrosine kinase receptor. The tyrosine kinase receptor transfers phosphate groups to tyrosine molecules. Signaling molecules bind to the extracellular domain of two nearby tyrosine kinase receptors, which then dimerize. Phosphates are then added to tyrosine residues on the intracellular domain of the receptors and can then transmit the signal to the next messenger within the cytoplasm.

Key Points

- Intracellular receptors are located in the cytoplasm of the cell and are activated by hydrophobic ligand molecules that can pass through the plasma membrane.
- Cell-surface receptors bind to an external ligand molecule and convert an extracellular signal into an intracellular signal.
- Three general categories of cell-surface receptors include: ion -channel, G- protein, and enzyme -linked protein receptors.
- Ion channel -linked receptors bind a ligand and open a channel through the membrane that allows specific ions to pass through.
- G-protein-linked receptors bind a ligand and activate a membrane protein called a G-protein, which then interacts with either an ion channel or an enzyme in the membrane.
- Enzyme-linked receptors are cell-surface receptors with intracellular domains that are associated with an enzyme.

Key Terms

- **integral protein**: a protein molecule (or assembly of proteins) that is permanently attached to the biological membrane
- **transcription**: the synthesis of RNA under the direction of DNA

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SECTION OVERVIEW

9.3: Intracellular Receptors

9.3.1: Nuclear Hormone Receptors

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9.3.1: Nuclear Hormone Receptors

Another type of relatively simple, though much slower, signaling is seen in pathways in which the signals are steroid hormones, like estrogen or testosterone, pictured below. Steroid hormones, as you are aware, are related to cholesterol, and as hydrophobic molecules, they are able to cross the cell membrane by themselves. This is unusual, as most signals coming to cells are incapable of crossing the plasma membrane, and thus, must have cell surface receptors.

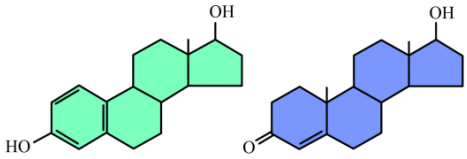


Figure 8.3.1: *Estradiol and Testosterone*

By contrast, steroid hormones have receptors inside the cell (intracellular receptors). Steroid hormone receptors are proteins that belong in a family known as the *nuclear receptors*. Nuclear hormone receptors are proteins with a double life: they are actually dormant transcription regulators. In the absence of signal, these receptors are in the cytoplasm, complexed with other proteins (HSP in Figure 8.3.2) and inactive. When a steroid hormone enters the cell, the nuclear hormone receptor binds the hormone and dissociates from the HSP. The receptors, then, with the hormone bound, translocate into the nucleus.

In the nucleus, Nuclear hormone receptors regulate the transcription of target genes by binding to their regulatory sequences (labeled HRE for hormone- response elements). The binding of the hormone-receptor complex to the regulatory elements of hormone-responsive genes modulates their expression. Because these responses involve gene expression, they are relatively slow. Most other signaling pathways, besides the two we have just discussed, involve multiple steps in which the original signal is passed on and amplified through a number of intermediate steps, before the cell responds to the signal.

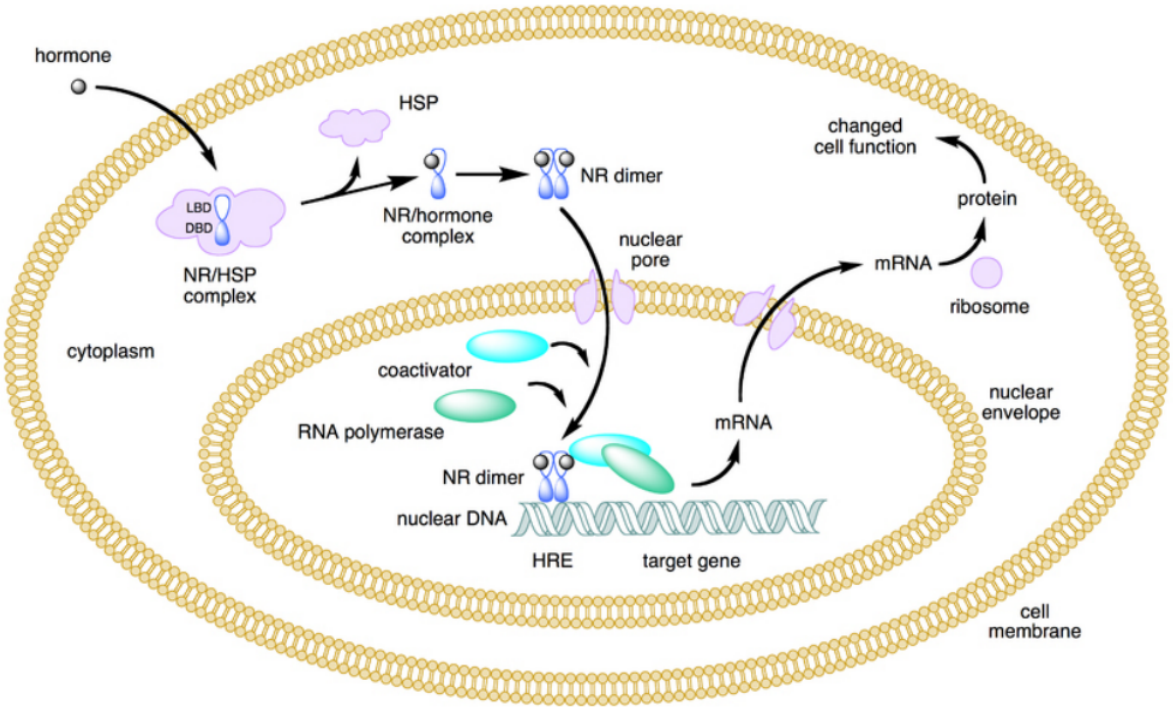


Figure 8.3.2: *Steroid hormones act by modulating expression of hormone-responsive genes*

We will now consider two signaling pathways, each mediated by a major class of cell surface receptor- the G-protein coupled receptors (GPCRs) and the receptor tyrosine kinases (RTKs). While the specific details of the signaling pathways that follow the binding of signals to each of these receptor types are different, it is easier to learn them when you can see what the pathways have

in common, namely, interaction of the signal with a receptor, followed by relaying the signal through a variable number of intermediate molecules, with the last of these molecules interacting with target protein(s) to modify their activity in the cell.

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SECTION OVERVIEW

9.4: Signal Transduction Through Receptor Kinases

9.4.1: Receptor Tyrosine Kinases (RTKs)

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9.4.1: Receptor Tyrosine Kinases (RTKs)

Receptor tyrosine kinases mediate responses to a large number of signals, including peptide hormones like insulin and growth factors like epidermal growth factor. Like the GPCRs, receptor tyrosine kinases bind a signal, then pass the message on through a series of intracellular molecules, the last of which acts on target proteins to change the state of the cell.

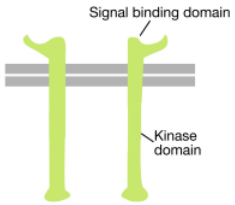


Figure 8.5.1: *Receptor Tyrosine Kinase before signal binding*

As the name suggests, a receptor tyrosine kinase is a cell surface receptor that also has a tyrosine kinase activity. The signal binding domain of the receptor tyrosine kinase is on the cell surface, while the tyrosine kinase enzymatic activity resides in the cytoplasmic part of the protein (see figure above). A transmembrane alpha helix connects these two regions of the receptor.

What happens when signal molecules bind to receptor tyrosine kinases?

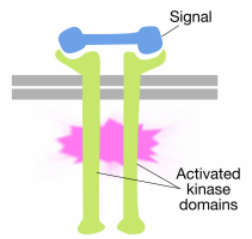


Figure 8.5.2: *Signal binding causes dimerization of receptor and activation of tyrosine kinase domains*

Binding of signal molecules to the extracellular domains of receptor tyrosine kinase molecules causes two receptor molecules to dimerize (come together and associate). This brings the cytoplasmic tails of the receptors close to each other and causes the tyrosine kinase activity of these tails to be turned on. The activated tails then phosphorylate each other on several tyrosine residues. This is called autophosphorylation.

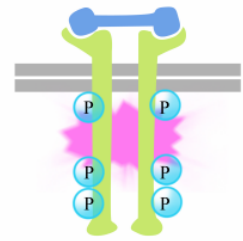


Figure 8.5.3: *Activated tyrosine kinase domains add phosphate onto each other*

The phosphorylation of tyrosines on the receptor tails triggers the assembly of an intracellular signaling complex on the tails. The newly phosphorylated tyrosines serve as binding sites for signaling proteins that then pass the message on to yet other proteins. An important protein that is subsequently activated by the signaling complexes on the receptor tyrosine kinases is called *Ras*.

The Ras protein is a monomeric guanine nucleotide binding protein that is associated with the cytosolic face of the plasma membrane (in fact, it is a lot like the alpha subunit of trimeric G-proteins). Just like the alpha subunit of a G- protein, Ras is active when GTP is bound to it and inactive when GDP is bound to it.Also, like the alpha subunit, Ras can hydrolyze the GTP to GDP.

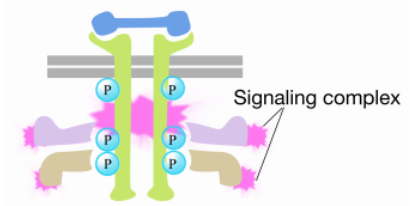


Figure 8.5.4: *Complex of signaling proteins assembles on phosphorylated RTK tails. This complex can activate Ras.*

When a signal arrives at the receptor tyrosine kinase, the receptor monomers come together and phosphorylate each others' tyrosines, triggering the assembly of a complex of proteins on the cytoplasmic tail of the receptor. One of the proteins in this complex interacts with Ras and stimulates the exchange of the GDP bound to the inactive Ras for a GTP. This activates the Ras.

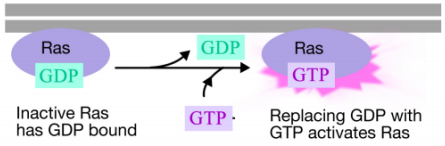


Figure 8.5.5: *Ras Activation*

Activated Ras triggers a phosphorylation cascade of three protein kinases, which relay and distribute the signal. These protein kinases are members of a group called the MAP kinases (Mitogen Activated Protein Kinases). The final kinase in this cascade phosphorylates various target proteins, including enzymes and transcriptional activators that regulate gene expression.

The phosphorylation of various enzymes can alter their activities, and set off new chemical reactions in the cell, while the phosphorylation of transcriptional activators can change which genes are expressed. The combined effect of changes in gene expression and protein activity alter the cell's physiological state.

Once again, in following the path of signal transduction mediated by RTKs, it is possible to discern the same basic pattern of events: a signal is bound by the extracellular domains of receptor tyrosine kinases, resulting in receptor dimerization and autophosphorylation of the cytosolic tails, thus conveying the message to the interior of the cell.

The message is passed on via a signalling complex to Ras which then stimulates a series of kinases. The terminal kinase in the cascade acts on target proteins and brings about in changes in protein activities and gene expression.

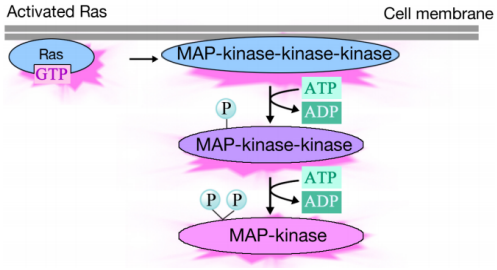


Figure 8.5.6: *Activated Ras Cascade*

The descriptions above provide a very simple sketch of some of the major classes of receptors and deal primarily with the mechanistic details of the steps by which signals received by various types of receptors bring about changes in cells. A major take-home lesson is the essential similarity of the different pathways.

Another point to keep in mind is that while we have looked at each individual pathway in isolation, a cell, at any given time receives multiple signals that set off a variety of different responses at once. The pathways described above show a considerable degree of "cross-talk" and the response to any given signal is affected by the other signals that the cell receives simultaneously. The multitude of different receptors, signals and the combinations thereof are the means by which cells are able to respond to an enormous variety of different circumstances.

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SECTION OVERVIEW

9.5: Signal Transduction Through G Protein Coupled Receptors

9.5.1: G-protein Coupled Receptors (GPCRs)

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9.5.1: G-protein Coupled Receptors (GPCRs)

G-protein coupled receptors are involved in responses of cells to many different kinds of signals, from epinephrine, to odors, to light. In fact, a variety of physiological phenomena including vision, taste, smell and the fight-or-flight response are mediated by GPCRs.

What are G-protein coupled receptors?

G-protein coupled receptors are cell surface receptors that pass on the signals that they receive with the help of guanine nucleotide binding proteins (a.k.a. G-proteins). Before thinking any further about the signaling pathways downstream of GPCRs, it is necessary to know a few important facts about these receptors and the G-proteins that assist them. Though there are hundreds of different G-protein coupled receptors, they all have the same basic structure: they all consist of a single polypeptide chain that threads back and forth seven times through the lipid bilayer of the plasma membrane. For this reason, they are sometimes called seven- pass transmembrane (7TM) receptors.

One end of the polypeptide forms the extracellular domain that binds the signal while the other end is in the cytosol of the cell.

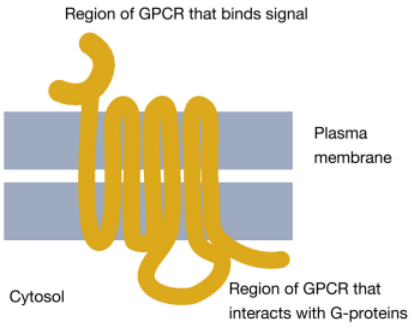


Figure 8.4.1: *G-protein coupled receptor*

When a ligand (signal) binds the extracellular domain of a GPCR, the receptor undergoes a conformational change that allows it to interact with a G-protein that will then pass the signal on to other intermediates in the signaling pathway.

What is a G-protein?

As noted above, a G-protein is a guanine nucleotide-binding protein that can interact with a G-protein linked receptor. G-proteins are associated with the cytosolic side of the plasma membrane, where they are ideally situated to interact with the cytosolic tail of the GPCR, when a signal binds to the GPCR.

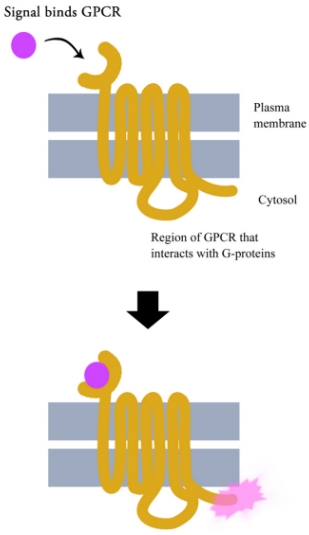


Figure 8.4.2: *G-protein coupled receptor signaling*

There are many different G-proteins, all of which share a characteristic structure- they are composed of three subunits called alpha, beta and gamma (aß.). Because of this, they are sometimes called heterotrimeric G proteins (hetero=different, trimeric= having three parts). The a subunit of such proteins can bind GDP or GTP and is capable of hydrolyzing a GTP molecule bound to it into GDP. In the unstimulated state of the cell, that is, in the absence of a signal bound to the GPCR, the G-proteins are found in the trimeric form (aß. bound together) and the a subunit has a GDP molecule bound to it.

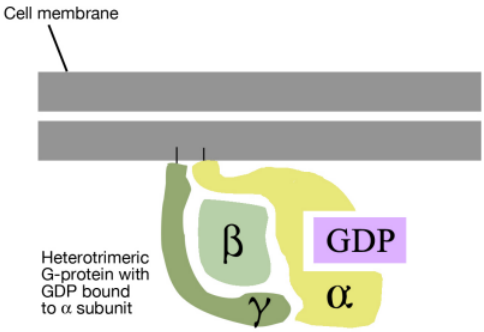


Figure 8.4.3: *G-protein with GDP Bound*

With this background on the structure and general properties of the GPCRs and the G-proteins, we can now look at what happens when a signal arrives at the cell surface and binds to a GPCR. The binding of a signal molecule by the extracellular part of the G-protein linked receptor causes the cytosolic tail of the receptor to interact with, and alter the conformation of, a G-protein. This has two consequences:

- First, the alpha subunit of the G- protein loses its GDP and binds a GTP instead.
- Second, the G-protein breaks up into the GTP-bound a part and the ß. part.

These two parts can diffuse freely along the cytosolic face of the plasma membrane and act upon their targets.

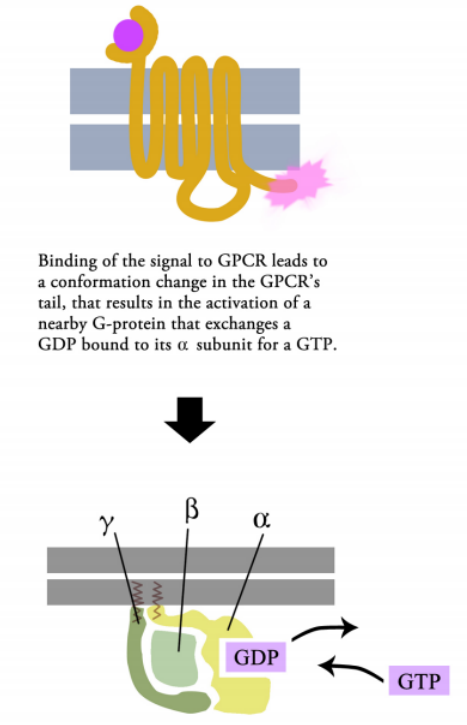


Figure 8.4.4: *G-protein Activation*

What happens when G-proteins interact with their target proteins? That depends on what the target is. G-proteins interact with different kinds of target proteins, of which we will examine two major categories:

Ion Channels

We have earlier seen that some gated ion channels can be opened or closed by the direct binding of neurotransmitters to a receptor that is an ion-channel protein. In other cases, ion channels are regulated by the binding of G-proteins. That is, instead of the signal directly binding to the ion channel, it binds to a GPCR, which activates a G-protein that then binds and opens the ion channel. The change in the distribution of ions across the plasma membrane causes a change in the membrane potential.

Specific Enzymes

The interaction of G-proteins with their target enzymes can regulate the activity of the enzyme, either increasing or decreasing its activity. Often the target enzyme will pass the signal on in another form to another part of the cell. As you might imagine, this kind of response takes a little longer than the kind where an ion channel is opened instantaneously. Two well-studied examples of enzymes whose activity is regulated by a G-protein are adenylate cyclase and phospholipase C. When adenylate cyclase is activated, the molecule cAMP is produced in large amounts.

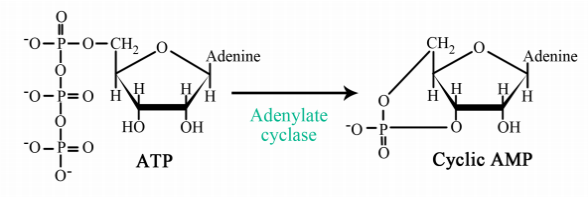


Figure 8.4.5: *Synthesis of cAMP*

When phospholipase C is activated, the molecules inositol trisphosphate (IP3) and diacylglycerol (DAG) are made. cAMP, IP3 and DAG are second messengers, small, diffusible molecules that can "spread the message" brought by the original signal, to other parts of the cell.

In these cases, the binding of a signal to the GPCR activated a G- protein, which in turn, activated an enzyme that makes a second messenger that can amplify the message in the cell. We will first trace the effects of activating adenylate cyclase and the resulting increase in cAMP.

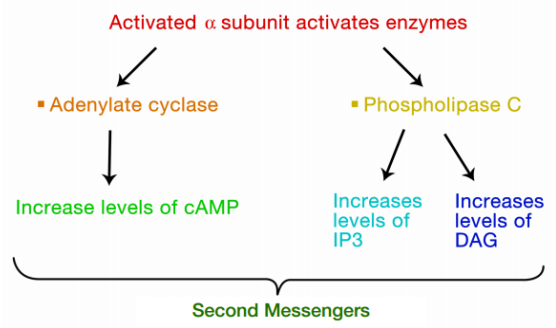


Figure 8.4.6: *Second Messengers*

What is the effect of elevated cAMP levels?

cAMP molecules bind to, and activate an enzyme, protein kinase A (PKA). PKA is composed of two catalytic and two regulatory subunits that are bound tightly together. Upon binding of cAMP the catalytic subunits are released from the regulatory subunits, allowing the enzyme to carry out its function, namely phosphorylating other proteins.

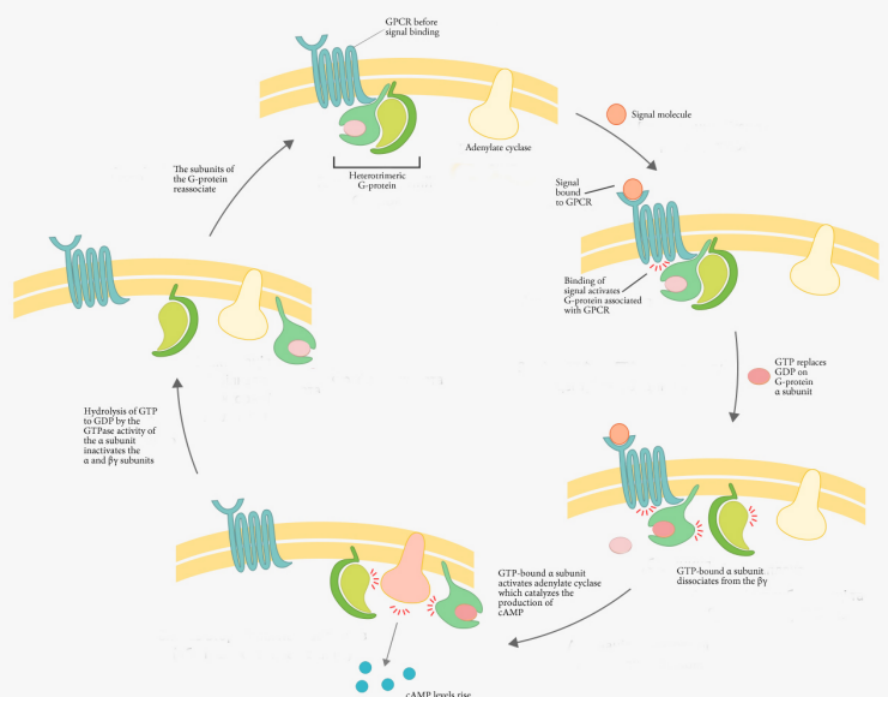


Figure 8.4.7: *G-protein Signaling Cycle*

Thus, cAMP can regulate the activity of PKA, which in turn, by phosphorylating other proteins can change their activity. The targets of PKA may be enzymes that are activated by phosphorylation, or they may be proteins that regulate transcription. The phosphorylation of a transcriptional activator, for example, may cause the activator to bind to a regulatory sequence on DNA and to increase the transcription of the gene it controls. The activation of previously inactive enzymes alters the state of the cell by changing the reactions that are occurring within the cell.

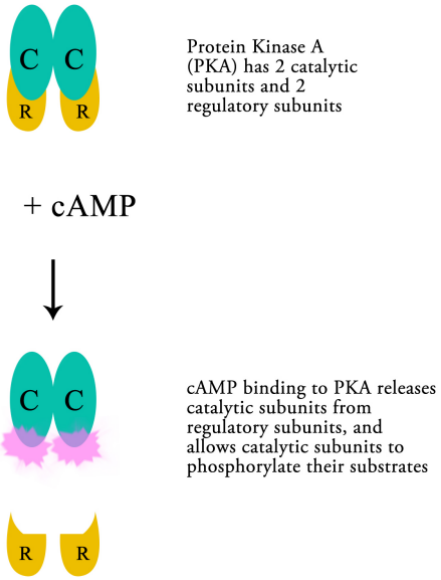


Figure 8.4.8: *Protein Kinase A Activation*

For example, the binding of epinephrine to its receptor on the cell surface, activates, through the action of G-proteins, and subsequent activation of PKA, the phosphorylation of glycogen phosphorylase. The resulting activation of glycogen phosphorylase leads to the breakdown of glycogen, releasing glucose (in the form of glucose-1-phosphate) for use by the cell. Changes in gene expression, likewise, lead to changes in the cell by altering the production of particular proteins in response to the signal.

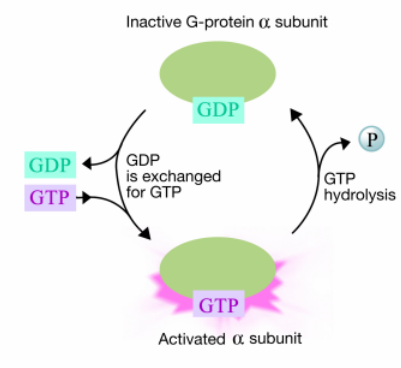


Figure 8.4.9: *G-protein nucleotide swapping*

Although the steps described above seem complicated, they follow the simple pattern outlined at the beginning of this section:

- Binding of signal to receptor
- Several steps where the signal is passed on through intermediate molecules (G-proteins, adenylate cyclase, cAMP, and finally, PKA)
- Phosphorylation of target proteins by the kinase, leading to changes in the cell.

Finally, if the signal binding to the receptor serves as a switch that sets these events in motion, there must be mechanisms to turn the pathway off. The first is at the level of the G-protein. Recall that the alpha subunit of the G-protein is in its free and activated state when it has GTP bound and that it associates with the beta- gamma subunits and has a GDP bound when it is inactive. We also know that the alpha subunit has an activity that enables it to hydrolyze GTP to GDP, as shown in the figure above left. This GTP-hydrolyzing activity makes it possible for the alpha subunit, once it has completed its task, to return to its GDP bound state, re-associate with the beta-gamma part and become inactive again.

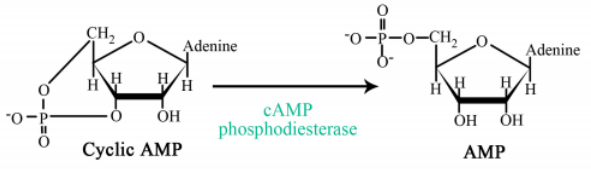


Figure 8.4.10: *cAMP Breakdown*

The second "off switch" is further down the signaling pathway, and controls the level of cAMP. We just noted that cAMP levels increase when adenylate cyclase is activated. When its job is done, cAMP is broken down by an enzyme called phosphodiesterase. When cAMP levels drop, PKA returns to its inactive state, putting a halt to the changes brought about by the activation of adenylate cyclase by an activated G-protein.

Let us now examine the events that follow the activation of Phospholipase C (PLC) by a G-protein. As we noted earlier, the activation of PLC results in the production of the second messengers IP3 and DAG. What do these molecules do?

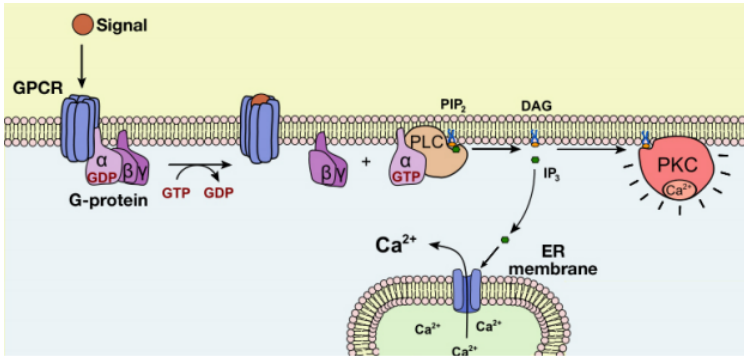


Figure 8.4.11: *Phospholipase C Signaling*

The IP3 and DAG produced by activated phospholipase C work together to activate a protein kinase. First, IP3 diffuses to the endoplasmic reticulum membrane where it binds to gated calcium ion channels. This causes calcium channels in the ER membrane to open and release large amounts of calcium into the cytoplasm from the ER lumen, as shown in the figure below.

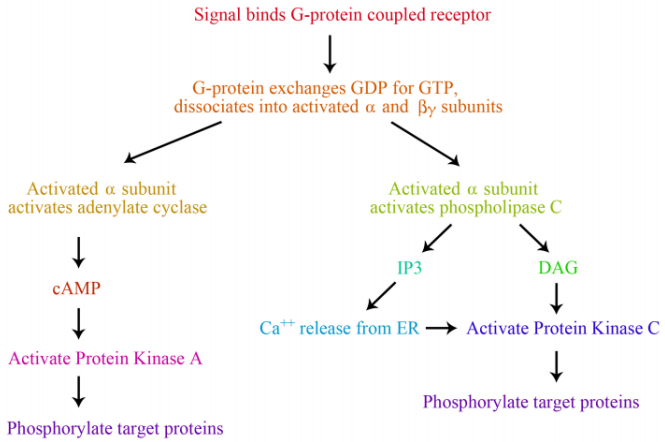


Figure 8.4.12: *Signaling Outcomes*

The increase in cytosolic calcium ion concentration has various effects, one of which is to activate a protein kinase called protein kinase C (C for calcium), together with the DAG made in the earlier step. Like PKA, Protein kinase C phosphorylates a variety of proteins in the cell, altering their activity and thus changing the state of the cell.

The pathways leading to PKC and PKA activation following the binding of a signal to a GPCR are summarized in Figure 8.4.12.

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CHAPTER OVERVIEW

10: How Cells Divide

10.1: Bacterial Cell Division

10.2: Eukaryotic Chromosomal Structure and Compaction

10.3: Overview of the Eukaryotic Cell Cycle

10.4: Interphase- Preparation for Mitosis

10.5: M phase- Chromosome Segregation and the Division of Cytoplasmic Contents

10.6: Control of the Cell Cycle

10.7: Genetics of Cancer

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10.1: Bacterial Cell Division

Skills to Develop

- Describe the process of binary fission in prokaryotes
- Explain how FtsZ and tubulin proteins are examples of homology

Prokaryotes, such as bacteria, propagate by binary fission. For unicellular organisms, cell division is the only method to produce new individuals. In both prokaryotic and eukaryotic cells, the outcome of cell reproduction is a pair of daughter cells that are genetically identical to the parent cell. In unicellular organisms, daughter cells are individuals.

To achieve the outcome of cloned offspring, certain steps are essential. The genomic DNA must be replicated and then allocated into the daughter cells; the cytoplasmic contents must also be divided to give both new cells the machinery to sustain life. In bacterial cells, the genome consists of a single, circular DNA chromosome; therefore, the process of cell division is simplified. Karyokinesis is unnecessary because there is no nucleus and thus no need to direct one copy of the multiple chromosomes into each daughter cell. This type of cell division is called binary (prokaryotic) fission.

Binary Fission

Due to the relative simplicity of the prokaryotes, the cell division process, called binary fission, is a less complicated and much more rapid process than cell division in eukaryotes. The single, circular DNA chromosome of bacteria is not enclosed in a nucleus, but instead occupies a specific location, the nucleoid, within the cell (Figure **10.1.1**). Although the DNA of the nucleoid is associated with proteins that aid in packaging the molecule into a compact size, there are no histone proteins and thus no nucleosomes in prokaryotes. The packing proteins of bacteria are, however, related to the cohesin and condensin proteins involved in the chromosome compaction of eukaryotes.

The bacterial chromosome is attached to the plasma membrane at about the midpoint of the cell. The starting point of replication, the origin, is close to the binding site of the chromosome to the plasma membrane (Figure **10.1.1**). Replication of the DNA is bidirectional, moving away from the origin on both strands of the loop simultaneously. As the new double strands are formed, each origin point moves away from the cell wall attachment toward the opposite ends of the cell. As the cell elongates, the growing membrane aids in the transport of the chromosomes. After the chromosomes have cleared the midpoint of the elongated cell, cytoplasmic separation begins. The formation of a ring composed of repeating units of a protein called FtsZ directs the partition between the nucleoids. Formation of the FtsZ ring triggers the accumulation of other proteins that work together to recruit new membrane and cell wall materials to the site. A septum is formed between the nucleoids, extending gradually from the periphery toward the center of the cell. When the new cell walls are in place, the daughter cells separate.

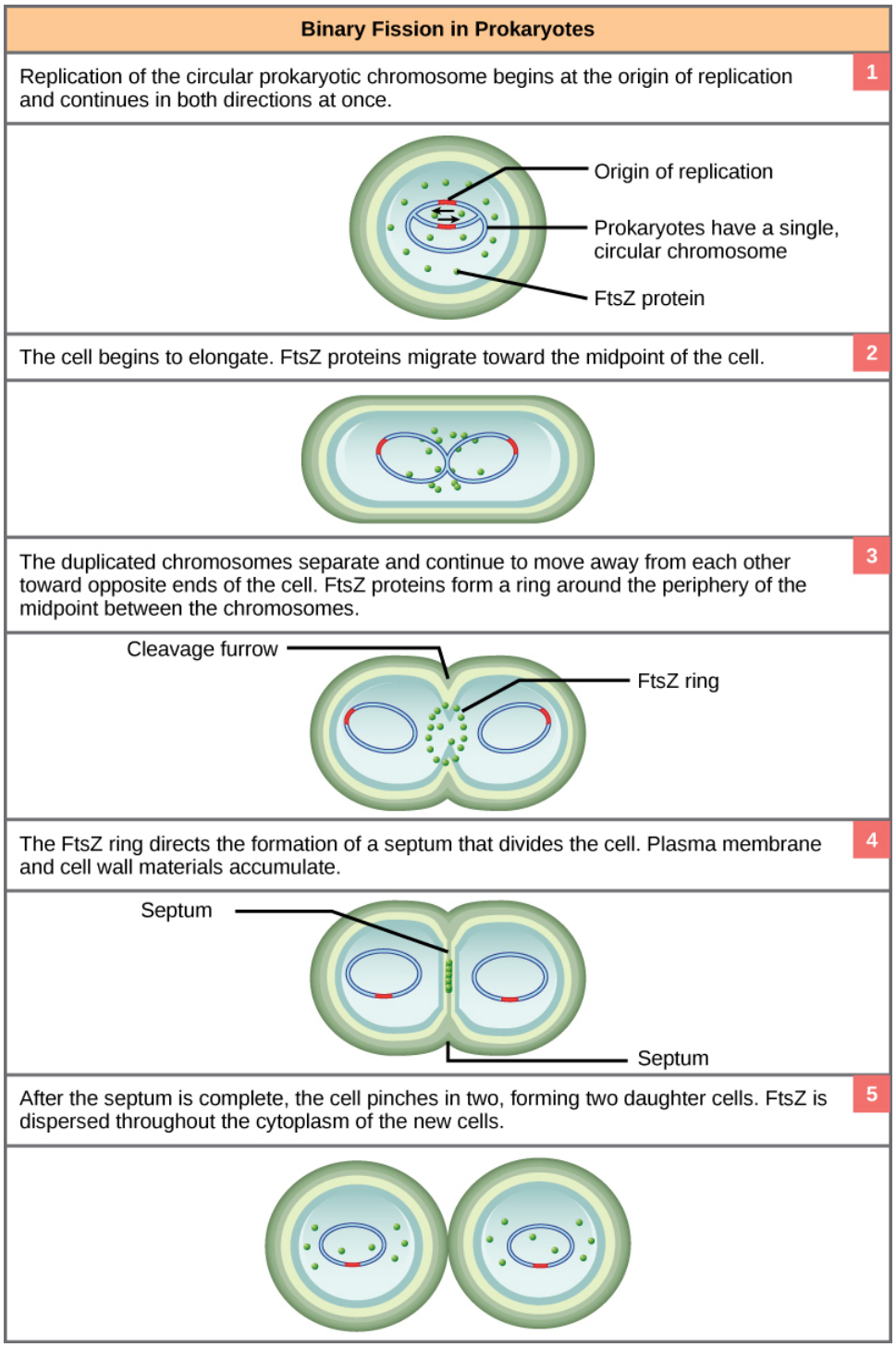


Figure **10.1.1**: These images show the steps of binary fission in prokaryotes. (credit: modification of work by "Mcstrother"/Wikimedia Commons)

Evolution Connection: Mitotic Spindle Apparatus

The precise timing and formation of the mitotic spindle is critical to the success of eukaryotic cell division. Prokaryotic cells, on the other hand, do not undergo karyokinesis and therefore have no need for a mitotic spindle. However, the FtsZ protein that plays such a vital role in prokaryotic cytokinesis is structurally and functionally very similar to tubulin, the building block of the microtubules that make up the mitotic spindle fibers that are necessary for eukaryotes. FtsZ proteins can form filaments, rings, and other three-dimensional structures that resemble the way tubulin forms microtubules, centrioles, and various

cytoskeletal components. In addition, both FtsZ and tubulin employ the same energy source, GTP (guanosine triphosphate), to rapidly assemble and disassemble complex structures.

FtsZ and tubulin are homologous structures derived from common evolutionary origins. In this example, FtsZ is the ancestor protein to tubulin (a modern protein). While both proteins are found in extant organisms, tubulin function has evolved and diversified tremendously since evolving from its FtsZ prokaryotic origin. A survey of mitotic assembly components found in present-day unicellular eukaryotes reveals crucial intermediary steps to the complex membrane-enclosed genomes of multicellular eukaryotes.

Table **10.1.1**: Cell Division Apparatus among Various Organisms

	Structure of genetic material	Division of nuclear material	Separation of daughter cells
Prokaryotes	There is no nucleus. The single, circular chromosome exists in a region of cytoplasm called the nucleoid.	Occurs through binary fission. As the chromosome is replicated, the two copies move to opposite ends of the cell by an unknown mechanism.	FtsZ proteins assemble into a ring that pinches the cell in two.
Some protists	Linear chromosomes exist in the nucleus.	Chromosomes attach to the nuclear envelope, which remains intact. The mitotic spindle passes through the envelope and elongates the cell. No centrioles exist.	Microfilaments form a cleavage furrow that pinches the cell in two.
Other protists	Linear chromosomes exist in the nucleus.	A mitotic spindle forms from the centrioles and passes through the nuclear membrane, which remains intact. Chromosomes attach to the mitotic spindle, which separates the chromosomes and elongates the cell.	Microfilaments form a cleavage furrow that pinches the cell in two.
Animal cells	Linear chromosomes exist in the nucleus.	A mitotic spindle forms from the centrosomes. The nuclear envelope dissolves. Chromosomes attach to the mitotic spindle, which separates the chromosomes and elongates the cell.	Microfilaments form a cleavage furrow that pinches the cell in two.

Summary

In both prokaryotic and eukaryotic cell division, the genomic DNA is replicated and then each copy is allocated into a daughter cell. In addition, the cytoplasmic contents are divided evenly and distributed to the new cells. However, there are many differences between prokaryotic and eukaryotic cell division. Bacteria have a single, circular DNA chromosome but no nucleus. Therefore, mitosis is not necessary in bacterial cell division. Bacterial cytokinesis is directed by a ring composed of a protein called FtsZ. Ingrowth of membrane and cell wall material from the periphery of the cells results in the formation of a septum that eventually constructs the separate cell walls of the daughter cells.

binary fission
prokaryotic cell division process

FtsZ
tubulin-like protein component of the prokaryotic cytoskeleton that is important in prokaryotic cytokinesis (name origin: **F**ilamenting **t**emperature-**s**ensitive mutant **Z**)

origin
(also, ORI) region of the prokaryotic chromosome where replication begins (origin of replication)

septum
structure formed in a bacterial cell as a precursor to the separation of the cell into two daughter cells

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10.2: Eukaryotic Chromosomal Structure and Compaction

Learning Objectives

- Describe the levels of chromsomal structure and compaction

Eukaryotic Chromosomal Structure and Compaction

If the DNA from all 46 chromosomes in a human cell nucleus was laid out end to end, it would measure approximately two meters. However, the diameter would be only 2 nm. Considering that the size of a typical human cell is about 10 µm (100,000 cells lined up to equal one meter), DNA must be tightly packaged to fit in the cell's nucleus. At the same time, it must also be readily accessible for the genes to be expressed. During some stages of the cell cycle, the long strands of DNA are condensed into compact chromosomes. There are a number of ways that chromosomes are compacted to fit in the cell's nucleus and be accessible for gene expression.

In the first level of compaction, short stretches of the DNA double helix wrap around a core of eight histone proteins at regular intervals along the entire length of the chromosome. The DNA-histone complex is called chromatin. The beadlike, histone DNA complex is called a nucleosome. DNA connecting the nucleosomes is called linker DNA. A DNA molecule in this form is about seven times shorter than the double helix without the histones. The beads are about 10 nm in diameter, in contrast with the 2-nm diameter of a DNA double helix. The next level of compaction occurs as the nucleosomes and the linker DNA between them are coiled into a 30-nm chromatin fiber. This coiling further shortens the chromosome so that it is now about 50 times shorter than the extended form. In the third level of packing, a variety of fibrous proteins is used to pack the chromatin. These fibrous proteins also ensure that each chromosome in a non-dividing cell occupies a particular area of the nucleus that does not overlap with that of any other chromosome.

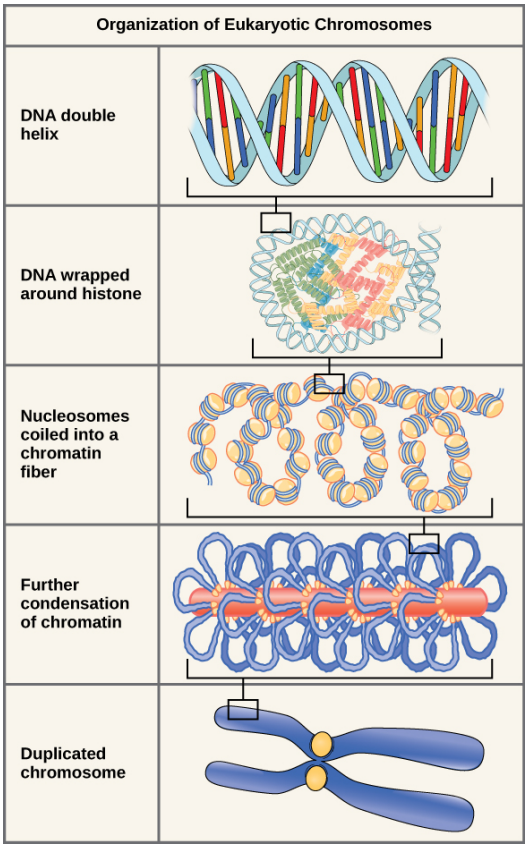


Figure 10.2.1: Levels of DNA Compaction: Double-stranded DNA wraps around histone proteins to form nucleosomes that have the appearance of "beads on a string." The nucleosomes are coiled into a 30-nm chromatin fiber. When a cell undergoes mitosis, the chromosomes condense even further.

DNA replicates in the S phase of interphase. After replication, the chromosomes are composed of two linked sister chromatids. When fully compact, the pairs of identically-packed chromosomes are bound to each other by cohesin proteins. The connection between the sister chromatids is closest in a region called the centromere. The conjoined sister chromatids, with a diameter of about 1 µm, are visible under a light microscope. The centromeric region is highly condensed and will appear as a constricted area.

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Key Points

- During some stages of the cell cycle, the long strands of DNA are condensed into compact chromosomes to fit in the cell's nucleus.
- In the first level of compaction, short stretches of the DNA double helix wrap around a core of eight histone proteins at regular intervals along the entire length of the chromosome.
- The DNA surrouding the histone core is called a nucleosome; the DNA-histone complex is called chromatin.
- The second level of compaction occurs as the nucleosomes and the linker DNA between them are coiled into a 30-nm chromatin fiber, which shortens the chromosome so it's about 50 times shorter than the extended form.
- After replication, the chromosomes are composed of two linked sister chromatids; when fully compact, the pairs of identically-packed chromosomes are bound to each other by cohesin proteins.
- The connection between the sister chromatids is closest in a region called the centromere; this region is highly condensed.

Key Terms

- **nucleosome**: any of the subunits that repeat in chromatin; a coil of DNA surrounding a histone core
- **histone**: any of various simple water-soluble proteins that are rich in the basic amino acids lysine and arginine and are complexed with DNA in the nucleosomes of eukaryotic chromatin
- **chromatin**: a complex of DNA, RNA, and proteins within the cell nucleus out of which chromosomes condense during cell division

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10.3: Overview of the Eukaryotic Cell Cycle

A eukaryotic cell cannot divide into two, the two into four, etc. unless two processes alternate:

- **doubling** of its genome (**DNA**) in **S phase** (synthesis phase) of the cell cycle;
- **halving** of that genome during mitosis (**M phase**).

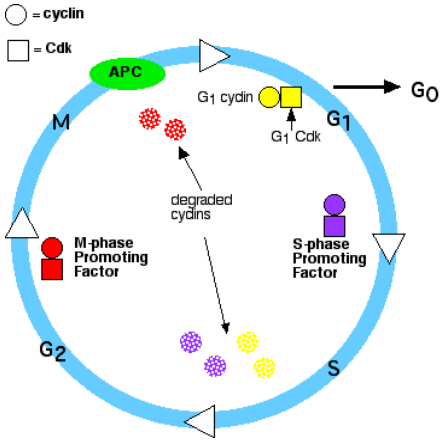


Figure 7.2.1 Cell Cycle: *The cell cycle consists of: **G1** = growth and preparation of the chromosomes for replication, **S** = synthesis of DNA and duplication of the centrosome, **G2** = preparation for **M** = mitosis. When a cell is in any phase of the cell cycle other than mitosis, it is often said to be in **interphase**.*

Control of the Cell Cycle

The passage of a cell through the cell cycle is controlled by proteins in the cytoplasm. Among the main players in animal cells are:

- Their levels in the cell rise and fall with the stages of the cell cycle.
- Their levels in the cell remain fairly stable, but each must bind the appropriate cyclin (whose levels fluctuate) in order to be activated. They add phosphate groups to a variety of protein substrates that control processes in the cell cycle.
- The **anaphase-promoting complex (APC)**. (The APC is also called the **cyclosome**, and the complex is often designated as the **APC/C**.) The APC/C
  - triggers the events leading to destruction of **cohesin** (as described below) thus allowing the sister chromatids to separate
  - degrades the mitotic (B) cyclins

Steps in the cycle

- A rising level of **G_1-cyclins** bind to their Cdks and signal the cell to prepare the chromosomes for replication.
- A rising level of **S-phase promoting factor** (**SPF**) — which includes A cyclins bound to Cdk2 — enters the nucleus and prepares the cell to duplicate its DNA (and its centrosomes).
- As DNA replication continues, cyclin E is destroyed, and the level of mitotic cyclins begins to rise (in G_2).
- Translocation of **M-phase promoting factor** (the complex of mitotic [B] cyclins with the M-phase Cdk [Cdk1]) into the nucleus initiates
  - assembly of the mitotic spindle
  - breakdown of the nuclear envelope
  - cessation of all gene transcription
  - condensation of the chromosomes
- These events take the cell to **metaphase** of mitosis.
- At this point, the M-phase promoting factor activates the **anaphase-promoting complex** (**APC/C**) which
  - allows the sister chromatids at the metaphase plate to separate and move to the poles (= anaphase), completing mitosis.

> Separation of the sister chromatids depends on the breakdown of the **cohesin** that has been holding them together. It works like this.
>
> - Cohesin breakdown is caused by a protease called **separase** (also known as separin).

- Separase is kept **inactive** until late metaphase by an inhibitory chaperone called **securin**.
- Anaphase begins when the anaphase promoting complex (APC/C) destroys securin (by tagging it with ubiquitin for deposit in a proteasome) thus ending its inhibition of separase and allowing
- separase to break down cohesin

    - destroys **B cyclins**. This is also done by attaching them to **ubiquitin** which targets them for destruction by **proteasomes**.
    - turns on synthesis of G_1 cyclins (D) for the next turn of the cycle.
    - degrades geminin, a protein that has kept the freshly-synthesized DNA in S phase from being re-replicated before mitosis.

This is only one of the mechanisms by which the cell ensures that every portion of its genome is copied once — and only once — during S phase

Some cells deliberately cut the cell cycle short allowing repeated S phases without completing mitosis and/or cytokinesis. This is called **endoreplication**.

Meiosis and the Cell Cycle

The special behavior of the chromosomes in meiosis I requires some special controls. Nonetheless, passage through the cell cycle in meiosis I (as well as meiosis II, which is essentially a mitotic division) uses many of the same players, e.g., **MPF** and **APC**. (In fact, MPF is also called **m**aturation-**p**romoting **f**actor for its role in meiosis I and II of developing oocytes.

Quality Control of the Cell Cycle

The cell has several systems for interrupting the cell cycle if something goes wrong.

DNA damage checkpoints. These sense DNA damage both before the cell enters S phase (a G_1 checkpoint) as well as after S phase (a G_2 checkpoint). Damage to DNA before the cell enters S phase inhibits the action of Cdk2 thus stopping the progression of the cell cycle until the damage can be repaired. If the damage is so severe that it cannot be repaired, the cell self-destructs by apoptosis. Damage to DNA after S phase (the G_2 checkpoint), inhibits the action of Cdk1 thus preventing the cell from proceeding from G_2 to mitosis. A check on the successful replication of DNA during S phase. If replication stops at any point on the DNA, progress through the cell cycle is halted until the problem is solved.

Spindle checkpoints. Some of these that have been discovered to detect any failure of spindle fibers to attach to **kinetochores** and arrest the cell in **metaphase** until all the kinetochores are attached correctly. They detect improper alignment of the spindle itself and block cytokinesis. Furthermore, they trigger apoptosis if the damage is irreparable. All the checkpoints examined require the services of a complex of proteins. Mutations in the genes encoding some of these have been associated with cancer; that is, they are oncogenes. This should not be surprising since checkpoint failures allow the cell to continue dividing despite damage to its integrity.

Examples of checkpoints

p53

The p53 protein senses DNA damage and can halt progression of the cell cycle in G_1 (by blocking the activity of Cdk2). Both copies of the *p53* gene must be mutated for this to fail so mutations in *p53* are recessive, and *p53* qualifies as a **tumor suppressor** gene.

The p53 protein is also a key player in **apoptosis**, forcing "bad" cells to commit suicide. So if the cell has only mutant versions of the protein, it can live on — perhaps developing into a cancer. More than half of all human cancers do, in fact, harbor *p53* mutations and have no functioning p53 protein.

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10.4: Interphase- Preparation for Mitosis

Learning Objectives

- Describe the events that occur during Interphase

Interphase

During interphase, the cell undergoes normal growth processes while also preparing for cell division. In order for a cell to move from interphase into the mitotic phase, many internal and external conditions must be met. The three stages of interphase are called G_1, S, and G_2 .

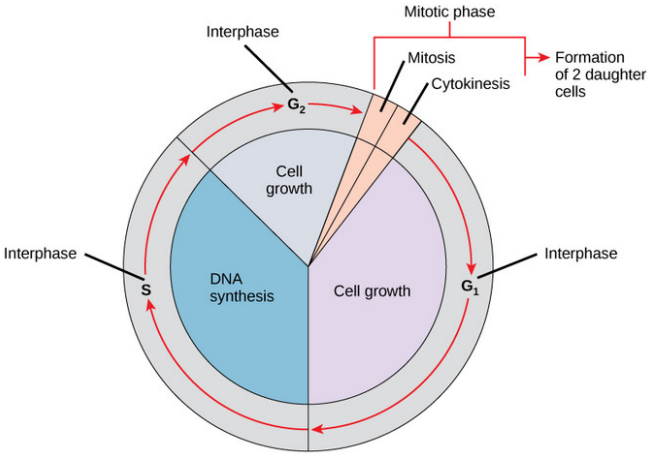


Figure **10.4.1**: The Stages of Interphase and the Cell Cycle: The cell cycle consists of interphase and the mitotic phase. During interphase, the cell grows and the nuclear DNA is duplicated. Interphase is followed by the mitotic phase. During the mitotic phase, the duplicated chromosomes are segregated and distributed into daughter nuclei. The cytoplasm is usually divided as well, resulting in two daughter cells.

G_1 Phase (First Gap)

The first stage of interphase is called the G_1 phase (first gap) because, from a microscopic aspect, little change is visible. However, during the G_1 stage, the cell is quite active at the biochemical level. The cell grows and accumulates the building blocks of chromosomal DNA and the associated proteins as well as sufficient energy reserves to complete the task of replicating each chromosome in the nucleus.

S Phase (Synthesis of DNA)

The synthesis phase of interphase takes the longest because of the complexity of the genetic material being duplicated. Throughout interphase, nuclear DNA remains in a semi-condensed chromatin configuration. In the S phase, DNA replication results in the formation of identical pairs of DNA molecules, sister chromatids, that are firmly attached to the centromeric region. The centrosome is duplicated during the S phase. The two centrosomes will give rise to the mitotic spindle, the apparatus that orchestrates the movement of chromosomes during mitosis. At the center of each animal cell, the centrosomes of animal cells are associated with a pair of rod-like objects, the centrioles, which are at right angles to each other. Centrioles help organize cell division. Centrioles are not present in the centrosomes of other eukaryotic species, such as plants and most fungi.

G_2 Phase (Second Gap)

In the G_2 phase, the cell replenishes its energy stores and synthesizes proteins necessary for chromosome manipulation. Some cell organelles are duplicated, and the cytoskeleton is dismantled to provide resources for the mitotic phase. There may be additional cell growth during G_2. The final preparations for the mitotic phase must be completed before the cell is able to enter the first stage of mitosis.

Key Points

- There are three stages of interphase: G_1 (first gap), S (synthesis of new DNA), and G_2 (second gap).
- Cells spend most of their lives in interphase, specifically in the S phase where genetic material must be copied.
- The cell grows and carries out biochemical functions, such as protein synthesis, in the G_1 phase.
- During the S phase, DNA is duplicated into two sister chromatids, and centrosomes, which give rise to the mitotic spindle, are also replicated.
- In the G_2 phase, energy is replenished, new proteins are synthesized, the cytoskeleton is dismantled, and additional growth occurs.

Key Terms

- **interphase**: the stage in the life cycle of a cell where the cell grows and DNA is replicated
- **sister chromatid**: either of the two identical strands of a chromosome (DNA material) that separate during mitosis
- **mitotic spindle**: the apparatus that orchestrates the movement of chromosomes during mitosis

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10.5: M phase- Chromosome Segregation and the Division of Cytoplasmic Contents

Learning Objectives

- Describe the events that occur at the different stages of mitosis

The Mitotic Phase

The mitotic phase is a multistep process during which the duplicated chromosomes are aligned, separated, and move into two new, identical daughter cells. The first portion of the mitotic phase is called karyokinesis or nuclear division. The second portion of the mitotic phase, called cytokinesis, is the physical separation of the cytoplasmic components into the two daughter cells.

Karyokinesis (Mitosis)

Karyokinesis, also known as mitosis, is divided into a series of phases (prophase, prometaphase, metaphase, anaphase, and telophase) that result in the division of the cell nucleus.

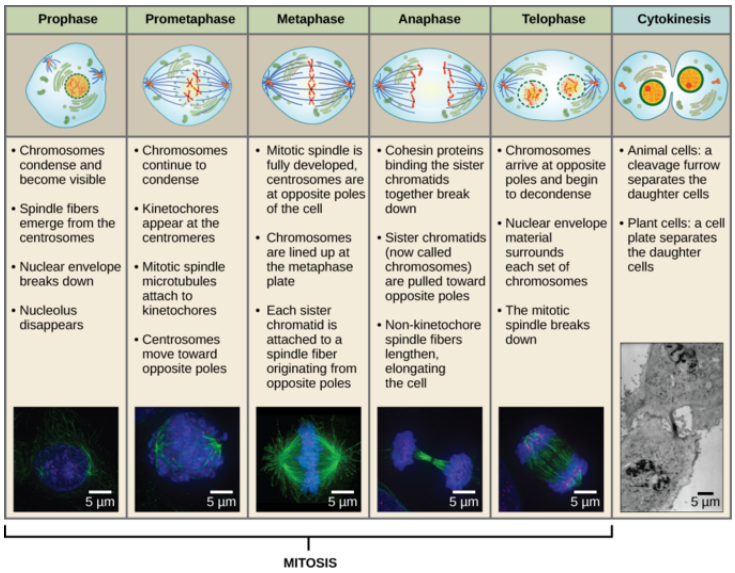


Figure **10.5.1**: Stages of the Cell Cycle: Karyokinesis (or mitosis) is divided into five stages: prophase, prometaphase, metaphase, anaphase, and telophase. The images at the bottom were taken by fluorescence microscopy (hence, the black background) of cells artificially stained by fluorescent dyes: blue fluorescence indicates DNA (chromosomes) and green fluorescence indicates microtubules (spindle apparatus).

During prophase, the “first phase,” the nuclear envelope starts to dissociate into small vesicles. The membranous organelles (such as the Golgi apparatus and endoplasmic reticulum) fragment and disperse toward the periphery of the cell. The nucleolus disappears and the centrosomes begin to move to opposite poles of the cell. Microtubules that will eventually form the mitotic spindle extend between the centrosomes, pushing them farther apart as the microtubule fibers lengthen. The sister chromatids begin to coil more tightly with the aid of condensin proteins and become visible under a light microscope.

During prometaphase, the “first change phase,” many processes that began in prophase continue to advance. The remnants of the nuclear envelope fragment. The mitotic spindle continues to develop as more microtubules assemble and stretch across the length of the former nuclear area. Chromosomes become more condensed and discrete. Each sister chromatid develops a protein structure called a kinetochore in the centromeric region. The proteins of the kinetochore attract and bind mitotic spindle microtubules.

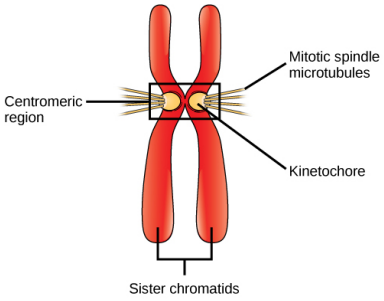


Figure 10.5.1: Kinetochore and Mitotic Spindle: During prometaphase, mitotic spindle microtubules from opposite poles attach to each sister chromatid at the kinetochore. In anaphase, the connection between the sister chromatids breaks down and the microtubules pull the chromosomes toward opposite poles.

During metaphase, the “change phase,” all the chromosomes are aligned on a plane called the metaphase plate, or the equatorial plane, midway between the two poles of the cell. The sister chromatids are still tightly attached to each other by cohesin proteins. At this time, the chromosomes are maximally condensed.

During anaphase, the “upward phase,” the cohesin proteins degrade, and the sister chromatids separate at the centromere. Each chromatid, now called a chromosome, is pulled rapidly toward the centrosome to which its microtubule is attached. The cell becomes visibly elongated (oval shaped) as the polar microtubules slide against each other at the metaphase plate where they overlap.

During telophase, the “distance phase,” the chromosomes reach the opposite poles and begin to decondense (unravel), relaxing into a chromatin configuration. The mitotic spindles are depolymerized into tubulin monomers that will be used to assemble cytoskeletal components for each daughter cell. Nuclear envelopes form around the chromosomes and nucleosomes appear within the nuclear area.

Cytokinesis

Cytokinesis, or “cell motion,” is the second main stage of the mitotic phase during which cell division is completed via the physical separation of the cytoplasmic components into two daughter cells. Division is not complete until the cell components have been apportioned and completely separated into the two daughter cells. Although the stages of mitosis are similar for most eukaryotes, the process of cytokinesis is quite different for eukaryotes that have cell walls, such as plant cells.

In cells such as animal cells, which lack cell walls, cytokinesis follows the onset of anaphase. A contractile ring composed of actin filaments forms just inside the plasma membrane at the former metaphase plate. The actin filaments pull the equator of the cell inward, forming a fissure. This fissure or “crack” is called the cleavage furrow. The furrow deepens as the actin ring contracts; eventually the membrane is cleaved in two.

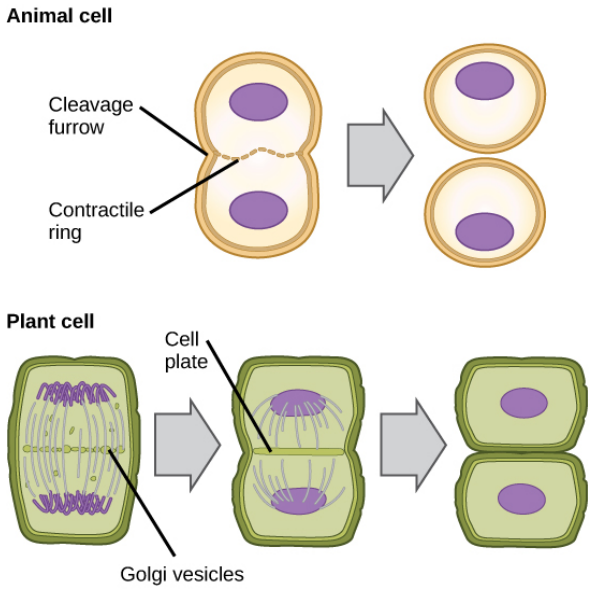


Figure **10.5.1**: Cytokinesis: During cytokinesis in animal cells, a ring of actin filaments forms at the metaphase plate. The ring contracts, forming a cleavage furrow, which divides the cell in two. In plant cells, Golgi vesicles coalesce at the former metaphase plate, forming a phragmoplast. A cell plate formed by the fusion of the vesicles of the phragmoplast grows from the center toward the cell walls and the membranes of the vesicles fuse to form a plasma membrane that divides the cell in two.

In plant cells, a new cell wall must form between the daughter cells. During interphase, the Golgi apparatus accumulates enzymes, structural proteins, and glucose molecules prior to breaking into vesicles and dispersing throughout the dividing cell. During telophase, these Golgi vesicles are transported on microtubules to form a phragmoplast (a vesicular structure) at the metaphase plate. There, the vesicles fuse and coalesce from the center toward the cell walls; this structure is called a cell plate. As more vesicles fuse, the cell plate enlarges until it merges with the cell walls at the periphery of the cell. Enzymes use the glucose that has accumulated between the membrane layers to build a new cell wall. The Golgi membranes become parts of the plasma membrane on either side of the new cell wall.

G_0 Phase

Not all cells adhere to the classic cell cycle pattern in which a newly-formed daughter cell immediately enters the preparatory phases of interphase, closely followed by the mitotic phase. Cells in G_0 phase are not actively preparing to divide. The cell is in a quiescent (inactive) stage that occurs when cells exit the cell cycle. Some cells enter G_0 temporarily until an external signal triggers the onset of G_1. Other cells that never or rarely divide, such as mature cardiac muscle and nerve cells, remain in G_0 permanently.

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Key Points

- During prophase, the nucleus disappears, spindle fibers form, and DNA condenses into chromosomes (sister chromatids).
- During metaphase, the sister chromatids align along the equator of the cell by attaching their centromeres to the spindle fibers.
- During anaphase, sister chromatids are separated at the centromere and are pulled towards opposite poles of the cell by the mitotic spindle.
- During telophase, chromosomes arrive at opposite poles and unwind into thin strands of DNA, the spindle fibers disappear, and the nuclear membrane reappears.
- Cytokinesis is the actual splitting of the cell membrane; animal cells pinch apart, while plant cells form a cell plate that becomes the new cell wall.
- Cells enter the G_0 (inactive) phase after they exit the cell cycle when they are not actively preparing to divide; some cells remain in G_0 phase permanently.

Key Terms

- **karyokinesis**: (mitosis) the first portion of mitotic phase in which division of the cell nucleus takes place
- **centrosome**: an organelle near the nucleus in the cytoplasm of most organisms that controls the organization of its microtubules and gives rise to the mitotic spindle
- **cytokinesis**: the second portion of the mitotic phase in which the cytoplasm of a cell divides following the division of the nucleus

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10.6: Control of the Cell Cycle

Skills to Develop

- Understand how the cell cycle is controlled by mechanisms both internal and external to the cell
- Explain how the three internal control checkpoints occur at the end of G_1, at the G_2/M transition, and during metaphase
- Describe the molecules that control the cell cycle through positive and negative regulation

The length of the cell cycle is highly variable, even within the cells of a single organism. In humans, the frequency of cell turnover ranges from a few hours in early embryonic development, to an average of two to five days for epithelial cells, and to an entire human lifetime spent in G_0 by specialized cells, such as cortical neurons or cardiac muscle cells. There is also variation in the time that a cell spends in each phase of the cell cycle. When fast-dividing mammalian cells are grown in culture (outside the body under optimal growing conditions), the length of the cycle is about 24 hours. In rapidly dividing human cells with a 24-hour cell cycle, the G_1 phase lasts approximately nine hours, the S phase lasts 10 hours, the G_2 phase lasts about four and one-half hours, and the M phase lasts approximately one-half hour. In early embryos of fruit flies, the cell cycle is completed in about eight minutes. The timing of events in the cell cycle is controlled by mechanisms that are both internal and external to the cell.

Regulation of the Cell Cycle by External Events

Both the initiation and inhibition of cell division are triggered by events external to the cell when it is about to begin the replication process. An event may be as simple as the death of a nearby cell or as sweeping as the release of growth-promoting hormones, such as human growth hormone (HGH). A lack of HGH can inhibit cell division, resulting in dwarfism, whereas too much HGH can result in gigantism. Crowding of cells can also inhibit cell division. Another factor that can initiate cell division is the size of the cell; as a cell grows, it becomes inefficient due to its decreasing surface-to-volume ratio. The solution to this problem is to divide.

Whatever the source of the message, the cell receives the signal, and a series of events within the cell allows it to proceed into interphase. Moving forward from this initiation point, every parameter required during each cell cycle phase must be met or the cycle cannot progress.

Regulation at Internal Checkpoints

It is essential that the daughter cells produced be exact duplicates of the parent cell. Mistakes in the duplication or distribution of the chromosomes lead to mutations that may be passed forward to every new cell produced from an abnormal cell. To prevent a compromised cell from continuing to divide, there are internal control mechanisms that operate at three main cell cycle checkpoints. A checkpoint is one of several points in the eukaryotic cell cycle at which the progression of a cell to the next stage in the cycle can be halted until conditions are favorable. These checkpoints occur near the end of G_1, at the G_2/M transition, and during metaphase (Figure **10.6.1**).

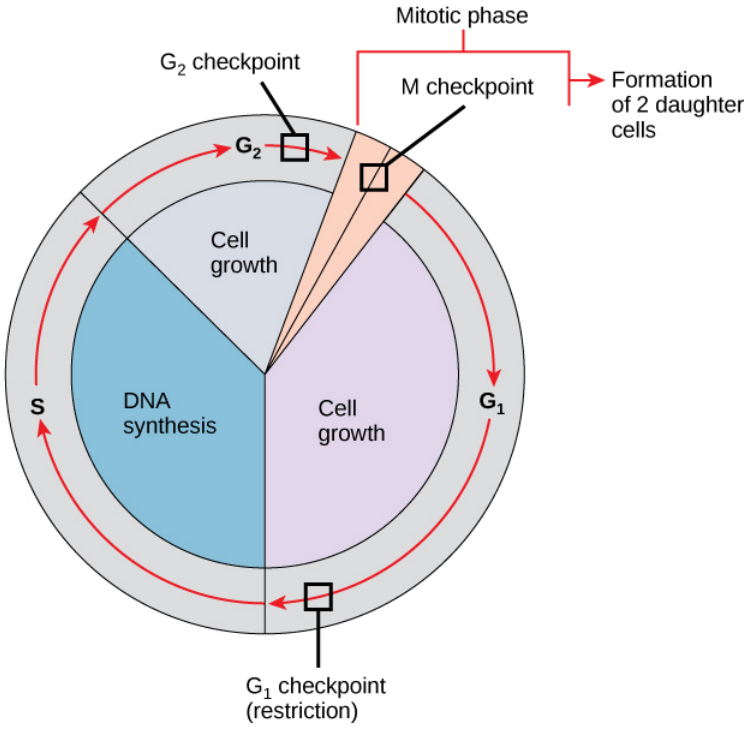


Figure **10.6.3**: The cell cycle is controlled at three checkpoints. The integrity of the DNA is assessed at the G_1 checkpoint. Proper chromosome duplication is assessed at the G_2 checkpoint. Attachment of each kinetochore to a spindle fiber is assessed at the M checkpoint.

The G_1 Checkpoint

The G_1 checkpoint determines whether all conditions are favorable for cell division to proceed. The G_1 checkpoint, also called the restriction point (in yeast), is a point at which the cell irreversibly commits to the cell division process. External influences, such as growth factors, play a large role in carrying the cell past the G_1 checkpoint. In addition to adequate reserves and cell size, there is a check for genomic DNA damage at the G_1 checkpoint. A cell that does not meet all the requirements will not be allowed to progress into the S phase. The cell can halt the cycle and attempt to remedy the problematic condition, or the cell can advance into G_0 and await further signals when conditions improve.

The G_2 Checkpoint

The G_2 checkpoint bars entry into the mitotic phase if certain conditions are not met. As at the G_1 checkpoint, cell size and protein reserves are assessed. However, the most important role of the G_2 checkpoint is to ensure that all of the chromosomes have been replicated and that the replicated DNA is not damaged. If the checkpoint mechanisms detect problems with the DNA, the cell cycle is halted, and the cell attempts to either complete DNA replication or repair the damaged DNA.

The M Checkpoint

The M checkpoint occurs near the end of the metaphase stage of karyokinesis. The M checkpoint is also known as the spindle checkpoint, because it determines whether all the sister chromatids are correctly attached to the spindle microtubules. Because the separation of the sister chromatids during anaphase is an irreversible step, the cycle will not proceed until the kinetochores of each pair of sister chromatids are firmly anchored to at least two spindle fibers arising from opposite poles of the cell.

Link to Learning

Watch what occurs at the G_1, G_2, and M checkpoints by visiting this website to see an animation of the cell cycle.

Regulator Molecules of the Cell Cycle

In addition to the internally controlled checkpoints, there are two groups of intracellular molecules that regulate the cell cycle. These regulatory molecules either promote progress of the cell to the next phase (positive regulation) or halt the cycle (negative regulation). Regulator molecules may act individually, or they can influence the activity or production of other regulatory proteins. Therefore, the failure of a single regulator may have almost no effect on the cell cycle, especially if more than one mechanism controls the same event. Conversely, the effect of a deficient or non-functioning regulator can be wide-ranging and possibly fatal to the cell if multiple processes are affected.

Positive Regulation of the Cell Cycle

Two groups of proteins, called cyclins and cyclin-dependent kinases (Cdks), are responsible for the progress of the cell through the various checkpoints. The levels of the four cyclin proteins fluctuate throughout the cell cycle in a predictable pattern (Figure **10.6.2**). Increases in the concentration of cyclin proteins are triggered by both external and internal signals. After the cell moves to the next stage of the cell cycle, the cyclins that were active in the previous stage are degraded.

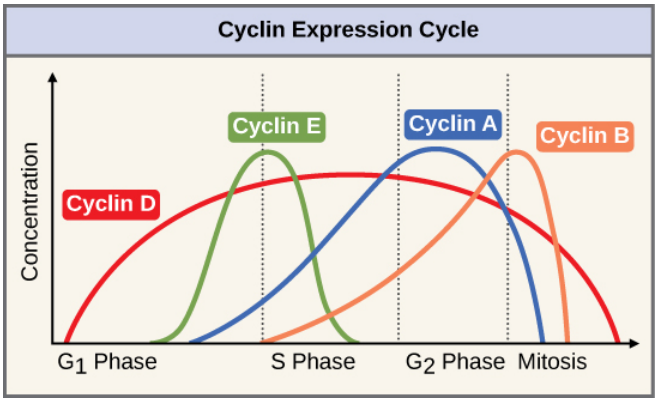


Figure **10.6.2**: The concentrations of cyclin proteins change throughout the cell cycle. There is a direct correlation between cyclin accumulation and the three major cell cycle checkpoints. Also note the sharp decline of cyclin levels following each checkpoint (the transition between phases of the cell cycle), as cyclin is degraded by cytoplasmic enzymes. (credit: modification of work by "WikiMiMa"/Wikimedia Commons)

Cyclins regulate the cell cycle only when they are tightly bound to Cdks. To be fully active, the Cdk/cyclin complex must also be phosphorylated in specific locations. Like all kinases, Cdks are enzymes (kinases) that phosphorylate other proteins. Phosphorylation activates the protein by changing its shape. The proteins phosphorylated by Cdks are involved in advancing the cell to the next phase. (Figure **10.6.3**). The levels of Cdk proteins are relatively stable throughout the cell cycle; however, the concentrations of cyclin fluctuate and determine when Cdk/cyclin complexes form. The different cyclins and Cdks bind at specific points in the cell cycle and thus regulate different checkpoints.

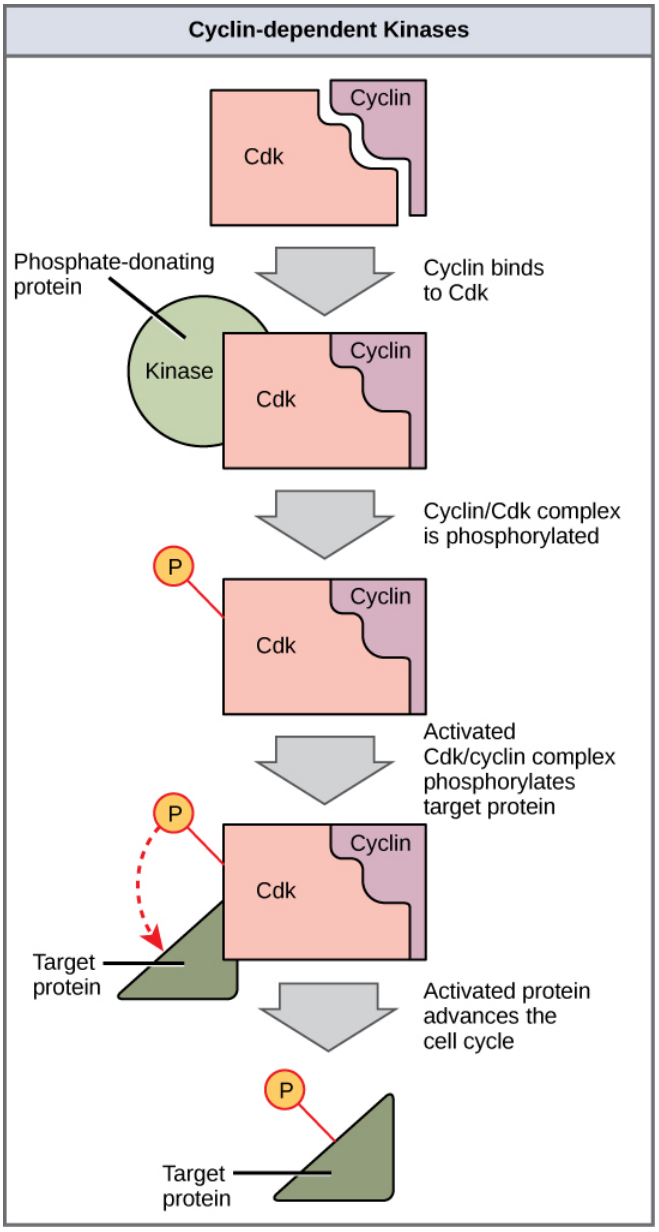


Figure **10.6.3**: Cyclin-dependent kinases (Cdks) are protein kinases that, when fully activated, can phosphorylate and thus activate other proteins that advance the cell cycle past a checkpoint. To become fully activated, a Cdk must bind to a cyclin protein and then be phosphorylated by another kinase.

Since the cyclic fluctuations of cyclin levels are based on the timing of the cell cycle and not on specific events, regulation of the cell cycle usually occurs by either the Cdk molecules alone or the Cdk/cyclin complexes. Without a specific concentration of fully activated cyclin/Cdk complexes, the cell cycle cannot proceed through the checkpoints.

Although the cyclins are the main regulatory molecules that determine the forward momentum of the cell cycle, there are several other mechanisms that fine-tune the progress of the cycle with negative, rather than positive, effects. These mechanisms essentially block the progression of the cell cycle until problematic conditions are resolved. Molecules that prevent the full activation of Cdks are called Cdk inhibitors. Many of these inhibitor molecules directly or indirectly monitor a particular cell cycle event. The block placed on Cdks by inhibitor molecules will not be removed until the specific event that the inhibitor monitors is completed.

Negative Regulation of the Cell Cycle

The second group of cell cycle regulatory molecules are negative regulators. Negative regulators halt the cell cycle. Remember that in positive regulation, active molecules cause the cycle to progress.

The best understood negative regulatory molecules are retinoblastoma protein (Rb), p53, and p21. Retinoblastoma proteins are a group of tumor-suppressor proteins common in many cells. The 53 and 21 designations refer to the functional molecular masses of the proteins (p) in kilodaltons. Much of what is known about cell cycle regulation comes from research conducted with cells that have lost regulatory control. All three of these regulatory proteins were discovered to be damaged or non-functional in cells that had begun to replicate uncontrollably (became cancerous). In each case, the main cause of the unchecked progress through the cell cycle was a faulty copy of the regulatory protein.

Rb, p53, and p21 act primarily at the G_1 checkpoint. p53 is a multi-functional protein that has a major impact on the commitment of a cell to division because it acts when there is damaged DNA in cells that are undergoing the preparatory processes during G_1. If damaged DNA is detected, p53 halts the cell cycle and recruits enzymes to repair the DNA. If the DNA cannot be repaired, p53 can trigger apoptosis, or cell suicide, to prevent the duplication of damaged chromosomes. As p53 levels rise, the production of p21 is triggered. p21 enforces the halt in the cycle dictated by p53 by binding to and inhibiting the activity of the Cdk/cyclin complexes. As a cell is exposed to more stress, higher levels of p53 and p21 accumulate, making it less likely that the cell will move into the S phase.

Rb exerts its regulatory influence on other positive regulator proteins. Chiefly, Rb monitors cell size. In the active, dephosphorylated state, Rb binds to proteins called transcription factors, most commonly, E2F (Figure 10.6.4). Transcription factors "turn on" specific genes, allowing the production of proteins encoded by that gene. When Rb is bound to E2F, production of proteins necessary for the G_1/S transition is blocked. As the cell increases in size, Rb is slowly phosphorylated until it becomes inactivated. Rb releases E2F, which can now turn on the gene that produces the transition protein, and this particular block is removed. For the cell to move past each of the checkpoints, all positive regulators must be "turned on," and all negative regulators must be "turned off."

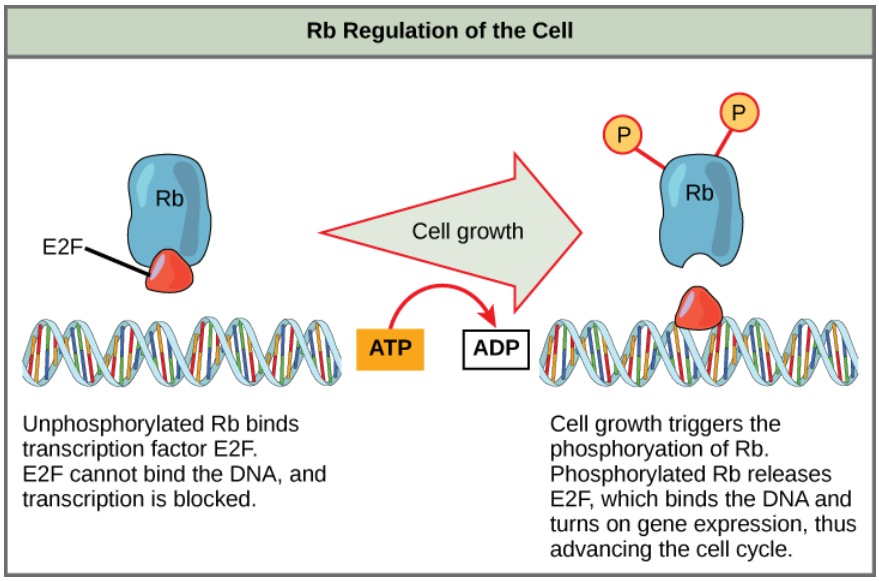


Figure 10.6.4: Rb halts the cell cycle and releases its hold in response to cell growth.

Exercise 10.6.1

Rb and other proteins that negatively regulate the cell cycle are sometimes called tumor suppressors. Why do you think the name tumor suppressor might be appropriate for these proteins?

Answer

Rb and other negative regulatory proteins control cell division and therefore prevent the formation of tumors. Mutations that prevent these proteins from carrying out their function can result in cancer.

Summary

Each step of the cell cycle is monitored by internal controls called checkpoints. There are three major checkpoints in the cell cycle: one near the end of G_1, a second at the G_2/M transition, and the third during metaphase. Positive regulator molecules allow the cell cycle to advance to the next stage. Negative regulator molecules monitor cellular conditions and can halt the cycle until specific requirements are met.

Glossary

cell cycle checkpoint
: mechanism that monitors the preparedness of a eukaryotic cell to advance through the various cell cycle stages

cyclin
: one of a group of proteins that act in conjunction with cyclin-dependent kinases to help regulate the cell cycle by phosphorylating key proteins; the concentrations of cyclins fluctuate throughout the cell cycle

cyclin-dependent kinase
: one of a group of protein kinases that helps to regulate the cell cycle when bound to cyclin; it functions to phosphorylate other proteins that are either activated or inactivated by phosphorylation

p21
: cell cycle regulatory protein that inhibits the cell cycle; its levels are controlled by p53

p53
: cell cycle regulatory protein that regulates cell growth and monitors DNA damage; it halts the progression of the cell cycle in cases of DNA damage and may induce apoptosis

retinoblastoma protein (Rb)
: regulatory molecule that exhibits negative effects on the cell cycle by interacting with a transcription factor (E2F)

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10.7: Genetics of Cancer

Skills to Develop

- Describe how cancer is caused by uncontrolled cell growth
- Understand how proto-oncogenes are normal cell genes that, when mutated, become oncogenes
- Describe how tumor suppressors function
- Explain how mutant tumor suppressors cause cancer

Cancer comprises many different diseases caused by a common mechanism: uncontrolled cell growth. Despite the redundancy and overlapping levels of cell cycle control, errors do occur. One of the critical processes monitored by the cell cycle checkpoint surveillance mechanism is the proper replication of DNA during the S phase. Even when all of the cell cycle controls are fully functional, a small percentage of replication errors (mutations) will be passed on to the daughter cells. If changes to the DNA nucleotide sequence occur within a coding portion of a gene and are not corrected, a gene mutation results. All cancers start when a gene mutation gives rise to a faulty protein that plays a key role in cell reproduction. The change in the cell that results from the malformed protein may be minor: perhaps a slight delay in the binding of Cdk to cyclin or an Rb protein that detaches from its target DNA while still phosphorylated. Even minor mistakes, however, may allow subsequent mistakes to occur more readily. Over and over, small uncorrected errors are passed from the parent cell to the daughter cells and amplified as each generation produces more non-functional proteins from uncorrected DNA damage. Eventually, the pace of the cell cycle speeds up as the effectiveness of the control and repair mechanisms decreases. Uncontrolled growth of the mutated cells outpaces the growth of normal cells in the area, and a tumor ("-oma") can result.

Proto-oncogenes

The genes that code for the positive cell cycle regulators are called proto-oncogenes. Proto-oncogenes are normal genes that, when mutated in certain ways, become oncogenes, genes that cause a cell to become cancerous. Consider what might happen to the cell cycle in a cell with a recently acquired oncogene. In most instances, the alteration of the DNA sequence will result in a less functional (or non-functional) protein. The result is detrimental to the cell and will likely prevent the cell from completing the cell cycle; however, the organism is not harmed because the mutation will not be carried forward. If a cell cannot reproduce, the mutation is not propagated and the damage is minimal. Occasionally, however, a gene mutation causes a change that increases the activity of a positive regulator. For example, a mutation that allows Cdk to be activated without being partnered with cyclin could push the cell cycle past a checkpoint before all of the required conditions are met. If the resulting daughter cells are too damaged to undergo further cell divisions, the mutation would not be propagated and no harm would come to the organism. However, if the atypical daughter cells are able to undergo further cell divisions, subsequent generations of cells will probably accumulate even more mutations, some possibly in additional genes that regulate the cell cycle.

The Cdk gene in the above example is only one of many genes that are considered proto-oncogenes. In addition to the cell cycle regulatory proteins, any protein that influences the cycle can be altered in such a way as to override cell cycle checkpoints. An oncogene is any gene that, when altered, leads to an increase in the rate of cell cycle progression.

Tumor Suppressor Genes

Like proto-oncogenes, many of the negative cell cycle regulatory proteins were discovered in cells that had become cancerous. Tumor suppressor genes are segments of DNA that code for negative regulator proteins, the type of regulators that, when activated, can prevent the cell from undergoing uncontrolled division. The collective function of the best-understood tumor suppressor gene proteins, Rb, p53, and p21, is to put up a roadblock to cell cycle progression until certain events are completed. A cell that carries a mutated form of a negative regulator might not be able to halt the cell cycle if there is a problem. Tumor suppressors are similar to brakes in a vehicle: Malfunctioning brakes can contribute to a car crash.

Mutated p53 genes have been identified in more than one-half of all human tumor cells. This discovery is not surprising in light of the multiple roles that the p53 protein plays at the G_1 checkpoint. A cell with a faulty p53 may fail to detect errors present in the genomic DNA (Figure **10.7.1**). Even if a partially functional p53 does identify the mutations, it may no longer be able to signal the necessary DNA repair enzymes. Either way, damaged DNA will remain uncorrected. At this point, a functional p53 will deem the

cell unsalvageable and trigger programmed cell death (apoptosis). The damaged version of p53 found in cancer cells, however, cannot trigger apoptosis.

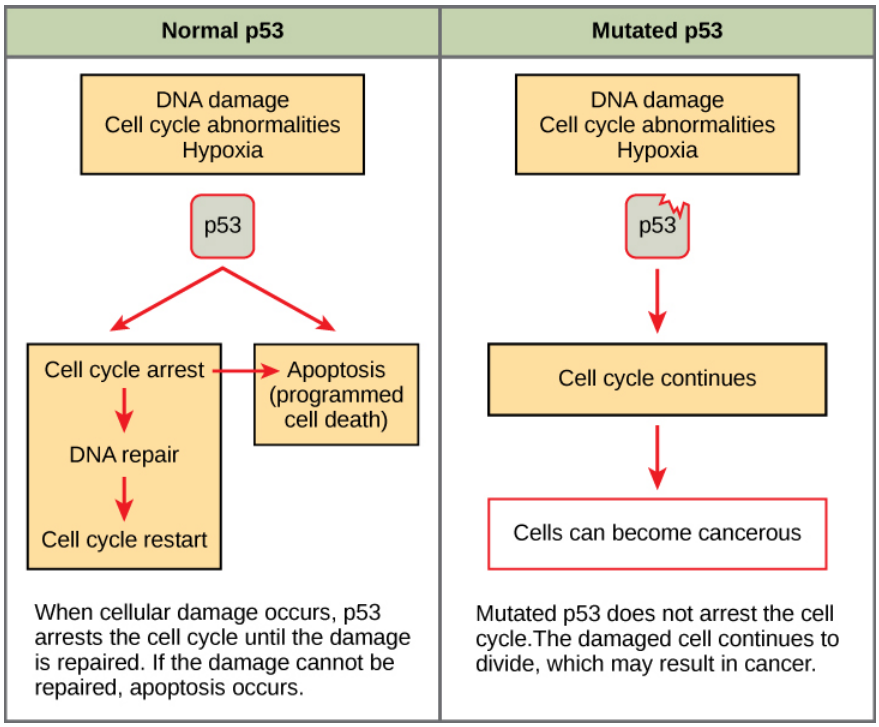


Figure 10.7.1: The role of normal p53 is to monitor DNA and the supply of oxygen (hypoxia is a condition of reduced oxygen supply). If damage is detected, p53 triggers repair mechanisms. If repairs are unsuccessful, p53 signals apoptosis. A cell with an abnormal p53 protein cannot repair damaged DNA and thus cannot signal apoptosis. Cells with abnormal p53 can become cancerous. (credit: modification of work by Thierry Soussi)

Exercise 10.7.1

Human papillomavirus can cause cervical cancer. The virus encodes E6, a protein that binds p53. Based on this fact and what you know about p53, what effect do you think E6 binding has on p53 activity?

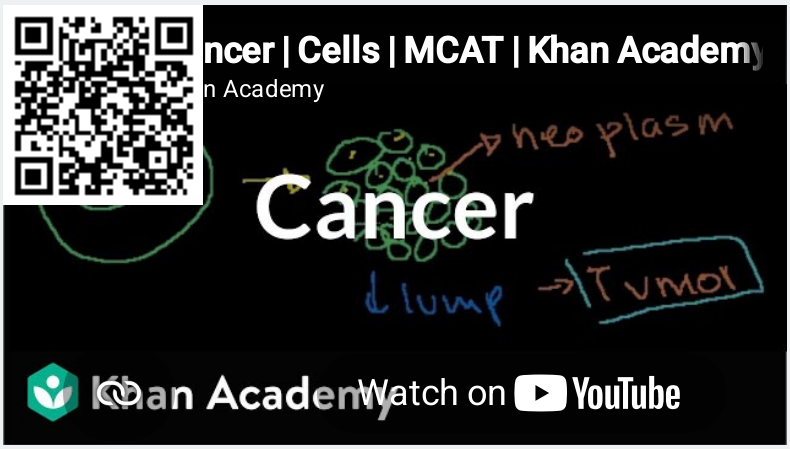
A. E6 activates p53
B. E6 inactivates p53
C. E6 mutates p53
D. E6 binding marks p53 for degradation

Answer

D. E6 binding marks p53 for degradation.

The loss of p53 function has other repercussions for the cell cycle. Mutated p53 might lose its ability to trigger p21 production. Without adequate levels of p21, there is no effective block on Cdk activation. Essentially, without a fully functional p53, the G_1 checkpoint is severely compromised and the cell proceeds directly from G_1 to S regardless of internal and external conditions. At the completion of this shortened cell cycle, two daughter cells are produced that have inherited the mutated p53 gene. Given the non-optimal conditions under which the parent cell reproduced, it is likely that the daughter cells will have acquired other mutations in addition to the faulty tumor suppressor gene. Cells such as these daughter cells quickly accumulate both oncogenes and non-functional tumor suppressor genes. Again, the result is tumor growth.

Link to Learning



Go to this website to watch an animation of how cancer results from errors in the cell cycle.

Summary

Cancer is the result of unchecked cell division caused by a breakdown of the mechanisms that regulate the cell cycle. The loss of control begins with a change in the DNA sequence of a gene that codes for one of the regulatory molecules. Faulty instructions lead to a protein that does not function as it should. Any disruption of the monitoring system can allow other mistakes to be passed on to the daughter cells. Each successive cell division will give rise to daughter cells with even more accumulated damage. Eventually, all checkpoints become nonfunctional, and rapidly reproducing cells crowd out normal cells, resulting in a tumor or leukemia (blood cancer).

Glossary

oncogene
: mutated version of a normal gene involved in the positive regulation of the cell cycle

proto-oncogene
: normal gene that when mutated becomes an oncogene

tumor suppressor gene
: segment of DNA that codes for regulator proteins that prevent the cell from undergoing uncontrolled division

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CHAPTER OVERVIEW

11: Sexual Reproduction and Meiosis

11.1: Sexual Reproduction Requires Meiosis

11.2: Features of Meiosis

11.2.1: Meiosis I

11.2.2: Meiosis II

11.3: The Process of Meiosis

11.4: Summing Up- Meiosis Versus Mitosis

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11.1: Sexual Reproduction Requires Meiosis

Sexual reproduction was an early evolutionary innovation after the appearance of eukaryotic cells. The fact that most eukaryotes reproduce sexually is evidence of its evolutionary success. In many animals, it is the only mode of reproduction. And yet, scientists recognize some real disadvantages to sexual reproduction. On the surface, offspring that are genetically identical to the parent may appear to be more advantageous. If the parent organism is successfully occupying a habitat, offspring with the same traits would be similarly successful. There is also the obvious benefit to an organism that can produce offspring by asexual budding, fragmentation, or asexual eggs. These methods of reproduction do not require another organism of the opposite sex. There is no need to expend energy finding or attracting a mate. That energy can be spent on producing more offspring. Indeed, some organisms that lead a solitary lifestyle have retained the ability to reproduce asexually. In addition, asexual populations only have female individuals, so every individual is capable of reproduction. In contrast, the males in sexual populations (half the population) are not producing offspring themselves. Because of this, an asexual population can grow twice as fast as a sexual population in theory. This means that in competition, the asexual population would have the advantage. All of these advantages to asexual reproduction, which are also disadvantages to sexual reproduction, should mean that the number of species with asexual reproduction should be more common.

However, multicellular organisms that exclusively depend on asexual reproduction are exceedingly rare. Why is sexual reproduction so common? This is one of the important questions in biology and has been the focus of much research from the latter half of the twentieth century until now. A likely explanation is that the variation that sexual reproduction creates among offspring is very important to the survival and reproduction of those offspring. The only source of variation in asexual organisms is mutation. This is the ultimate source of variation in sexual organisms. In addition, those different mutations are continually reshuffled from one generation to the next when different parents combine their unique genomes, and the genes are mixed into different combinations by the process of meiosis. Meiosis is the division of the contents of the nucleus that divides the chromosomes among gametes. Variation is introduced during meiosis, as well as when the gametes combine in fertilization.

EVOLUTION IN ACTION: The Red Queen Hypothesis

There is no question that sexual reproduction provides evolutionary advantages to organisms that employ this mechanism to produce offspring. The problematic question is why, even in the face of fairly stable conditions, sexual reproduction persists when it is more difficult and produces fewer offspring for individual organisms? Variation is the outcome of sexual reproduction, but why are ongoing variations necessary? Enter the Red Queen hypothesis, first proposed by Leigh Van Valen in 1973.[1] The concept was named in reference to the Red Queen's race in Lewis Carroll's book, *Through the Looking-Glass*, in which the Red Queen says one must run at full speed just to stay where one is.

All species coevolve with other organisms. For example, predators coevolve with their prey, and parasites coevolve with their hosts. A remarkable example of coevolution between predators and their prey is the unique coadaptation of night flying bats and their moth prey. Bats find their prey by emitting high-pitched clicks, but moths have evolved simple ears to hear these clicks so they can avoid the bats. The moths have also adapted behaviors, such as flying away from the bat when they first hear it, or dropping suddenly to the ground when the bat is upon them. Bats have evolved “quiet” clicks in an attempt to evade the moth’s hearing. Some moths have evolved the ability to respond to the bats’ clicks with their own clicks as a strategy to confuse the bats echolocation abilities.

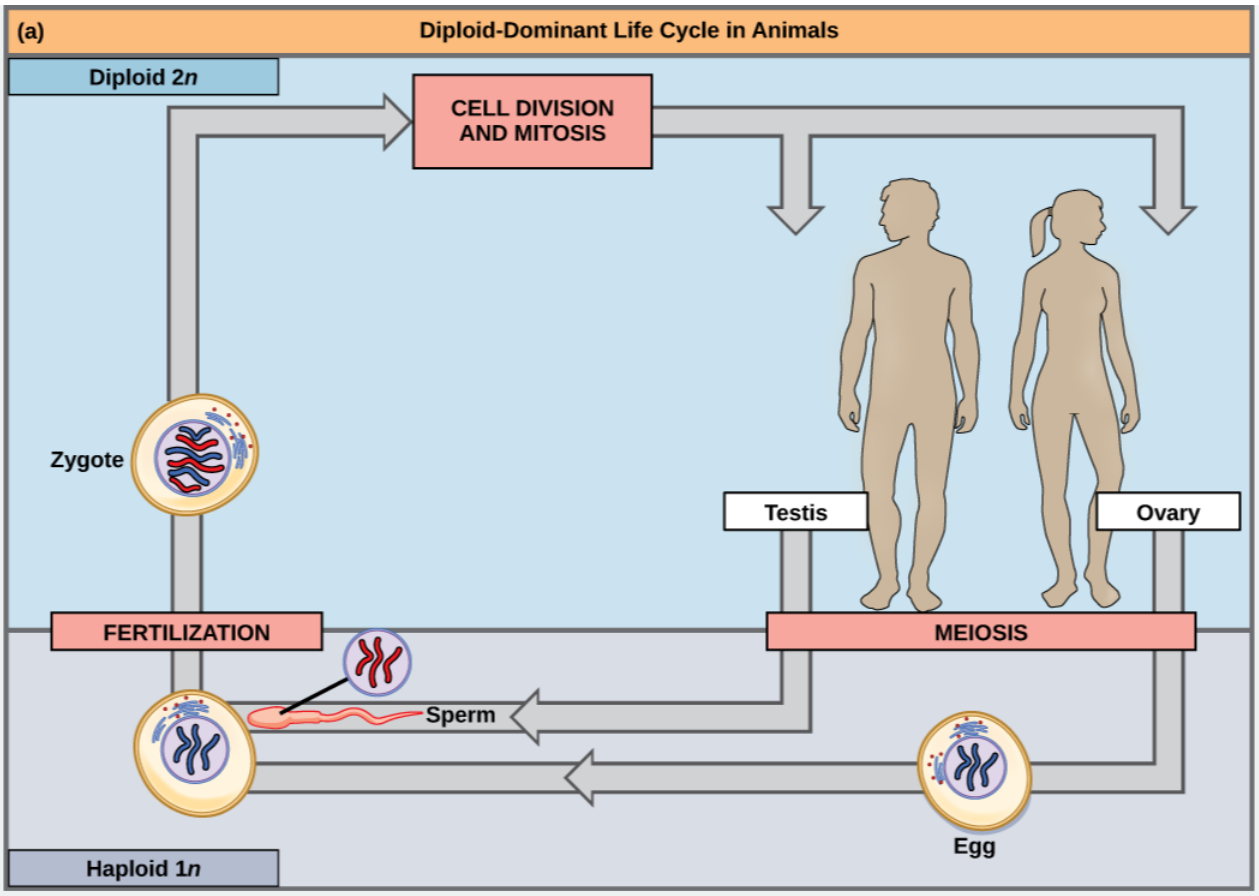
Each tiny advantage gained by favorable variation gives a species an edge over close competitors, predators, parasites, or even prey. The only method that will allow a coevolving species to keep its own share of the resources is also to continually improve its ability to survive and produce offspring. As one species gains an advantage, other species must also develop an advantage or they will be outcompeted. No single species progresses too far ahead because genetic variation among progeny of sexual reproduction provides all species with a mechanism to produce adapted individuals. Species whose individuals cannot keep up become extinct. The Red Queen’s catchphrase was, “It takes all the running you can do to stay in the same place.” This is an apt description of coevolution between competing species.

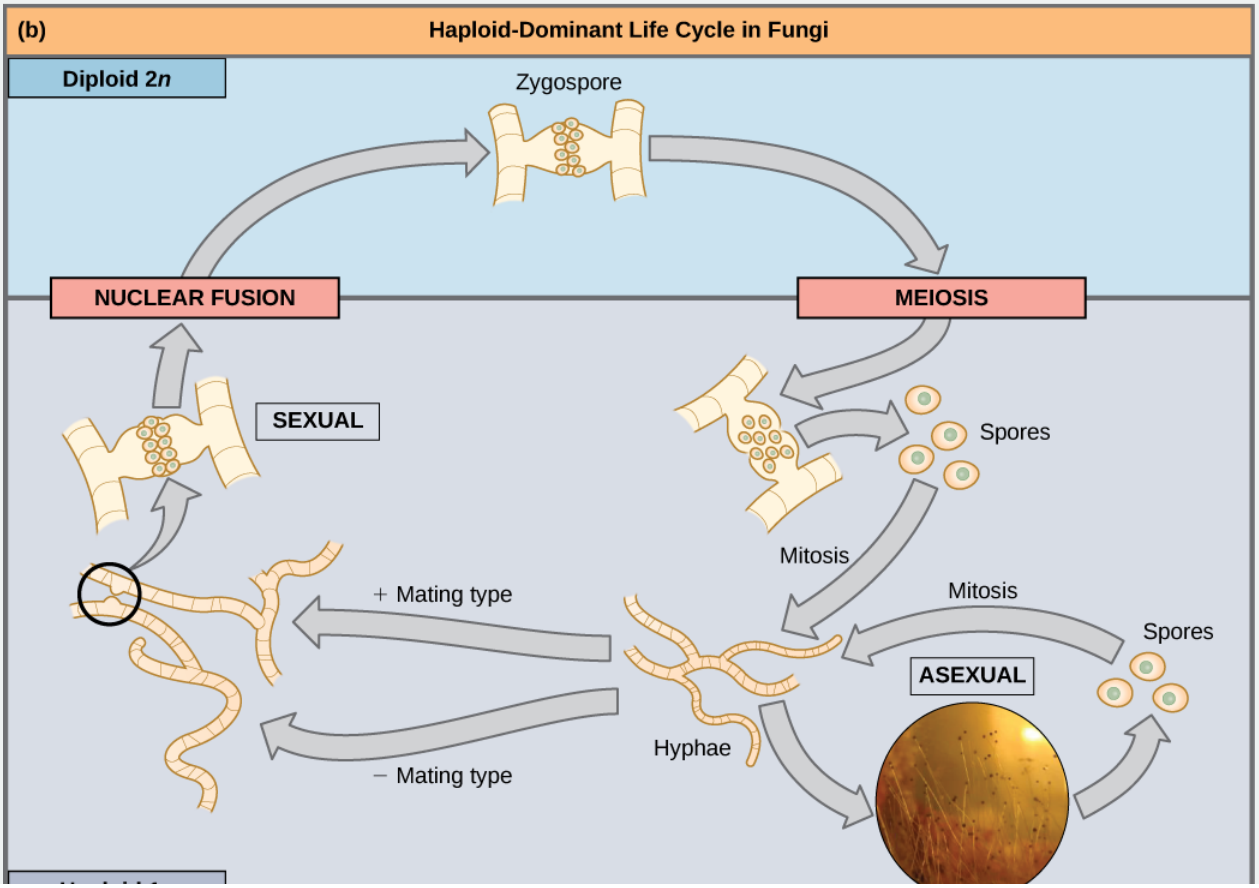
Life Cycles of Sexually Reproducing Organisms

Fertilization and meiosis alternate in sexual life cycles. What happens between these two events depends on the organism. The process of meiosis reduces the resulting gamete's chromosome number by half. Fertilization, the joining of two haploid gametes, restores the diploid condition. There are three main categories of life cycles in multicellular organisms: diploid-dominant, in which the multicellular diploid stage is the most obvious life stage (and there is no multicellular haploid stage), as with most animals including humans; haploid-dominant, in which the multicellular haploid stage is the most obvious life stage (and there is no multicellular diploid stage), as with all fungi and some algae; and alternation of generations, in which the two stages, haploid and diploid, are apparent to one degree or another depending on the group, as with plants and some algae.

Nearly all animals employ a diploid-dominant life-cycle strategy in which the only haploid cells produced by the organism are the gametes. The gametes are produced from diploid germ cells, a special cell line that only produces gametes. Once the haploid gametes are formed, they lose the ability to divide again. There is no multicellular haploid life stage. Fertilization occurs with the fusion of two gametes, usually from different individuals, restoring the diploid state (Figure **11.1.1a**).

ART CONNECTION


(a)
Diploid-Dominant Life Cycle in Animals
Diploid 2n
CELL DIVISION AND MITOSIS
Zygote
Testis
Ovary
FERTILIZATION
MEIOSIS
Sperm
Egg
Haploid 1n


(b)
Haploid-Dominant Life Cycle in Fungi
Diploid 2n
Zygospore
NUCLEAR FUSION
MEIOSIS
SEXUAL
Spores
Mitosis
+ Mating type
Mitosis
Spores
ASEXUAL
Hyphae
− Mating type

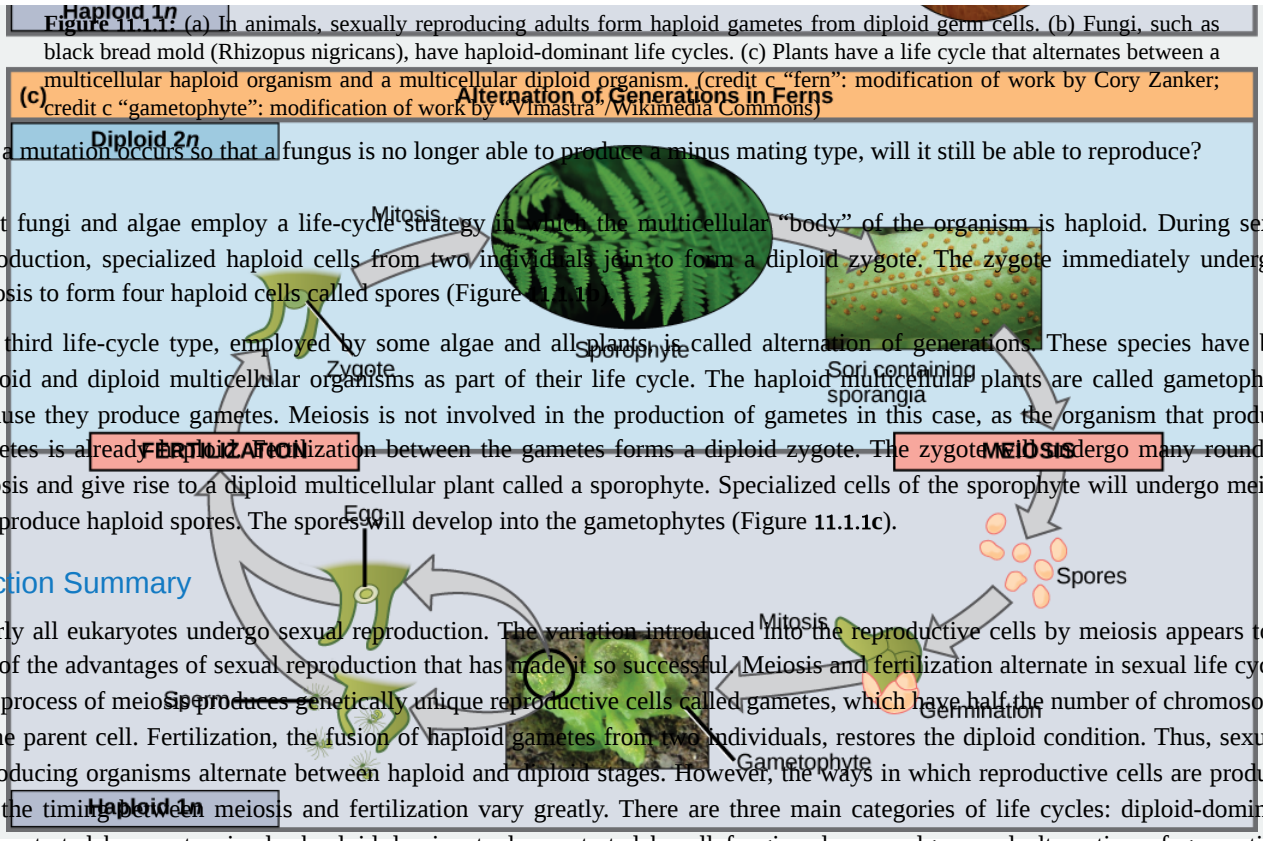


Figure 11.1.1: (a) In animals, sexually reproducing adults form haploid gametes from diploid germ cells. (b) Fungi, such as black bread mold (Rhizopus nigricans), have haploid-dominant life cycles. (c) Plants have a life cycle that alternates between a multicellular haploid organism and a multicellular diploid organism. (credit c "fern": modification of work by Cory Zanker; credit c "gametophyte": modification of work by "Vlmastra"/Wikimedia Commons)

If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

Most fungi and algae employ a life-cycle strategy in which the multicellular "body" of the organism is haploid. During sexual reproduction, specialized haploid cells from two individuals join to form a diploid zygote. The zygote immediately undergoes meiosis to form four haploid cells called spores (Figure 11.1.1b).

The third life-cycle type, employed by some algae and all plants, is called alternation of generations. These species have both haploid and diploid multicellular organisms as part of their life cycle. The haploid multicellular plants are called gametophytes because they produce gametes. Meiosis is not involved in the production of gametes in this case, as the organism that produces gametes is already haploid. Fertilization between the gametes forms a diploid zygote. The zygote will undergo many rounds of mitosis and give rise to a diploid multicellular plant called a sporophyte. Specialized cells of the sporophyte will undergo meiosis and produce haploid spores. The spores will develop into the gametophytes (Figure **11.1.1c**).

Section Summary

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells by meiosis appears to be one of the advantages of sexual reproduction that has made it so successful. Meiosis and fertilization alternate in sexual life cycles. The process of meiosis produces genetically unique reproductive cells called gametes, which have half the number of chromosomes as the parent cell. Fertilization, the fusion of haploid gametes from two individuals, restores the diploid condition. Thus, sexually reproducing organisms alternate between haploid and diploid stages. However, the ways in which reproductive cells are produced and the timing between meiosis and fertilization vary greatly. There are three main categories of life cycles: diploid-dominant, demonstrated by most animals; haploid-dominant, demonstrated by all fungi and some algae; and alternation of generations, demonstrated by plants and some algae.

Art Connections

Figure **11.1.1**: If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

Answer

Yes, it will be able to reproduce asexually.

Footnotes

1. 1 Leigh Van Valen, "A new evolutionary law," Evolutionary Theory 1 (1973): 1–30.

Glossary

alternation of generations
a life-cycle type in which the diploid and haploid stages alternate

diploid-dominant
a life-cycle type in which the multicellular diploid stage is prevalent

haploid-dominant
a life-cycle type in which the multicellular haploid stage is prevalent

gametophyte
a multicellular haploid life-cycle stage that produces gametes

germ cell
a specialized cell that produces gametes, such as eggs or sperm

life cycle

the sequence of events in the development of an organism and the production of cells that produce offspring

meiosis

a nuclear division process that results in four haploid cells

sporophyte

a multicellular diploid life-cycle stage that produces spores

Contributors and Attributions

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SECTION OVERVIEW

11.2: Features of Meiosis

11.2.1: Meiosis I

11.2.2: Meiosis II

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11.2.1: Meiosis I

Learning Objectives

- Describe the stages and results of meiosis I

Meiosis I

Meiosis is preceded by an interphase consisting of three stages. The G_1 phase (also called the first gap phase) initiates this stage and is focused on cell growth. The S phase is next, during which the DNA of the chromosomes is replicated. This replication produces two identical copies, called sister chromatids, that are held together at the centromere by cohesin proteins. The centrosomes, which are the structures that organize the microtubules of the meiotic spindle, also replicate. Finally, during the G_2 phase (also called the second gap phase), the cell undergoes the final preparations for meiosis.

Prophase I

During prophase I, chromosomes condense and become visible inside the nucleus. As the nuclear envelope begins to break down, homologous chromosomes move closer together. The synaptonemal complex, a lattice of proteins between the homologous chromosomes, forms at specific locations, spreading to cover the entire length of the chromosomes. The tight pairing of the homologous chromosomes is called synapsis. In synapsis, the genes on the chromatids of the homologous chromosomes are aligned with each other. The synaptonemal complex also supports the exchange of chromosomal segments between non-sister homologous chromatids in a process called crossing over. The crossover events are the first source of genetic variation produced by meiosis. A single crossover event between homologous non-sister chromatids leads to an exchange of DNA between chromosomes. Following crossover, the synaptonemal complex breaks down and the cohesin connection between homologous pairs is also removed. At the end of prophase I, the pairs are held together only at the chiasmata; they are called tetrads because the four sister chromatids of each pair of homologous chromosomes are now visible.

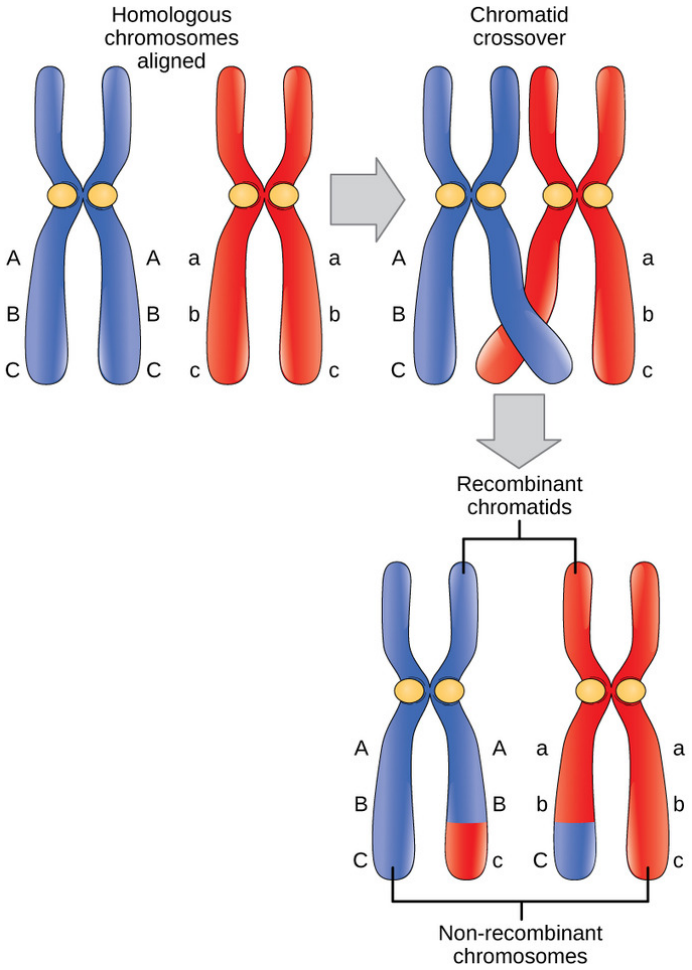


Figure **11.2.1.1**: Crossover between homologous chromosomes: Crossover occurs between non-sister chromatids of homologous chromosomes. The result is an exchange of genetic material between homologous chromosomes.

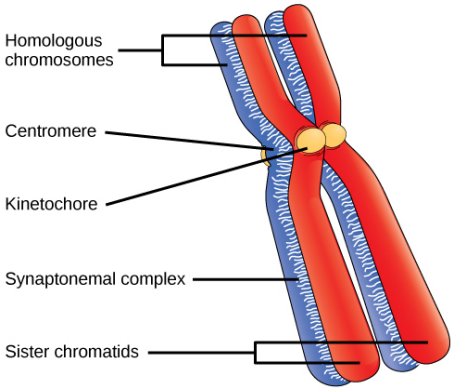


Figure **11.2.1.1**: Synapsis holds pairs of homologous chromosomes together: Early in prophase I, homologous chromosomes come together to form a synapse. The chromosomes are bound tightly together and in perfect alignment by a protein lattice called a synaptonemal complex and by cohesin proteins at the centromere.

Prometaphase I

The key event in prometaphase I is the formation of the spindle fiber apparatus where spindle fiber microtubules attach to the kinetochore proteins at the centromeres. Microtubules grow from centrosomes placed at opposite poles of the cell. The microtubules move toward the middle of the cell and attach to one of the two fused homologous chromosomes at the kinetochores. At the end of prometaphase I, each tetrad is attached to microtubules from both poles, with one homologous chromosome facing each pole. In addition, the nuclear membrane has broken down entirely.

Metaphase I

During metaphase I, the tetrads move to the metaphase plate with kinetochores facing opposite poles. The homologous pairs orient themselves randomly at the equator. This event is the second mechanism that introduces variation into the gametes or spores. In each cell that undergoes meiosis, the arrangement of the tetrads is different. The number of variations is dependent on the number of chromosomes making up a set. There are two possibilities for orientation at the metaphase plate. The possible number of alignments, therefore, equals 2n, where n is the number of chromosomes per set. Given these two mechanisms, it is highly unlikely that any two haploid cells resulting from meiosis will have the same genetic composition.

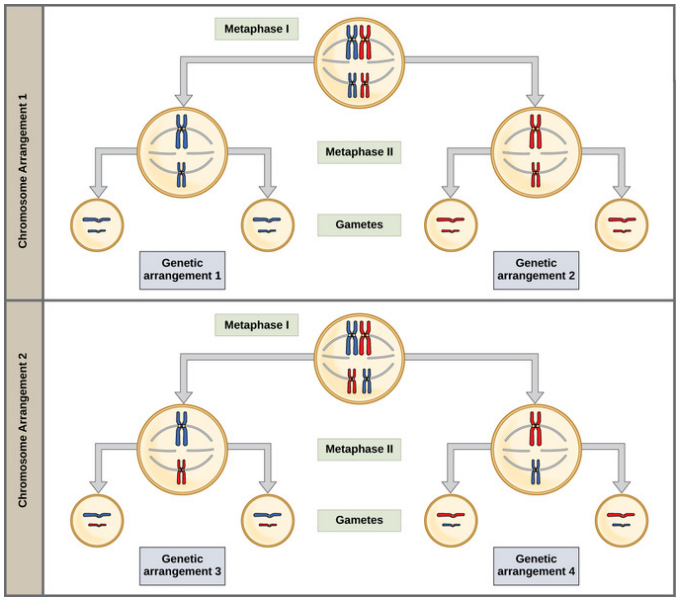


Figure **11.2.1.1**: Meiosis I ensures unique gametes: Random, independent assortment during metaphase I can be demonstrated by considering a cell with a set of two chromosomes (n = 2). In this case, there are two possible arrangements at the equatorial plane in metaphase I. The total possible number of different gametes is 2n, where n equals the number of chromosomes in a set. In this example, there are four possible genetic combinations for the gametes. With n = 23 in human cells, there are over 8 million possible combinations of paternal and maternal chromosomes.

Anaphase I

In anaphase I, the microtubules pull the attached chromosomes apart. The sister chromatids remain tightly bound together at the centromere. The chiasmata are broken in anaphase I as the microtubules attached to the fused kinetochores pull the homologous chromosomes apart.

Telophase I and Cytokinesis

In telophase I, the separated chromosomes arrive at opposite poles. In some organisms, the chromosomes decondense and nuclear envelopes form around the chromatids in telophase I. Then cytokinesis, the physical separation of the cytoplasmic components into two daughter cells, occurs without reformation of the nuclei. In nearly all species of animals and some fungi, cytokinesis separates the cell contents via a cleavage furrow (constriction of the actin ring that leads to cytoplasmic division). In plants, a cell plate is formed during cell cytokinesis by Golgi vesicles fusing at the metaphase plate. This cell plate will ultimately lead to the formation of cell walls that separate the two daughter cells.

Two haploid cells are the end result of the first meiotic division. The cells are haploid because at each pole there is just one of each pair of the homologous chromosomes. Therefore, only one full set of the chromosomes is present. Although there is only one chromosome set, each homolog still consists of two sister chromatids.

Key Points

- Meiosis is preceded by interphase which consists of the G_1 phase (growth), the S phase (DNA replication), and the G_2 phase.
- During prophase I, the homologous chromosomes condense and become visible as the x shape we know, pair up to form a tetrad, and exchange genetic material by crossing over.

- During prometaphase I, microtubules attach at the chromosomes' kinetochores and the nuclear envelope breaks down.
- In metaphase I, the tetrads line themselves up at the metaphase plate and homologous pairs orient themselves randomly.
- In anaphase I, centromeres break down and homologous chromosomes separate.
- In telophase I, chromosomes move to opposite poles; during cytokinesis the cell separates into two haploid cells.

Key Terms

- **crossing over**: the exchange of genetic material between homologous chromosomes that results in recombinant chromosomes
- **tetrad**: two pairs of sister chromatids (a dyad pair) aligned in a certain way and often on the equatorial plane during the meiosis process
- **chromatid**: either of the two strands of a chromosome that separate during meiosis

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11.2.2: Meiosis II

Learning Objectives

- Describe the stages and results of Meiosis II

Meiosis II

Meiosis II initiates immediately after cytokinesis, usually before the chromosomes have fully decondensed. In contrast to meiosis I, meiosis II resembles a normal mitosis. In some species, cells enter a brief interphase, or interkinesis, before entering meiosis II. Interkinesis lacks an S phase, so chromosomes are not duplicated. The two cells produced in meiosis I go through the events of meiosis II together. During meiosis II, the sister chromatids within the two daughter cells separate, forming four new haploid gametes. The mechanics of meiosis II is similar to mitosis, except that each dividing cell has only one set of homologous chromosomes.

Prophase II

If the chromosomes decondensed in telophase I, they condense again. If nuclear envelopes were formed, they fragment into vesicles. The centrosomes that were duplicated during interphase I move away from each other toward opposite poles and new spindles are formed.

Prometaphase II

The nuclear envelopes are completely broken down and the spindle is fully formed. Each sister chromatid forms an individual kinetochore that attaches to microtubules from opposite poles.

Metaphase II

The sister chromatids are maximally condensed and aligned at the equator of the cell.

Anaphase II

The sister chromatids are pulled apart by the kinetochore microtubules and move toward opposite poles. Non-kinetochore microtubules elongate the cell.

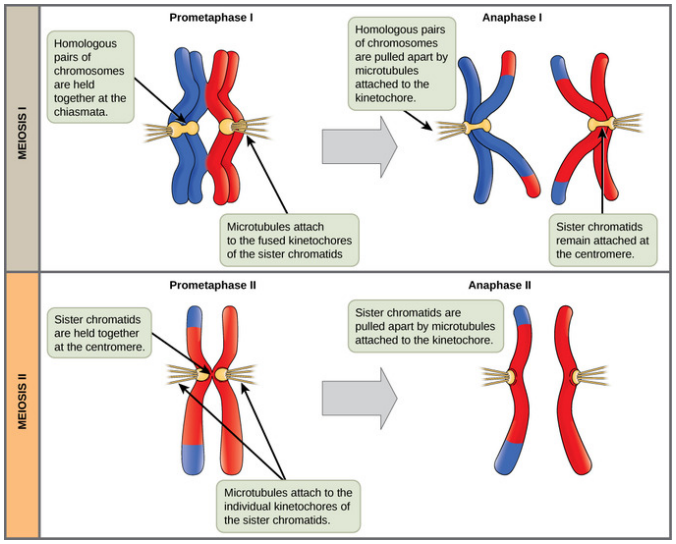


Figure 11.2.2.1: Meiosis I vs. Meiosis II: The process of chromosome alignment differs between meiosis I and meiosis II. In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes, and the homologous chromosomes are arranged at the midpoint of the cell in metaphase I. In anaphase I, the homologous chromosomes are separated. In prometaphase II, microtubules attach to the kinetochores of sister chromatids, and the sister chromatids are arranged at the midpoint of the cells in metaphase II. In anaphase II, the sister chromatids are separated.

Telophase II and Cytokinesis

The chromosomes arrive at opposite poles and begin to decondense. Nuclear envelopes form around the chromosomes. Cytokinesis separates the two cells into four unique haploid cells. At this point, the newly-formed nuclei are both haploid. The cells produced are genetically unique because of the random assortment of paternal and maternal homologs and because of the recombining of maternal and paternal segments of chromosomes (with their sets of genes) that occurs during crossover.

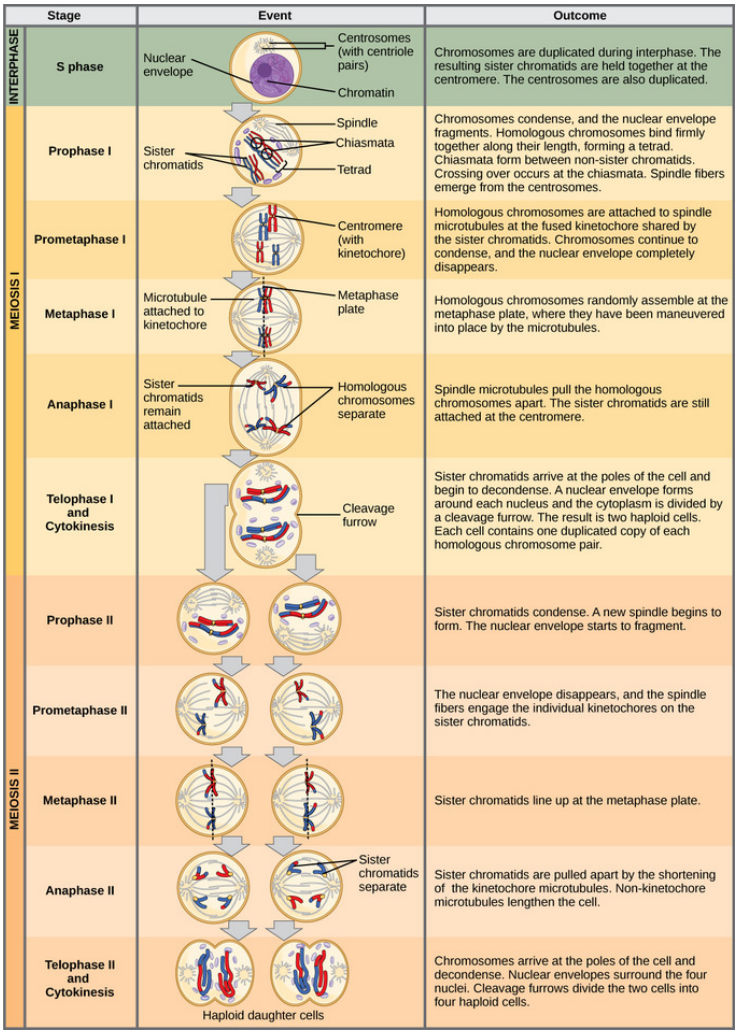


Figure 11.2.2.1: Complete Stages of Meiosis: An animal cell with a diploid number of four (2n = 4) proceeds through the stages of meiosis to form four haploid daughter cells.

Key Points

- During prophase II, chromsomes condense again, centrosomes that were duplicated during interphase I move away from each other toward opposite poles, and new spindles are formed.
- During prometaphase II, the nuclear envelopes are completely broken down, and each sister chromatid forms an individual kinetochore that attaches to microtubules from opposite poles.
- During metaphase II, sister chromatids are condensed and aligned at the equator of the cell.
- During anaphase II sister chromatids are pulled apart by the kinetochore microtubules and move toward opposite poles.
- During telophase II and cytokinesis, chromosomes arrive at opposite poles and begin to decondense; the two cells divide into four unique haploid cells.

Key Terms

- **meiosis II**: the second part of the meiotic process; the end result is production of four haploid cells from the two haploid cells produced in meiosis I

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11.3: The Process of Meiosis

Sexual reproduction requires fertilization, a union of two cells from two individual organisms. If those two cells each contain one set of chromosomes, then the resulting cell contains two sets of chromosomes. The number of sets of chromosomes in a cell is called its ploidy level. Haploid cells contain one set of chromosomes. Cells containing two sets of chromosomes are called diploid. If the reproductive cycle is to continue, the diploid cell must somehow reduce its number of chromosome sets before fertilization can occur again, or there will be a continual doubling in the number of chromosome sets in every generation. So, in addition to fertilization, sexual reproduction includes a nuclear division, known as meiosis, that reduces the number of chromosome sets.

Most animals and plants are diploid, containing two sets of chromosomes; in each somatic cell (the nonreproductive cells of a multicellular organism), the nucleus contains two copies of each chromosome that are referred to as homologous chromosomes. Somatic cells are sometimes referred to as “body” cells. Homologous chromosomes are matched pairs containing genes for the same traits in identical locations along their length. Diploid organisms inherit one copy of each homologous chromosome from each parent; all together, they are considered a full set of chromosomes. In animals, haploid cells containing a single copy of each homologous chromosome are found only within gametes. Gametes fuse with another haploid gamete to produce a diploid cell.

The nuclear division that forms haploid cells, which is called meiosis, is related to mitosis. As you have learned, mitosis is part of a cell reproduction cycle that results in identical daughter nuclei that are also genetically identical to the original parent nucleus. In mitosis, both the parent and the daughter nuclei contain the same number of chromosome sets—diploid for most plants and animals. Meiosis employs many of the same mechanisms as mitosis. However, the starting nucleus is always diploid and the nuclei that result at the end of a meiotic cell division are haploid. To achieve the reduction in chromosome number, meiosis consists of one round of chromosome duplication and two rounds of nuclear division. Because the events that occur during each of the division stages are analogous to the events of mitosis, the same stage names are assigned. However, because there are two rounds of division, the stages are designated with a “I” or “II.” Thus, meiosis I is the first round of meiotic division and consists of prophase I, prometaphase I, and so on. Meiosis I reduces the number of chromosome sets from two to one. The genetic information is also mixed during this division to create unique recombinant chromosomes. Meiosis II, in which the second round of meiotic division takes place in a way that is similar to mitosis, includes prophase II, prometaphase II, and so on.

Interphase

Meiosis is preceded by an interphase consisting of the G_1, S, and G_2 phases, which are nearly identical to the phases preceding mitosis. The G_1 phase is the first phase of interphase and is focused on cell growth. In the S phase, the DNA of the chromosomes is replicated. Finally, in the G_2 phase, the cell undergoes the final preparations for meiosis.

During DNA duplication of the S phase, each chromosome becomes composed of two identical copies (called sister chromatids) that are held together at the centromere until they are pulled apart during meiosis II. In an animal cell, the centrosomes that organize the microtubules of the meiotic spindle also replicate. This prepares the cell for the first meiotic phase.

Meiosis I

Early in prophase I, the chromosomes can be seen clearly microscopically. As the nuclear envelope begins to break down, the proteins associated with homologous chromosomes bring the pair close to each other. The tight pairing of the homologous chromosomes is called synapsis. In synapsis, the genes on the chromatids of the homologous chromosomes are precisely aligned with each other. An exchange of chromosome segments between non-sister homologous chromatids occurs and is called crossing over. This process is revealed visually after the exchange as chiasmata (singular = *chiasma*) (Figure **11.3.1**).

As prophase I progresses, the close association between homologous chromosomes begins to break down, and the chromosomes continue to condense, although the homologous chromosomes remain attached to each other at chiasmata. The number of chiasmata varies with the species and the length of the chromosome. At the end of prophase I, the pairs are held together only at chiasmata (Figure **11.3.1**) and are called tetrads because the four sister chromatids of each pair of homologous chromosomes are now visible.

The crossover events are the first source of genetic variation produced by meiosis. A single crossover event between homologous non-sister chromatids leads to a reciprocal exchange of equivalent DNA between a maternal chromosome and a paternal chromosome. Now, when that sister chromatid is moved into a gamete, it will carry some DNA from one parent of the individual

and some DNA from the other parent. The recombinant sister chromatid has a combination of maternal and paternal genes that did not exist before the crossover.

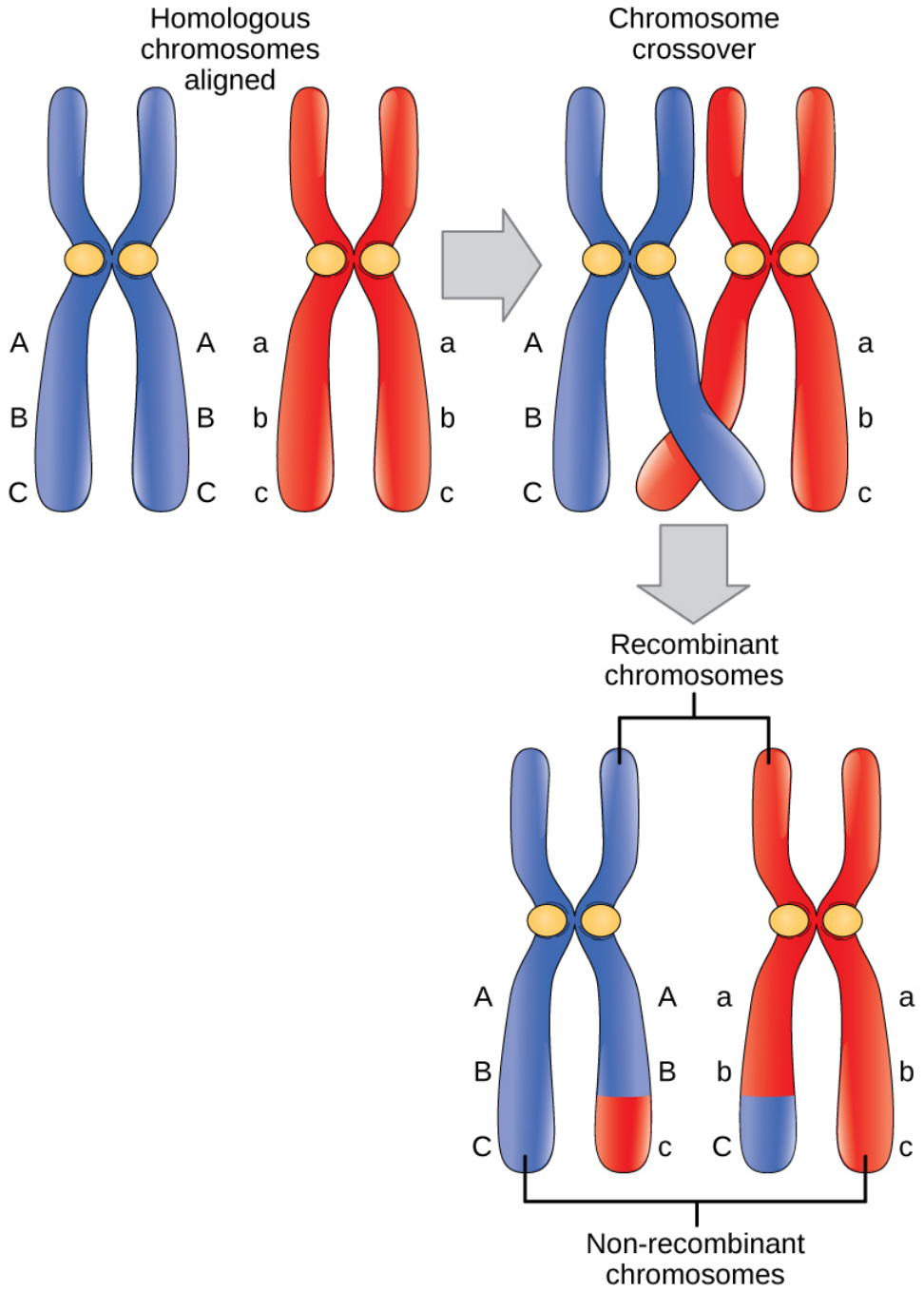


Figure 11.3.1: In this illustration of the effects of crossing over, the blue chromosome came from the individual's father and the red chromosome came from the individual's mother. Crossover occurs between non-sister chromatids of homologous chromosomes. The result is an exchange of genetic material between homologous chromosomes. The chromosomes that have a mixture of maternal and paternal sequence are called recombinant and the chromosomes that are completely paternal or maternal are called non-recombinant.

The key event in prometaphase I is the attachment of the spindle fiber microtubules to the kinetochore proteins at the centromeres. The microtubules assembled from centrosomes at opposite poles of the cell grow toward the middle of the cell. At the end of prometaphase I, each tetrad is attached to microtubules from both poles, with one homologous chromosome attached at one pole and the other homologous chromosome attached to the other pole. The homologous chromosomes are still held together at chiasmata. In addition, the nuclear membrane has broken down entirely.

During metaphase I, the homologous chromosomes are arranged in the center of the cell with the kinetochores facing opposite poles. The orientation of each pair of homologous chromosomes at the center of the cell is random.

This randomness, called independent assortment, is the physical basis for the generation of the second form of genetic variation in offspring. Consider that the homologous chromosomes of a sexually reproducing organism are originally inherited as two separate sets, one from each parent. Using humans as an example, one set of 23 chromosomes is present in the egg donated by the mother. The father provides the other set of 23 chromosomes in the sperm that fertilizes the egg. In metaphase I, these pairs line up at the midway point between the two poles of the cell. Because there is an equal chance that a microtubule fiber will encounter a maternally or paternally inherited chromosome, the arrangement of the tetrads at the metaphase plate is random. Any maternally inherited chromosome may face either pole. Any paternally inherited chromosome may also face either pole. The orientation of each tetrad is independent of the orientation of the other 22 tetrads.

In each cell that undergoes meiosis, the arrangement of the tetrads is different. The number of variations depends on the number of chromosomes making up a set. There are two possibilities for orientation (for each tetrad); thus, the possible number of alignments equals 2^n where n is the number of chromosomes per set. Humans have 23 chromosome pairs, which results in over eight million (2^{23}) possibilities. This number does not include the variability previously created in the sister chromatids by crossover. Given these two mechanisms, it is highly unlikely that any two haploid cells resulting from meiosis will have the same genetic composition (Figure **11.3.2**).

To summarize the genetic consequences of meiosis I: the maternal and paternal genes are recombined by crossover events occurring on each homologous pair during prophase I; in addition, the random assortment of tetrads at metaphase produces a unique combination of maternal and paternal chromosomes that will make their way into the gametes.

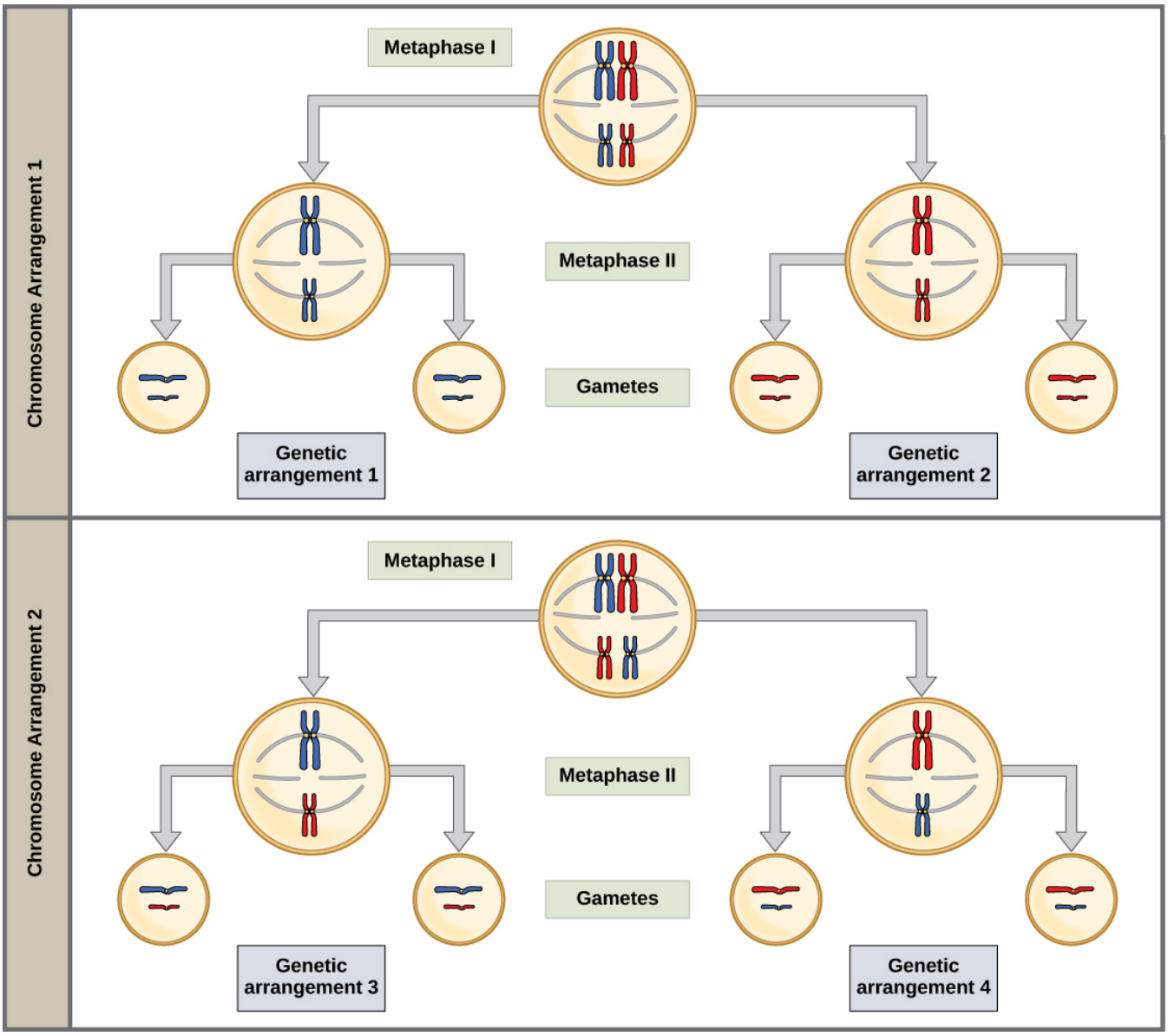


Figure 11.3.2: To demonstrate random, independent assortment at metaphase I, consider a cell with n = 2. In this case, there are two possible arrangements at the equatorial plane in metaphase I, as shown in the upper cell of each panel. These two possible orientations lead to the production of genetically different gametes. With more chromosomes, the number of possible arrangements increases dramatically.

In anaphase I, the spindle fibers pull the linked chromosomes apart. The sister chromatids remain tightly bound together at the centromere. It is the chiasma connections that are broken in anaphase I as the fibers attached to the fused kinetochores pull the homologous chromosomes apart (Figure **11.3.3**).

In telophase I, the separated chromosomes arrive at opposite poles. The remainder of the typical telophase events may or may not occur depending on the species. In some organisms, the chromosomes decondense and nuclear envelopes form around the chromatids in telophase I.

Cytokinesis, the physical separation of the cytoplasmic components into two daughter cells, occurs without reformation of the nuclei in other organisms. In nearly all species, cytokinesis separates the cell contents by either a cleavage furrow (in animals and some fungi), or a cell plate that will ultimately lead to formation of cell walls that separate the two daughter cells (in plants). At each pole, there is just one member of each pair of the homologous chromosomes, so only one full set of the chromosomes is present. This is why the cells are considered haploid—there is only one chromosome set, even though there are duplicate copies of

the set because each homolog still consists of two sister chromatids that are still attached to each other. However, although the sister chromatids were once duplicates of the same chromosome, they are no longer identical at this stage because of crossovers.

CONCEPT IN ACTION

Review the process of meiosis, observing how chromosomes align and migrate, at this site.

Meiosis II

In meiosis II, the connected sister chromatids remaining in the haploid cells from meiosis I will be split to form four haploid cells. In some species, cells enter a brief interphase, or interkinesis, that lacks an S phase, before entering meiosis II. Chromosomes are not duplicated during interkinesis. The two cells produced in meiosis I go through the events of meiosis II in synchrony. Overall, meiosis II resembles the mitotic division of a haploid cell.

In prophase II, if the chromosomes decondensed in telophase I, they condense again. If nuclear envelopes were formed, they fragment into vesicles. The centrosomes duplicated during interkinesis move away from each other toward opposite poles, and new spindles are formed. In prometaphase II, the nuclear envelopes are completely broken down, and the spindle is fully formed. Each sister chromatid forms an individual kinetochore that attaches to microtubules from opposite poles. In metaphase II, the sister chromatids are maximally condensed and aligned at the center of the cell. In anaphase II, the sister chromatids are pulled apart by the spindle fibers and move toward opposite poles.

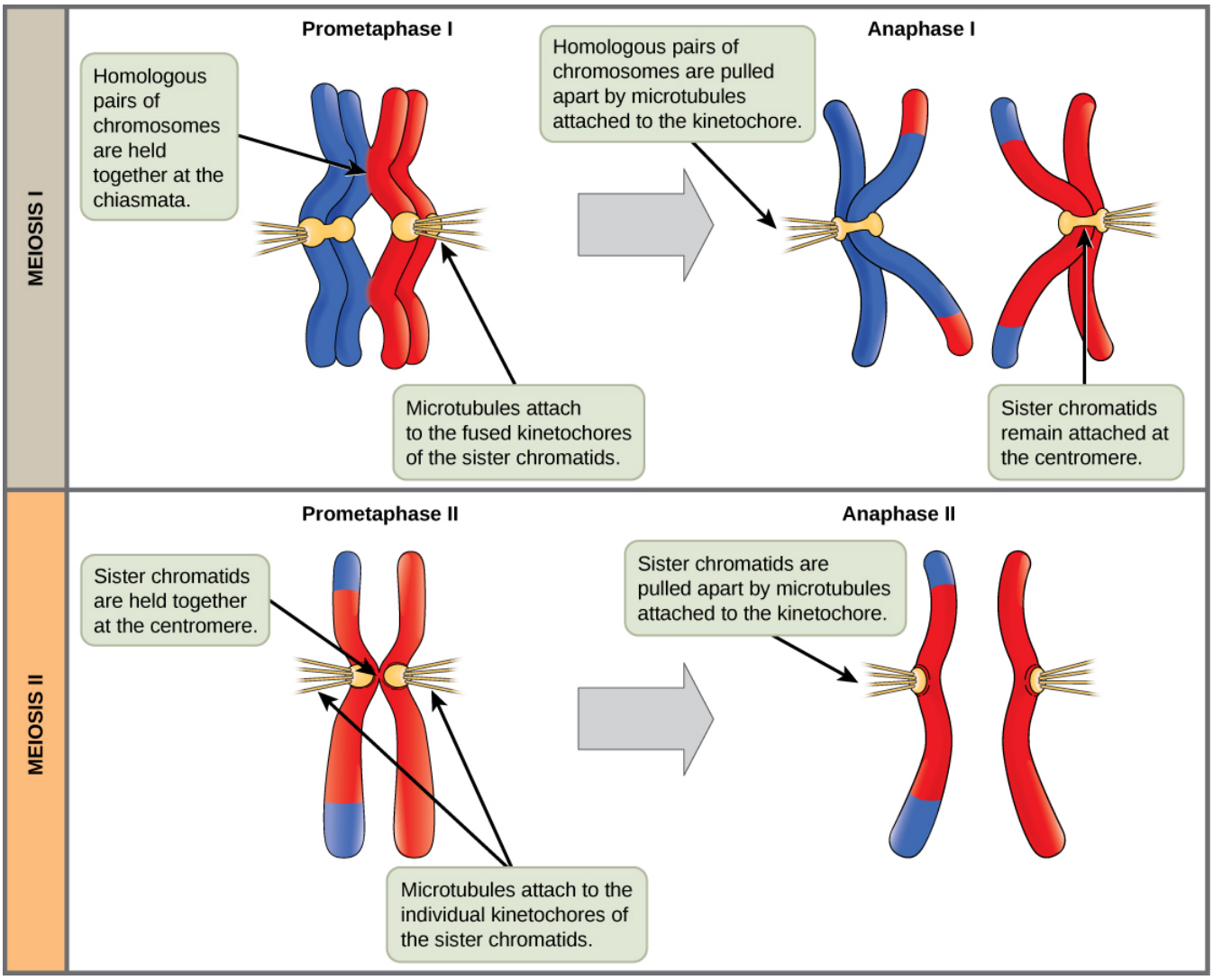


Figure 11.3.3: In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes. In anaphase I, the homologous chromosomes are separated. In prometaphase II, microtubules attach to individual kinetochores of sister chromatids. In anaphase II, the sister chromatids are separated.

In telophase II, the chromosomes arrive at opposite poles and begin to decondense. Nuclear envelopes form around the chromosomes. Cytokinesis separates the two cells into four genetically unique haploid cells. At this point, the nuclei in the newly produced cells are both haploid and have only one copy of the single set of chromosomes. The cells produced are genetically unique because of the random assortment of paternal and maternal homologs and because of the recombination of maternal and paternal segments of chromosomes—with their sets of genes—that occurs during crossover.

Comparing Meiosis and Mitosis

Mitosis and meiosis, which are both forms of division of the nucleus in eukaryotic cells, share some similarities, but also exhibit distinct differences that lead to their very different outcomes. Mitosis is a single nuclear division that results in two nuclei, usually partitioned into two new cells. The nuclei resulting from a mitotic division are genetically identical to the original. They have the same number of sets of chromosomes: one in the case of haploid cells, and two in the case of diploid cells. On the other hand, meiosis is two nuclear divisions that result in four nuclei, usually partitioned into four new cells. The nuclei resulting from meiosis are never genetically identical, and they contain one chromosome set only—this is half the number of the original cell, which was diploid (Figure **11.3.4**).

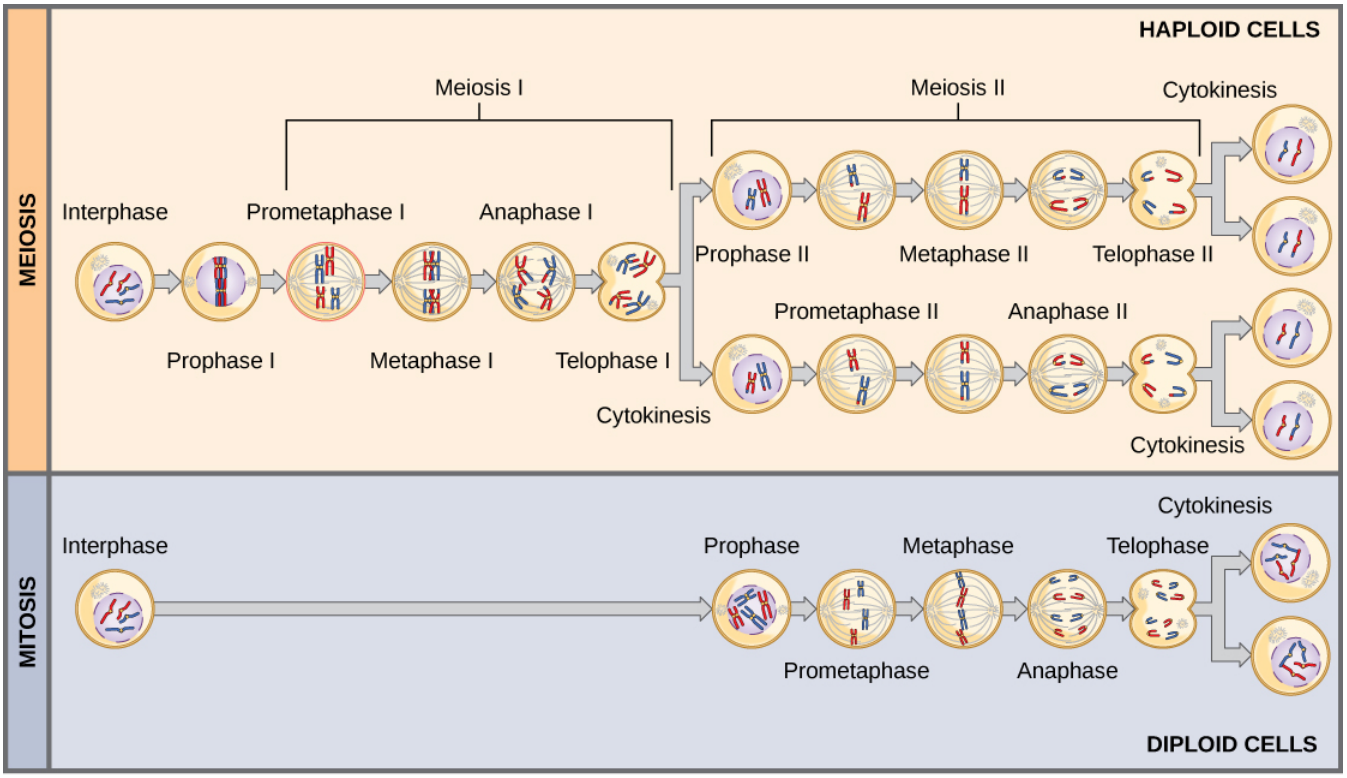
The differences in the outcomes of meiosis and mitosis occur because of differences in the behavior of the chromosomes during each process. Most of these differences in the processes occur in meiosis I, which is a very different nuclear division than mitosis.

In meiosis I, the homologous chromosome pairs become associated with each other, are bound together, experience chiasmata and crossover between sister chromatids, and line up along the metaphase plate in tetrads with spindle fibers from opposite spindle poles attached to each kinetochore of a homolog in a tetrad. All of these events occur only in meiosis I, never in mitosis.

Homologous chromosomes move to opposite poles during meiosis I so the number of sets of chromosomes in each nucleus-to-be is reduced from two to one. For this reason, meiosis I is referred to as a reduction division. There is no such reduction in ploidy level in mitosis.

Meiosis II is much more analogous to a mitotic division. In this case, duplicated chromosomes (only one set of them) line up at the center of the cell with divided kinetochores attached to spindle fibers from opposite poles. During anaphase II, as in mitotic anaphase, the kinetochores divide and one sister chromatid is pulled to one pole and the other sister chromatid is pulled to the other pole. If it were not for the fact that there had been crossovers, the two products of each meiosis II division would be identical as in mitosis; instead, they are different because there has always been at least one crossover per chromosome. Meiosis II is not a reduction division because, although there are fewer copies of the genome in the resulting cells, there is still one set of chromosomes, as there was at the end of meiosis I.

Cells produced by mitosis will function in different parts of the body as a part of growth or replacing dead or damaged cells. They may even be involved in asexual reproduction in some organisms. Cells produced by meiosis in a diploid-dominant organism such as an animal will only participate in sexual reproduction.



						OUTCOME
PROCESS	DNA synthesis	Synapsis of homologous chromosomes	Crossover	Homologous chromosomes line up at metaphase plate	Sister chromatids line up at metaphase plate	Number and genetic composition of daughter cells
MEIOSIS	Occurs in S phase of interphase	During prophase I	During prophase I	During metaphase I	During metaphase II	Four haploid cells at the end of meiosis II
MITOSIS	Occurs in S phase of interphase	Does not occur in mitosis	Does not occur in mitosis	Does not occur in mitosis	During metaphase	Two diploid cells at the end of mitosis

Figure 11.3.4: Meiosis and mitosis are both preceded by one round of DNA replication; however, meiosis includes two nuclear divisions. The four daughter cells resulting from meiosis are haploid and genetically distinct. The daughter cells resulting from mitosis are diploid and identical to the parent cell.

CONCEPT IN ACTION

For an animation comparing mitosis and meiosis, go to this website.

Section Summary

Sexual reproduction requires that diploid organisms produce haploid cells that can fuse during fertilization to form diploid offspring. The process that results in haploid cells is called meiosis. Meiosis is a series of events that arrange and separate

chromosomes into daughter cells. During the interphase of meiosis, each chromosome is duplicated. In meiosis, there are two rounds of nuclear division resulting in four nuclei and usually four haploid daughter cells, each with half the number of chromosomes as the parent cell. During meiosis, variation in the daughter nuclei is introduced because of crossover in prophase I and random alignment at metaphase I. The cells that are produced by meiosis are genetically unique.

Meiosis and mitosis share similarities, but have distinct outcomes. Mitotic divisions are single nuclear divisions that produce daughter nuclei that are genetically identical and have the same number of chromosome sets as the original cell. Meiotic divisions are two nuclear divisions that produce four daughter nuclei that are genetically different and have one chromosome set rather than the two sets the parent cell had. The main differences between the processes occur in the first division of meiosis. The homologous chromosomes separate into different nuclei during meiosis I causing a reduction of ploidy level. The second division of meiosis is much more similar to a mitotic division.

Glossary

chiasmata
(singular = *chiasma*) the structure that forms at the crossover points after genetic material is exchanged

crossing over
(also, recombination) the exchange of genetic material between homologous chromosomes resulting in chromosomes that incorporate genes from both parents of the organism forming reproductive cells

fertilization
the union of two haploid cells typically from two individual organisms

interkinesis
a period of rest that may occur between meiosis I and meiosis II; there is no replication of DNA during interkinesis

meiosis I
the first round of meiotic cell division; referred to as reduction division because the resulting cells are haploid

meiosis II
the second round of meiotic cell division following meiosis I; sister chromatids are separated from each other, and the result is four unique haploid cells

recombinant
describing something composed of genetic material from two sources, such as a chromosome with both maternal and paternal segments of DNA

reduction division
a nuclear division that produces daughter nuclei each having one-half as many chromosome sets as the parental nucleus; meiosis I is a reduction division

somatic cell
all the cells of a multicellular organism except the gamete-forming cells

synapsis
the formation of a close association between homologous chromosomes during prophase I

tetrad
two duplicated homologous chromosomes (four chromatids) bound together by chiasmata during prophase I

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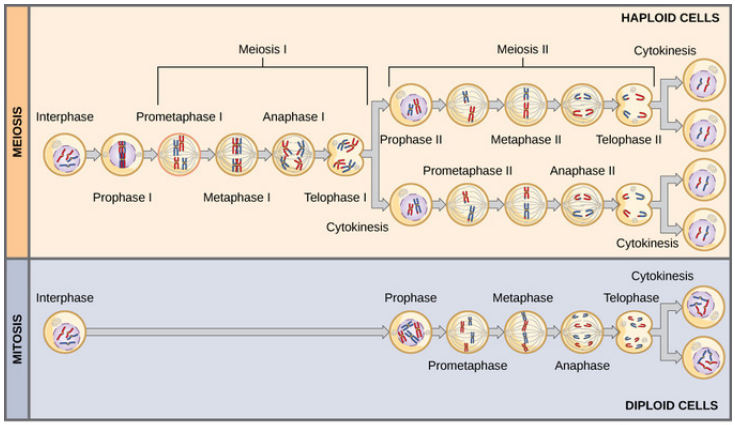
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11.4: Summing Up- Meiosis Versus Mitosis

Learning Objectives

- Compare and contrast mitosis and meiosis

Mitosis and meiosis are both forms of division of the nucleus in eukaryotic cells. They share some similarities, but also exhibit distinct differences that lead to very different outcomes. The purpose of mitosis is cell regeneration, growth, and asexual reproduction,while the purpose of meiosis is the production of gametes for sexual reproduction. Mitosis is a single nuclear division that results in two nuclei that are usually partitioned into two new daughter cells. The nuclei resulting from a mitotic division are genetically identical to the original nucleus. They have the same number of sets of chromosomes, one set in the case of haploid cells and two sets in the case of diploid cells. In most plants and all animal species, it is typically diploid cells that undergo mitosis to form new diploid cells. In contrast, meiosis consists of two nuclear divisions resulting in four nuclei that are usually partitioned into four new haploid daughter cells. The nuclei resulting from meiosis are not genetically identical and they contain one chromosome set only. This is half the number of chromosome sets in the original cell, which is diploid.



	OUTCOME
PROCESS	Number and genetic composition of daughter cells
MEIOSIS	Four haploid cells at the end of meiosis II
MITOSIS	Two diploid cells at the end of mitosis

PROCESS	DNA synthesis	Synapsis of homologous chromosomes	Crossover	Homologous chromosomes line up at metaphase plate	Sister chromatids line up at metaphase plate	Number and genetic composition of daughter cells
MEIOSIS	Occurs in S phase of interphase	During prophase I	During prophase I	During metaphase I	During metaphase II	Four haploid cells at the end of meiosis II
MITOSIS	Occurs in S phase of interphase	Does not occur in mitosis	Does not occur in mitosis	Does not occur in mitosis	During metaphase	Two diploid cells at the end of mitosis

Figure **11.4.1**: Comparing Meiosis and Mitosis: Meiosis and mitosis are both preceded by one round of DNA replication; however, meiosis includes two nuclear divisions. The four daughter cells resulting from meiosis are haploid and genetically distinct. The daughter cells resulting from mitosis are diploid and identical to the parent cell.

The main differences between mitosis and meiosis occur in meiosis I. In meiosis I, the homologous chromosome pairs become associated with each other and are bound together with the synaptonemal complex. Chiasmata develop and crossover occurs between homologous chromosomes, which then line up along the metaphase plate in tetrads with kinetochore fibers from opposite spindle poles attached to each kinetochore of a homolog in a tetrad. All of these events occur only in meiosis I.

When the tetrad is broken up and the homologous chromosomes move to opposite poles, the ploidy level is reduced from two to one. For this reason, meiosis I is referred to as a reduction division. There is no such reduction in ploidy level during mitosis.

Meiosis II is much more similar to a mitotic division. In this case, the duplicated chromosomes (only one set, as the homologous pairs have now been separated into two different cells) line up on the metaphase plate with divided kinetochores attached to kinetochore fibers from opposite poles. During anaphase II and mitotic anaphase, the kinetochores divide and sister chromatids, now referred to as chromosomes, are pulled to opposite poles. The two daughter cells of mitosis, however, are identical, unlike the daughter cells produced by meiosis. They are different because there has been at least one crossover per chromosome. Meiosis II is

not a reduction division because, although there are fewer copies of the genome in the resulting cells, there is still one set of chromosomes, as there was at the end of meiosis I. Meiosis II is, therefore, referred to as equatorial division.

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Key Points

- For the most part, in mitosis, diploid cells are partitioned into two new diploid cells, while in meiosis, diploid cells are partitioned into four new haploid cells.
- In mitosis, the daughter cells have the same number of chromosomes as the parent cell, while in meiosis, the daughter cells have half the number of chromosomes as the parent.

- The daughter cells produced by mitosis are identical, whereas the daughter cells produced by meiosis are different because crossing over has occurred.
- The events that occur in meiosis but not mitosis include homologous chromosomes pairing up, crossing over, and lining up along the metaphase plate in tetrads.
- Meiosis II and mitosis are not reduction division like meiosis I because the number of chromosomes remains the same; therefore, meiosis II is referred to as equatorial division.
- When the homologous chromosomes separate and move to opposite poles during meiosis I, the ploidy level is reduced from two to one, which is referred to as a reduction division.

Key Terms

- **reduction division**: the first of the two divisions of meiosis, a type of cell division
- **ploidy**: the number of homologous sets of chromosomes in a cell
- **equatorial division**: a process of nuclear division in which each chromosome divides equally such that the number of chromosomes remains the same from parent to daughter cells

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CHAPTER OVERVIEW

12: Patterns of Inheritance

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12.1.2: Mendel’s Model System

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SECTION OVERVIEW

12.1: The Mystery of Heredity

12.1.1: Introduction to Mendelian Inheritance

12.1.2: Mendel's Model System

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12.1.1: Introduction to Mendelian Inheritance

Learning Objectives

- Describe the traits of pea plants that were studied by Mendel

Gregor Mendel and the Study of Genetics

Genetics is the study of heredity, or the passing of traits from parents to offspring. Gregor Johann Mendel set the framework for genetics long before chromosomes or genes had been identified, at a time when meiosis was not well understood. For his work, Mendel is often referred to as the "father of modern genetics. " Mendel selected a simple biological system, garden peas, and conducted methodical, quantitative analyses using large sample sizes.



Figure **12.1.1.1**: Gregor Mendel: Gregor Johann Mendel was a German-speaking Moravian scientist and Augustinian friar who gained posthumous fame as the founder of the modern science of genetics.

Mendel entered the Augustinian St. Thomas's Abbey and began his training as a priest. He began studying heredity using mice, but his bishop did not like one of his friars studying animal sex, so he switched to plants. Mendel grew and studied around 29,000 garden pea plants in a monastery's garden, where he analyzed seven characteristics of the garden pea plants: flower color (purple or white), seed texture (wrinkled or round), seed color (yellow or green), stem length (long or short), pod color (yellow or green), pod texture (inflated or constricted), and flower position (axial or terminal). Based on the appearance, or phenotypes, of the seven traits, Mendel developed genotypes for those traits.

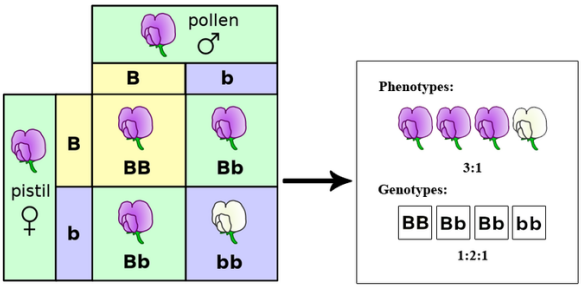


Figure **12.1.1.1**: Appearance and genetic makeup of garden pea plant flowers: Based on Mendel's experiments, the genotype of the pea flowers could be determined from the phenotypes of the flowers.

Because of Mendel's work, the fundamental principles of heredity were revealed, which are often referred to as Mendel's Laws of Inheritance. We now know that genes, carried on chromosomes, are the basic functional units of heredity with the capability to be replicated, expressed, or mutated. Today, the postulates put forth by Mendel form the basis of classical, or Mendelian, genetics. Not all genes are transmitted from parents to offspring according to Mendelian genetics, but Mendel's experiments serve as an excellent starting point for thinking about inheritance.

Mendel made all of his observations and findings crossing individual plants. We can now view a human karyotype of all of the chromosomes in an individual to visualize chromosomal abnormalities in offspring, even before birth. Shortly after Mendel proposed that traits were determined by what are now known as genes, other researchers observed that different traits were often inherited together, and thereby deduced that the genes were physically linked by being located on the same chromosome. Mendel's work was the beginning of many of the advances in molecular biology over the years.

Key Points

- Mendel studied seven characteristics of the garden pea plants: flower color, seed texture, seed color, stem length, pod color, pod texture, and flower position to develop his Laws of Inheritance.
- Genetics is the study of genes passed from parents to offspring.
- Genes are the basic fundamental units of heredity.

Key Terms

- **genetics**: The branch of biology that deals with the transmission and variation of inherited characteristics, in particular chromosomes and DNA.

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12.1.2: Mendel's Model System

Learning Objectives

- Describe the scientific reasons for the success of Mendel's experimental work

Mendel's Model System

Mendel's seminal work was accomplished using the garden pea, *Pisum sativum*, to study inheritance. Pea plant reproduction is easily manipulated; large quantities of garden peas could be cultivated simultaneously, allowing Mendel to conclude that his results did not occur simply by chance. The garden pea also grows to maturity within one season; several generations could be evaluated over a relatively short time.

Pea plants have both male and female parts and can easily be grown in large numbers. For this reason, garden pea plants can either self-pollinate or cross-pollinate with other pea plants. In the absence of outside manipulation, this species naturally self-fertilizes: ova (the eggs) within individual flowers are fertilized by pollen (containing the sperm cell) from the same flower. The sperm and the eggs that produce the next generation of plants both come from the same parent. What's more, the flower petals remain sealed tightly until after pollination, preventing pollination from other plants. The result is highly inbred, or "true-breeding," pea plants. These are plants that always produce offspring that look like the parent. Today, we know that these "true-breeding" plants are homozygous for most traits.

A gardener or researcher, such as Mendel, can cross-pollinate these same plants by manually applying sperm from one plant to the pistil (containing the ova) of another plant. Now the sperm and eggs come from different parent plants. When Mendel cross-pollinated a true-breeding plant that only produced yellow peas with a true-breeding plant that only produced green peas, he found that the first generation of offspring is always all yellow peas. The green pea trait did not show up. However, if this first generation of yellow pea plants were allowed to self-pollinate, the following or second generation had a ratio of 3:1 yellow to green peas.

In this and all the other pea plant traits Mendel followed, one form of the trait was "dominant" over another so it masked the presence of the other "recessive" form in the first generation after cross-breeding two homozygous plants.. Even if the phenotype (visible form) is hidden, the genotype (allele controlling that form of the trait) can be passed on to next generation and produce the recessive form in the second generation. By experimenting with true-breeding pea plants, Mendel avoided the appearance of unexpected (recombinant) traits in offspring that might occur if the plants were not true breeding.



Figure **12.1.2.1**: Mendel's Experiments With Peas: Experimenting with thousands of garden peas, Mendel uncovered the fundamentals of genetics.

Key Points

- Mendel used true-breeding plants in his experiments. These plants, when self-fertilized, always produce offspring with the same phenotype.
- Pea plants are easily manipulated, grow in one season, and can be grown in large quantities; these qualities allowed Mendel to conduct methodical, quantitative analyses using large sample sizes.
- Based on his experiments with the garden peas, Mendel found that one phenotype was always dominant over another recessive phenotype for the same trait.

Key Terms

- **phenotype**: the observable characteristics of an organism, often resulting from its genetic information or a combination of genetic information and environmental factors
- **genotype**: the specific genetic information of a cell or organism, usually a description of the allele or alleles relating to a specific gene.
- **true-breeding plant**: a plant that always produces offspring of the same phenotype when self-fertilized; one that is homozygous for the trait being followed.

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SECTION OVERVIEW

12.2: Monohybrid Crosses- The Principle of Segregation

12.2.1: Pedigree Analysis

12.2.2: Inferring the Mode of Inheritance

12.2.3: Phenotypes and Genotypes

12.2.4: Mendelian Crosses

12.2.5: Mendel's Law of Segregation

12.2.6: The Punnett Square Approach for a Monohybrid Cross

12.2.7: Garden Pea Characteristics Revealed the Basics of Heredity

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12.2.1: Pedigree Analysis

Pedigree charts are diagrams that show the phenotypes and/or genotypes for a particular organism and its ancestors. While commonly used in human families to track genetic diseases, they can be used for any species and any inherited trait. Geneticists use a standardized set of symbols to represent an individual's sex, family relationships and phenotype. These diagrams are used to determine the **mode of inheritance** of a particular disease or trait, and to predict the probability of its appearance among offspring. Pedigree analysis is therefore an important tool in both basic research and **genetic counseling**.

Each pedigree chart represents all of the available information about the inheritance of a single trait (most often a disease) within a family. The pedigree chart is therefore drawn using factual information, but there is always some possibility of errors in this information, especially when relying on family members' recollections or even clinical diagnoses. In real pedigrees, further complications can arise due to **incomplete penetrance** (including age of onset) and **variable expressivity** of disease alleles, but for the examples presented in this book, we will presume complete accuracy of the pedigrees. A pedigree may be drawn when trying to determine the nature of a newly discovered disease, or when an individual with a family history of a disease wants to know the probability of passing the disease on to their children. In either case, a tree is drawn, as shown in Figure **12.2.1.2**, with circles to represent females, and squares to represent males. Matings are drawn as a line joining a male and female, while a consanguineous mating (closely related is two lines.

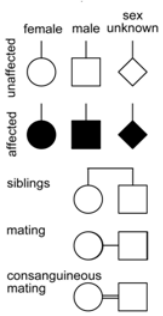


Figure **12.2.1.2**: Symbols used in drawing a pedigree. (Original-Deyholos-CC:AN)

The affected individual that brings the family to the attention of a geneticist is called the **proband** (or propositus). If an individual is known to have symptoms of the disease (**affected**), the symbol is filled in. Sometimes a half-filled in symbol is used to indicate a known **carrier** of a disease; this is someone who does not have any symptoms of the disease, but who passed the disease on to subsequent generations because they are a heterozygote. Note that when a pedigree is constructed, it is often unknown whether a particular individual is a carrier or not, so not all carriers are always explicitly indicated in a pedigree. For simplicity, in this chapter we will assume that the pedigrees presented are accurate, and represent fully penetrant traits.

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12.2.2: Inferring the Mode of Inheritance

Given a pedigree of an uncharacterized disease or trait, one of the first tasks is to determine which modes of inheritance are possible and then which mode of inheritance is most likely. This information is essential in calculating the probability that the trait will be inherited in any future offspring. We will mostly consider five major types of inheritance: autosomal dominant (AD), autosomal recessive (AR), X-linked dominant (XD), X-linked recessive (XR), and Y-linked (Y).

Autosomal Dominant (AD)

When a disease is caused by a dominant allele of a gene, every person with that allele will show symptoms of the disease (assuming complete penetrance), and only one disease allele needs to be inherited for an individual to be affected. Thus, every affected individual must have an affected parent. A pedigree with affected individuals in every generation is typical of AD diseases. However, beware that other modes of inheritance can also show the disease in every generation, as described below. It is also possible for an affected individual with an AD disease to have a family without any affected children, if the affected parent is a heterozygote. This is particularly true in small families, where the probability of every child inheriting the normal, rather than disease allele is not extremely small. Note that AD diseases are usually rare in populations, therefore affected individuals with AD diseases tend to be heterozygotes (otherwise, both parents would have had to been affected with the same rare disease). Achondroplastic dwarfism, and polydactyly are both examples of human conditions that may follow an AD mode of inheritance.

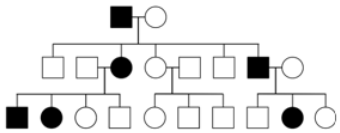


Figure **12.2.2.3**: A pedigree consistent with AD inheritance. (Original-Deyholos-CC:AN)

X-linked dominant (XD)

In X-linked dominant inheritance, the gene responsible for the disease is located on the X-chromosome, and the allele that causes the disease is dominant to the normal allele in females. Because females have twice as many X-chromosomes as males, females tend to be more frequently affected than males in the population. However, not all pedigrees provide sufficient information to distinguish XD and AD. One definitive indication that a trait is inherited as AD, and not XD, is that an affected father passes the disease to a son; this type of transmission is not possible with XD, since males inherit their X chromosome from their mothers.

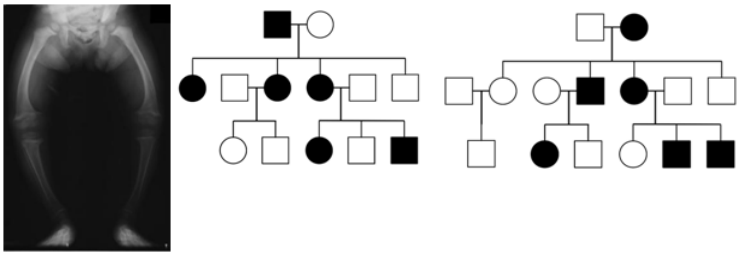


Figure **12.2.2.5**: Some types of rickets may follow an XD mode of inheritance. (Wikipedia-Mrish-CC:AS) (middle and left) Two pedigrees consistent with XD inheritance. (Original-Deyholos_CC:AN)

Autosomal recessive (AR)

Diseases that are inherited in an autosomal recessive pattern require that both parents of an affected individual carry at least one copy of the disease allele. With AR traits, many individuals in a pedigree can be carriers, probably without knowing it. Compared to pedigrees of dominant traits, AR pedigrees tend to show fewer affected individuals and are more likely than AD or XD to “skip a generation”. Thus, the major feature that distinguishes AR from AD or XD is that unaffected individuals can have affected offspring.



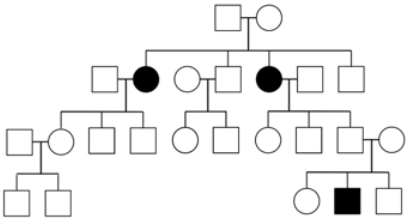
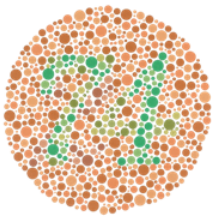


Figure **12.2.2.6**: (left) Many inborn errors of metabolism, such as phenylketonuria (PKU) are inherited as AR. Newborns are often tested for a few of the most common metabolic diseases. (Wikipedia-U.S. Air Force photo/Staff Sgt. Eric T. Sheler-PD) (right) A pedigree consistent with AR inheritance. (Original-Deyholos_CC:AN)

X-linked recessive (XR)

Because males have only one X-chromosome, any male that inherits an X-linked recessive disease allele will be affected by it (assuming complete penetrance). Therefore, in XR modes of inheritance, males tend to be affected more frequently than females in a population. This is in contrast to AR and AD, where both sexes tend to be affected equally, and XD, in which females are affected more frequently. Note, however, in the small sample sizes typical of human families, it is usually not possible to accurately determine whether one sex is affected more frequently than others. On the other hand, one feature of a pedigree that can be used to definitively establish that an inheritance pattern is not XR is the presence of an affected daughter from unaffected parents; because she would have had to inherit one X-chromosome from her father, he would also have been affected in XR.



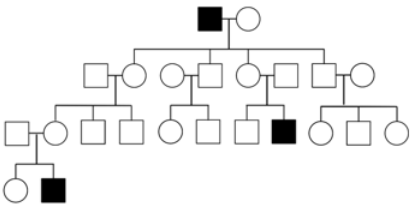


Figure **12.2.2.8**: Some forms of colour blindness are inherited as XR-traits. Colour blindness is diagnosed using tests such as this. Ishihara Test. (Wikipedia-unknown-PD) (right) A pedigree consistent with XR inheritance. (Original-Deyholos-CC:AN)

Y-linked and Mitochondrial Inheritance.

Two additional modes are **Y-linked** and **Mitochondrial inheritance**.

Only males are affected in human Y-linked inheritance (and other species with the X/Y sex determining system). There is only father to son transmission. This is the easiest mode of inheritance to identify, but it is one of the rarest because there are so few genes located on the Y-chromosome. An example of Y-linked inheritance is the **hairy-ear-rim** phenotype seen in some Indian families. As expected this trait is passed on from father to all sons and no daughters. Y-chromosome DNA polymorphisms can be used to follow the male lineage in large families or through ancient ancestral lineages. For example, the Y-chromosome of Mongolian ruler Genghis Khan (1162-1227 CE), and his male relatives, accounts for ~8% of the Y-chromosome lineage of men in Asia (0.5% world wide).

Mutations in Mitochondrial DNA are inherited through the maternal line (from your mother). There are some human diseases associated with mutations in mitochondria genes. These mutations can affect both males and females, but males cannot pass them on as the mitochondria are inherited via the egg, not the sperm. Mitochondrial DNA polymorphisms are also used to investigate evolutionary lineages, both ancient and recent. Because of the relative similarity of sequence mtDNA is also used in species identification in ecology studies.

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12.2.3: Phenotypes and Genotypes

Learning Objectives

- Distinguish between the phenotype and the genotype of an organism

Phenotypes and Genotypes

The observable traits expressed by an organism are referred to as its phenotype. An organism's underlying genetic makeup, consisting of both physically visible and non-expressed alleles, is called its genotype. Johann Gregor Mendel's (1822–1884) hybridization experiments demonstrate the difference between phenotype and genotype.

Mendel crossed or mated two true-breeding (self-pollinating) garden peas, *Pisum saivum*, by manually transferring pollen from the anther of a mature pea plant of one variety to the stigma of a separate mature pea plant of the second variety. Plants used in first-generation crosses were called P_0, or parental generation one, plants. Mendel collected the seeds belonging to the P_0plants that resulted from each cross and grew them the following season. These offspring were called the F_1, or the first filial (filial = offspring, daughter or son), generation. Once Mendel examined the characteristics in the F_1 generation of plants, he allowed them to self-fertilize naturally. He then collected and grew the seeds from the F_1 plants to produce the F_2, or second filial, generation.

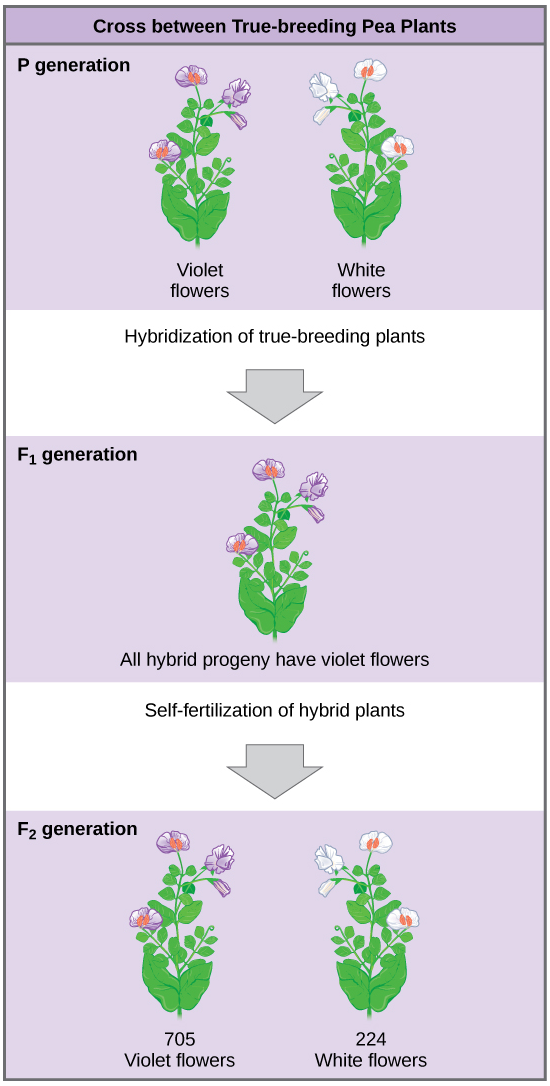


Figure **12.2.3.1**: Mendelian crosses: In one of his experiments on inheritance patterns, Mendel crossed plants that were true-breeding for violet flower color with plants true-breeding for white flower color (the P generation). The resulting hybrids in the F_1 generation all had violet flowers. In the F_2 generation, approximately three-quarters of the plants had violet flowers, and one-quarter had white flowers.

When true-breeding plants in which one parent had white flowers and one had violet flowers were cross-fertilized, all of the F1 hybrid offspring had violet flowers. That is, the hybrid offspring were phenotypically identical to the true-breeding parent with violet flowers. However, we know that the allele donated by the parent with white flowers was not simply lost because it reappeared in some of the F2 offspring. Therefore, the F1 plants must have been genotypically different from the parent with violet flowers.

In his 1865 publication, Mendel reported the results of his crosses involving seven different phenotypes, each with two contrasting traits. A trait is defined as a variation in the physical appearance of a heritable characteristic. The characteristics included plant height, seed texture, seed color, flower color, pea pod size, pea pod color, and flower position. To fully examine each characteristic, Mendel generated large numbers of F_1 and F_2 plants, reporting results from 19,959 F_2 plants alone. His findings were consistent. First, Mendel confirmed that he had plants that bred true for white or violet flower color. Regardless of how many generations Mendel examined, all self-crossed offspring of parents with white flowers had white flowers, and all self-crossed offspring of parents with violet flowers had violet flowers. In addition, Mendel confirmed that, other than flower color, the pea plants were physically identical.

Key Points

- Mendel used pea plants with seven distinct traits or phenotypes to determine the pattern of inheritance and the underlying genotypes.
- Mendel found that crossing two purebred pea plants which expressed different traits resulted in an F_1generation where all the pea plants expressed the same trait or phenotype.
- When Mendel allowed the F_1 plants to self-fertilize, the F_2 generation showed two different phenotypes, indicating that the F_1 plants had different genotypes.

Key Terms

- **phenotype**: the appearance of an organism based on a multifactorial combination of genetic traits and environmental factors, especially used in pedigrees
- **genotype**: the combination of alleles, situated on corresponding chromosomes, that determines a specific trait of an individual, such as “Aa” or “aa”

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12.2.4: Mendelian Crosses

Learning Objectives

- Identify Mendelian crosses

Mendelian Crosses

Mendel performed crosses, which involved mating two true-breeding individuals that have different traits. In the pea, which is a naturally self-pollinating plant, this is done by manually transferring pollen from the anther of a mature pea plant of one variety to the stigma of a separate mature pea plant of the second variety. In plants, pollen carries the male gametes (sperm) to the stigma, a sticky organ that traps pollen and allows the sperm to move down the pistil to the female gametes (ova) below. To prevent the pea plant that was receiving pollen from self-fertilizing and confounding his results, Mendel painstakingly removed all of the anthers from the plant's flowers before they had a chance to mature.

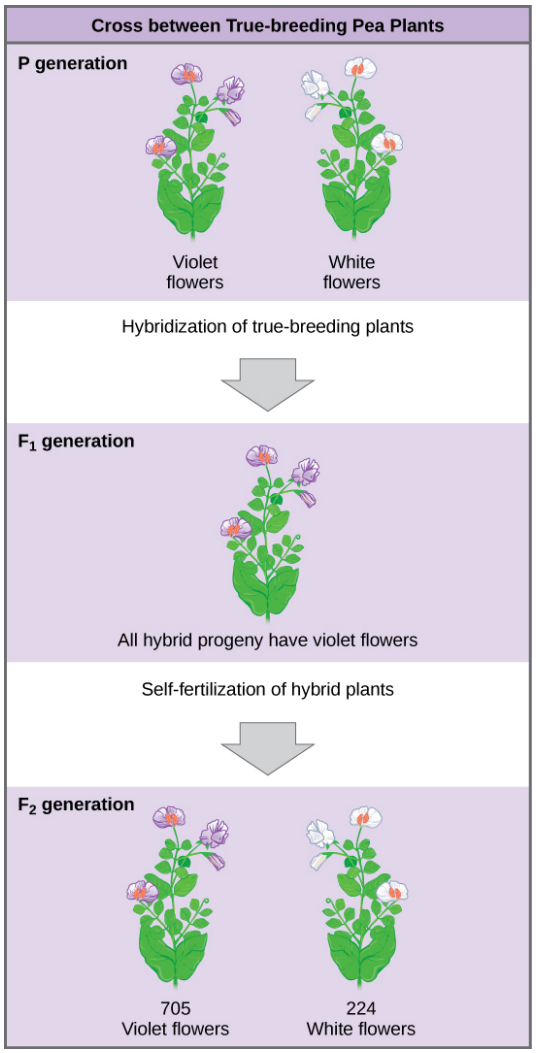


Figure 12.2.4.1: Mendelian Crosses: In one of his experiments on inheritance patterns, Mendel crossed plants that were true-breeding for violet flower color with plants true-breeding for white flower color (the P generation). The resulting hybrids in the F1 generation all had violet flowers. In the F2 generation, approximately three-quarters of the plants had violet flowers, while one-quarter had white flowers.

Plants used in first-generation crosses were called P_0, or parental generation one, plants. Mendel collected the seeds belonging to the P_0 plants that resulted from each cross and grew them the following season. These offspring were called the F_1, or the first filial (filial = offspring, daughter or son), generation. Once Mendel examined the characteristics in the F_1generation of plants, he allowed

them to self-fertilize naturally. He then collected and grew the seeds from the F_1 plants to produce the F_2, or second filial, generation. Mendel's experiments extended beyond the F_2 generation to the F_3 and F_4generations, and so on, but it was the ratio of characteristics in the P_0−F_1−F_2 generations that were the most intriguing and became the basis for Mendel's postulates.

Key Points

- Mendel carefully controlled his experiments by removing the anthers from the pea plants before they matured.
- First generation pea plants were called parental generation, P_0, while the following generations were called filial, F_n, where n is the number of generations from P_0.
- The ratio of characteristics in the P_0−F_1−F_2 generations became the basis for Mendel's postulates.

Key Terms

- **filial**: of a generation or generations descending from a specific previous one
- **parental**: of the generation of organisms that produce a hybrid

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12.2.5: Mendel's Law of Segregation

Learning Objectives

- Apply the law of segregation to determine the chances of a particular genotype arising from a genetic cross

Equal Segregation of Alleles

Observing that true-breeding pea plants with contrasting traits gave rise to F_1 generations that all expressed the dominant trait and F_2 generations that expressed the dominant and recessive traits in a 3:1 ratio, Mendel proposed the law of segregation. The law of segregation states that each individual that is a diploid has a pair of alleles (copy) for a particular trait. Each parent passes an allele at random to their offspring resulting in a diploid organism. The allele that contains the dominant trait determines the phenotype of the offspring. In essence, the law states that copies of genes separate or segregate so that each gamete receives only one allele.

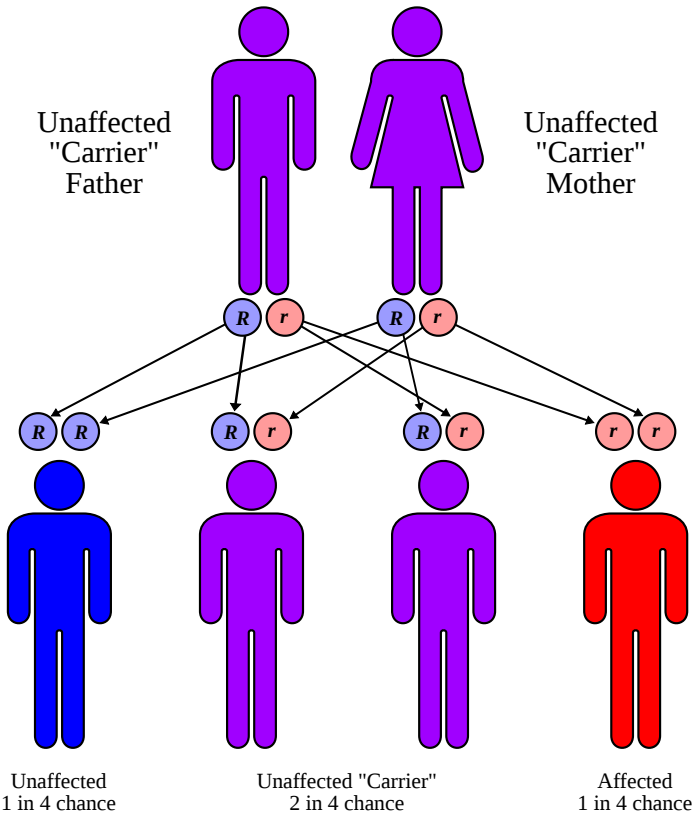


Figure **12.2.5.1**: The Law of Segregation states that alleles segregate randomly into gametes: When gametes are formed, each allele of one parent segregates randomly into the gametes, such that half of the parent's gametes carry each allele.

For the F_2 generation of a monohybrid cross, the following three possible combinations of genotypes could result: homozygous dominant, heterozygous, or homozygous recessive. Because heterozygotes could arise from two different pathways (receiving one dominant and one recessive allele from either parent), and because heterozygotes and homozygous dominant individuals are phenotypically identical, the law supports Mendel's observed 3:1 phenotypic ratio. The equal segregation of alleles is the reason we can apply the Punnett square to accurately predict the offspring of parents with known genotypes.

The physical basis of Mendel's law of segregation is the first division of meiosis in which the homologous chromosomes with their different versions of each gene are segregated into daughter nuclei. The behavior of homologous chromosomes during meiosis can account for the segregation of the alleles at each genetic locus to different gametes. As chromosomes separate into different gametes during meiosis, the two different alleles for a particular gene also segregate so that each gamete acquires one of the two alleles. In Mendel's experiments, the segregation and the independent assortment during meiosis in the F1 generation give rise to

the F2 phenotypic ratios observed by Mendel. The role of the meiotic segregation of chromosomes in sexual reproduction was not understood by the scientific community during Mendel's lifetime.

Key Points

- Each gamete acquires one of the two alleles as chromosomes separate into different gametes during meiosis.
- Heterozygotes, which posess one dominant and one recessive allele, can receive each allele from either parent and will look identical to homozygous dominant individuals; the Law of Segregation supports Mendel's observed 3:1 phenotypic ratio.
- Mendel proposed the Law of Segregation after observing that pea plants with two different traits produced offspring that all expressed the dominant trait, but the following generation expressed the dominant and recessive traits in a 3:1 ratio.

Key Terms

- **law of segregation**: a diploid individual possesses a pair of alleles for any particular trait and each parent passes one of these randomly to its offspring

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12.2.6: The Punnett Square Approach for a Monohybrid Cross

Learning Objectives

- Describe the Punnett square approach to a monohybrid cross

Punnett Square Approach to a Monohybrid Cross

When fertilization occurs between two true-breeding parents that differ in only one characteristic, the process is called a monohybrid cross, and the resulting offspring are monohybrids. Mendel performed seven monohybrid crosses involving contrasting traits for each characteristic. On the basis of his results in F_1 and F_2 generations, Mendel postulated that each parent in the monohybrid cross contributed one of two paired unit factors to each offspring and that every possible combination of unit factors was equally likely.

To demonstrate a monohybrid cross, consider the case of true-breeding pea plants with yellow versus green pea seeds. The dominant seed color is yellow; therefore, the parental genotypes were YY (homozygous dominant) for the plants with yellow seeds and yy (homozygous recessive) for the plants with green seeds, respectively. A Punnett square, devised by the British geneticist Reginald Punnett, can be drawn that applies the rules of probability to predict the possible outcomes of a genetic cross or mating and their expected frequencies.To prepare a Punnett square, all possible combinations of the parental alleles are listed along the top (for one parent) and side (for the other parent) of a grid, representing their meiotic segregation into haploid gametes. Then the combinations of egg and sperm are made in the boxes in the table to show which alleles are combining. Each box then represents the diploid genotype of a zygote, or fertilized egg, that could result from this mating. Because each possibility is equally likely, genotypic ratios can be determined from a Punnett square. If the pattern of inheritance (dominant or recessive) is known, the phenotypic ratios can be inferred as well. For a monohybrid cross of two true-breeding parents, each parent contributes one type of allele. In this case, only one genotype is possible. All offspring are Yy and have yellow seeds.

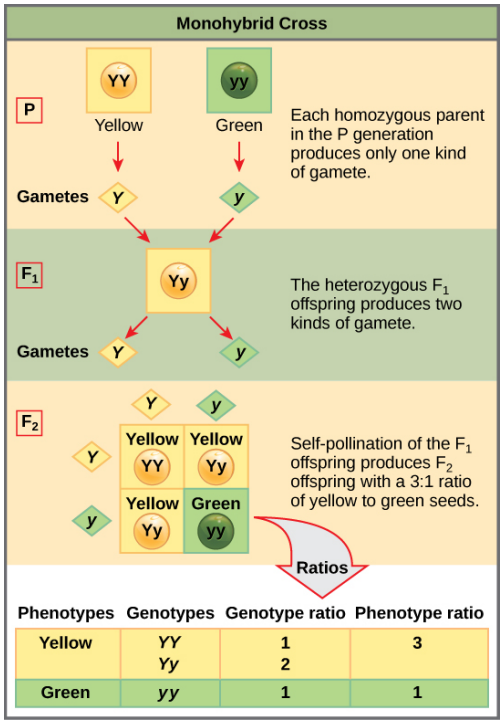


Figure **12.2.6.1**: Punnett square analysis of a monohytbrid cross: In the P generation, pea plants that are true-breeding for the dominant yellow phenotype are crossed with plants with the recessive green phenotype. This cross produces F1 heterozygotes with a yellow phenotype. Punnett square analysis can be used to predict the genotypes of the F2 generation.

A self-cross of one of the Yy heterozygous offspring can be represented in a 2 × 2 Punnett square because each parent can donate one of two different alleles. Therefore, the offspring can potentially have one of four allele combinations: YY, Yy, yY, or yy. Notice that there are two ways to obtain the Yy genotype: a Y from the egg and a y from the sperm, or a y from the egg and a Y from the

sperm. Both of these possibilities must be counted. Recall that Mendel's pea-plant characteristics behaved in the same way in reciprocal crosses. Therefore, the two possible heterozygous combinations produce offspring that are genotypically and phenotypically identical despite their dominant and recessive alleles deriving from different parents. They are grouped together. Because fertilization is a random event, we expect each combination to be equally likely and for the offspring to exhibit a ratio of YY:Yy:yy genotypes of 1:2:1. Furthermore, because the YY and Yy offspring have yellow seeds and are phenotypically identical, applying the sum rule of probability, we expect the offspring to exhibit a phenotypic ratio of 3 yellow:1 green. Indeed, working with large sample sizes, Mendel observed approximately this ratio in every F_2 generation resulting from crosses for individual traits.

Beyond predicting the offspring of a cross between known homozygous or heterozygous parents, Mendel also developed a way to determine whether an organism that expressed a dominant trait was a heterozygote or a homozygote. Called the test cross, this technique is still used by plant and animal breeders. In a test cross, the dominant-expressing organism is crossed with an organism that is homozygous recessive for the same characteristic. If the dominant-expressing organism is a homozygote, then all F_1 offspring will be heterozygotes expressing the dominant trait. Alternatively, if the dominant expressing organism is a heterozygote, the F_1 offspring will exhibit a 1:1 ratio of heterozygotes and recessive homozygotes. The test cross further validates Mendel's postulate that pairs of unit factors segregate equally.

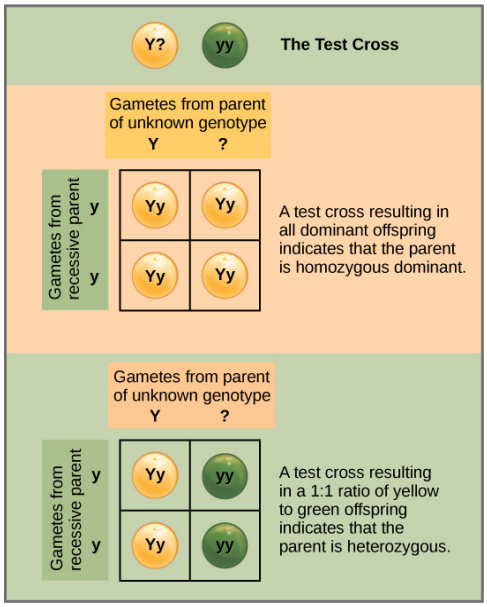


Figure **12.2.6.1**: Example of a test cross: A test cross can be performed to determine whether an organism expressing a dominant trait is a homozygote or a heterozygote.

Key Points

- Fertilization between two true-breeding parents that differ in only one characteristic is called a monohybrid cross.
- For a monohybrid cross of two true-breeding parents, each parent contributes one type of allele resulting in all of the offspring with the same genotype.
- A test cross is a way to determine whether an organism that expressed a dominant trait was a heterozygote or a homozygote.

Key Terms

- **monohybrid**: a hybrid between two species that only have a difference of one gene
- **homozygous**: of an organism in which both copies of a given gene have the same allele
- **heterozygous**: of an organism which has two different alleles of a given gene
- **Punnett square**: a graphical representation used to determine the probability of an offspring expressing a particular genotype

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12.2.7: Garden Pea Characteristics Revealed the Basics of Heredity

Learning Objectives

- Evaluate the results of F1 and F2 generations from Mendelian crosses of peas

Garden Pea Characteristics Revealed the Basics of Heredity

To fully examine each of the seven traits in garden peas, Mendel generated large numbers of F_1 and F_2 plants, reporting results from 19,959 F_2 plants alone. His findings were consistent.

What results did Mendel find in his crosses for flower color? First, Mendel confirmed that he had plants that bred true for white or violet flower color. Regardless of how many generations Mendel examined, all self-crossed offspring of parents with white flowers had white flowers, and all self-crossed offspring of parents with violet flowers had violet flowers. In addition, Mendel confirmed that, other than flower color, the pea plants were physically identical.

Once these validations were complete, Mendel applied the pollen from a plant with violet flowers to the stigma of a plant with white flowers. After gathering and sowing the seeds that resulted from this cross, Mendel found that 100 percent of the F_1hybrid generation had violet flowers. Conventional wisdom at that time would have predicted the hybrid flowers to be pale violet or for hybrid plants to have equal numbers of white and violet flowers. In other words, the contrasting parental traits were expected to blend in the offspring. Instead, Mendel's results demonstrated that the white flower trait in the F_1 generation had completely disappeared.

Importantly, Mendel did not stop his experimentation there. He allowed the F_1 plants to self-fertilize and found that, of F_2-generation plants, 705 had violet flowers and 224 had white flowers. This was a ratio of 3.15 violet flowers per one white flower, or approximately 3:1. When Mendel transferred pollen from a plant with violet flowers to the stigma of a plant with white flowers and vice versa, he obtained about the same ratio regardless of which parent, male or female, contributed which trait. This is called a reciprocal cross: a paired cross in which the respective traits of the male and female in one cross become the respective traits of the female and male in the other cross. For the other six characteristics Mendel examined, the F_1 and F_2generations behaved in the same way as they had for flower color. One of the two traits would disappear completely from the F_1 generation only to reappear in the F_2 generation at a ratio of approximately 3:1.

Upon compiling his results for many thousands of plants, Mendel concluded that the characteristics could be divided into expressed and latent traits. He called these, respectively, dominant and recessive traits. Dominant traits are those that are inherited unchanged in a hybridization. Recessive traits become latent, or disappear, in the offspring of a hybridization. The recessive trait does, however, reappear in the progeny of the hybrid offspring. An example of a dominant trait is the violet-flower trait. For this same characteristic (flower color), white-colored flowers are a recessive trait. The fact that the recessive trait reappeared in the F_2 generation meant that the traits remained separate (not blended) in the plants of the F_1 generation. Mendel also proposed that plants possessed two copies of the trait for the flower-color characteristic and that each parent transmitted one of its two copies to its offspring, where they came together. Moreover, the physical observation of a dominant trait could mean that the genetic composition of the organism included two dominant versions of the characteristic or that it included one dominant and one recessive version. Conversely, the observation of a recessive trait meant that the organism lacked any dominant versions of this characteristic.

The Results of Mendel's Garden Pea Hybridizations				
Characteristic	**Contrasting P0 Traits**	**F1 Offspring Traits**	**F2 Offspring Traits**	**F2 Trait Ratios**
Flower color	Violet vs. white	100 percent violet	705 violet 224 white	3.15:1
Flower position	Axial vs. terminal	100 percent axial	651 axial 207 terminal	3.14:1
Plant height	Tall vs. dwarf	100 percent tall	787 tall 277 dwarf	2.84:1
Seed texture	Round vs. wrinkled	100 percent round	5,474 round 1,850 wrinkled	2.96:1
Seed color	Yellow vs. green	100 percent yellow	6,022 yellow 2,001 green	3.01:1
Pea pod texture	Inflated vs. constricted	100 percent inflated	882 inflated 299 constricted	2.95:1
Pea pod color	Green vs. yellow	100 percent green	428 green 152 yellow	2.82:1

Figure **12.2.7.1**: Results of Mendel's Garden Pea Hybridizations: Mendel conducted thousands of experiments and found the same ratios of offspring every time, regardless of which trait he examined.

Key Points

- Dominant traits are inherited unchanged from one generation to the next.
- Recessive traits disappear in the first filial generation, but reappear in the second filial generation at a ratio of 3:1, dominant:recessive.
- In the F1 generation, Mendel found that one of the two options for each trait had disappeared (all offspring were identical phenotypes), while in the F_2 generation, the trait reappeared in 1/4 of the offspring (a 3:1 ratio).

Key Terms

- **hybrid**: offspring resulting from cross-breeding different entities, e.g. two different species or two purebred parent strains
- **recessive**: able to be covered up by a dominant trait
- **dominant**: a relationship between alleles of a gene, in which one allele masks the expression (phenotype) of another allele at the same locus

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12.3: Dihybrid Crosses and Mendel's Law of Independent Assortment

Learning Objectives

- Use the probability or forked line method to calculate the chance of any particular genotype arising from a genetic cross

Independent Assortment

Mendel's law of independent assortment states that genes do not influence each other with regard to the sorting of alleles into gametes: every possible combination of alleles for every gene is equally likely to occur. The independent assortment of genes can be illustrated by the dihybrid cross: a cross between two true-breeding parents that express different traits for two characteristics. Consider the characteristics of seed color and seed texture for two pea plants: one that has green, wrinkled seeds (yyrr) and another that has yellow, round seeds (YYRR). Because each parent is homozygous, the law of segregation indicates that the gametes for the green/wrinkled plant all are yr, while the gametes for the yellow/round plant are all YR. Therefore, the F_1 generation of offspring all are YyRr.

For the F2 generation, the law of segregation requires that each gamete receive either an R allele or an r allele along with either a Y allele or a y allele. The law of independent assortment states that a gamete into which an r allele sorted would be equally likely to contain either a Y allele or a y allele. Thus, there are four equally likely gametes that can be formed when the YyRr heterozygote is self-crossed as follows: YR, Yr, yR, and yr. Arranging these gametes along the top and left of a 4 × 4 Punnett square gives us 16 equally likely genotypic combinations. From these genotypes, we infer a phenotypic ratio of 9 round/yellow:3 round/green:3 wrinkled/yellow:1 wrinkled/green. These are the offspring ratios we would expect, assuming we performed the crosses with a large enough sample size.

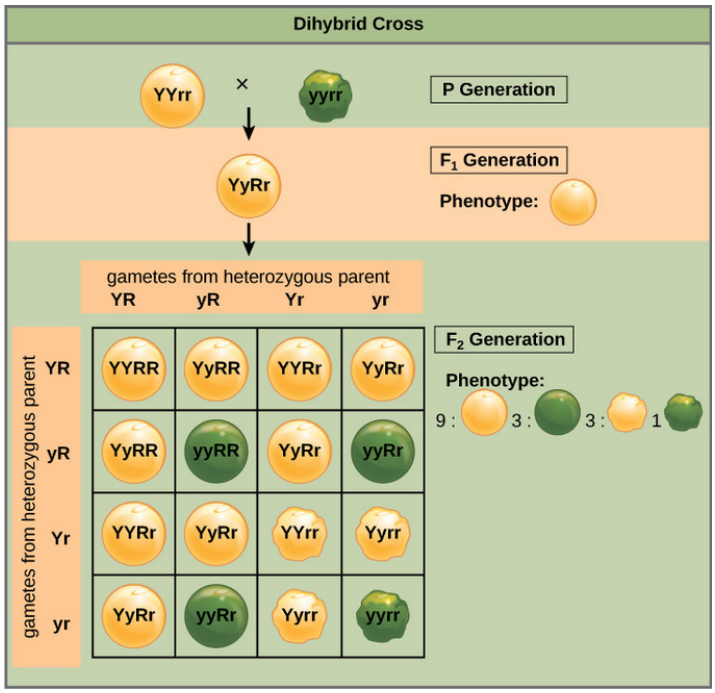


Figure **12.3.1**: Independent assortment of 2 genes: This dihybrid cross of pea plants involves the genes for seed color and texture.

Because of independent assortment and dominance, the 9:3:3:1 dihybrid phenotypic ratio can be collapsed into two 3:1 ratios, characteristic of any monohybrid cross that follows a dominant and recessive pattern. Ignoring seed color and considering only seed texture in the above dihybrid cross, we would expect that three-quarters of the F_2 generation offspring would be round and one-quarter would be wrinkled. Similarly, isolating only seed color, we would assume that three-quarters of the F_2offspring would be yellow and one-quarter would be green. The sorting of alleles for texture and color are independent events, so we can apply the product rule. Therefore, the proportion of round and yellow F_2 offspring is expected to be (3/4) × (3/4) = 9/16, and the proportion of wrinkled and green offspring is expected to be (1/4) × (1/4) = 1/16. These proportions are identical to those obtained using a

Punnett square. Round/green and wrinkled/yellow offspring can also be calculated using the product rule as each of these genotypes includes one dominant and one recessive phenotype. Therefore, the proportion of each is calculated as (3/4) × (1/4) = 3/16.

Forked-Line Method

When more than two genes are being considered, the Punnett-square method becomes unwieldy. For instance, examining a cross involving four genes would require a 16 × 16 grid containing 256 boxes. It would be extremely cumbersome to manually enter each genotype. For more complex crosses, the forked-line and probability methods are preferred.

To prepare a forked-line diagram for a cross between F_1 heterozygotes resulting from a cross between AABBCC and aabbcc parents, we first create rows equal to the number of genes being considered and then segregate the alleles in each row on forked lines according to the probabilities for individual monohybrid crosses. We then multiply the values along each forked path to obtain the F_2 offspring probabilities. Note that this process is a diagrammatic version of the product rule. The values along each forked pathway can be multiplied because each gene assorts independently. For a trihybrid cross, the F_2phenotypic ratio is 27:9:9:9:3:3:3:1.

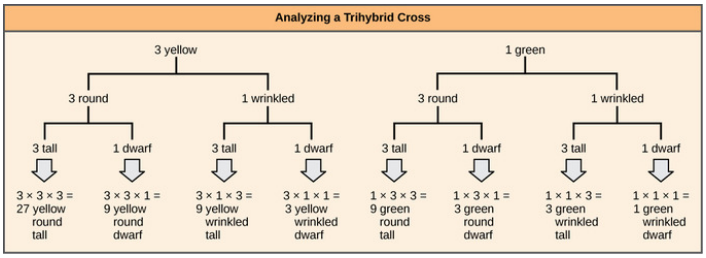


Figure **12.3.1**: Independent assortment of 3 genes: The forked-line method can be used to analyze a trihybrid cross. Here, the probability for color in the F2 generation occupies the top row (3 yellow:1 green). The probability for shape occupies the second row (3 round:1 wrinked), and the probability for height occupies the third row (3 tall:1 dwarf). The probability for each possible combination of traits is calculated by multiplying the probability for each individual trait. Thus, the probability of F2 offspring having yellow, round, and tall traits is 3 × 3 × 3, or 27.

Probability Method

While the forked-line method is a diagrammatic approach to keeping track of probabilities in a cross, the probability method gives the proportions of offspring expected to exhibit each phenotype (or genotype) without the added visual assistance.

To fully demonstrate the power of the probability method, however, we can consider specific genetic calculations. For instance, for a tetrahybrid cross between individuals that are heterozygotes for all four genes, and in which all four genes are sorting independently in a dominant and recessive pattern, what proportion of the offspring will be expected to be homozygous recessive for all four alleles? Rather than writing out every possible genotype, we can use the probability method. We know that for each gene the fraction of homozygous recessive offspring will be 1/4. Therefore, multiplying this fraction for each of the four genes, (1/4) × (1/4) × (1/4) × (1/4), we determine that 1/256 of the offspring will be quadruply homozygous recessive.

Key Points

- Mendel's law of independent assortment states that genes do not influence each other with regard to the sorting of alleles into gametes; every possible combination of alleles for every gene is equally likely to occur.
- The calculation of any particular genotypic combination of more than one gene is, therefore, the probability of the desired genotype at the first locus multiplied by the probability of the desired genotype at the other loci.
- The forked line method can be used to calculate the chances of all possible genotypic combinations from a cross, while the probability method can be used to calculate the chance of any one particular genotype that might result from that cross.

Key Terms

- **independent assortment**: separate genes for separate traits are passed independently of one another from parents to offspring

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12.4: Rules of Probability for Mendelian Inheritance

Learning Objectives

- Calculate the probability of traits of pea plants using Mendelian crosses

Probability Basics

Probabilities are mathematical measures of likelihood. The empirical probability of an event is calculated by dividing the number of times the event occurs by the total number of opportunities for the event to occur. Empirical probabilities come from observations such as those of Mendel. An example of a genetic event is a round seed produced by a pea plant. Mendel demonstrated that the probability of the event "round seed" was guaranteed to occur in the F_1 offspring of true-breeding parents, one of which has round seeds and one of which has wrinkled seeds. When the F_1 plants were subsequently self-crossed, the probability of any given F_2 offspring having round seeds was now three out of four. In other words, in a large population of F_2 offspring chosen at random, 75 percent were expected to have round seeds, whereas 25 percent were expected to have wrinkled seeds. Using large numbers of crosses, Mendel was able to calculate probabilities and use these to predict the outcomes of other crosses.

The Product Rule

Mendel demonstrated that the pea-plant characteristics he studied were transmitted as discrete units from parent to offspring. Mendel also determined that different characteristics were transmitted independently of one another and could be considered in separate probability analyses. For instance, performing a cross between a plant with green, wrinkled seeds and a plant with yellow, round seeds produced offspring that had a 3:1 ratio of green:yellow seeds and a 3:1 ratio of round:wrinkled seeds. The characteristics of color and texture did not influence each other.

The product rule of probability can be applied to this phenomenon of the independent transmission of characteristics. It states that the probability of two independent events occurring together can be calculated by multiplying the individual probabilities of each event occurring alone. Imagine that you are rolling a six-sided die (D) and flipping a penny (P) at the same time. The die may roll any number from 1–6 ($D_{\#}$), whereas the penny may turn up heads (P_H) or tails (P_T). The outcome of rolling the die has no effect on the outcome of flipping the penny and vice versa. There are 12 possible outcomes, and each is expected to occur with equal probability: D_1P_H, D_1P_T, D_2P_H, D_2P_T, D_3P_H, D_3P_T, D_4P_H, D_4P_T, D_5P_H, D_5P_T, D_6P_H, D_6P_T.

Of the 12 possible outcomes, the die has a 2/12 (or 1/6) probability of rolling a two, and the penny has a 6/12 (or 1/2) probability of coming up heads. The probability that you will obtain the combined outcome 2 and heads is: $(D_2) \times (P_H) = (1/6) \times (1/2)$ or 1/12. The word "and" is a signal to apply the product rule. Consider how the product rule is applied to a dihybrid: the probability of having both dominant traits in the F_2 progeny is the product of the probabilities of having the dominant trait for each characteristic.

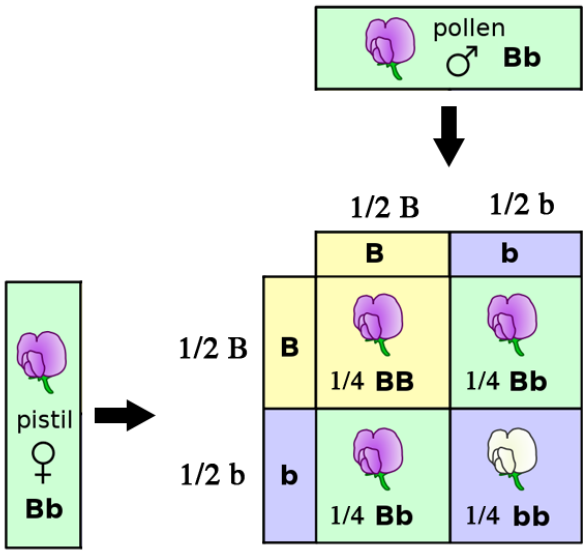


Figure **12.4.1**: Role of probability in segregation of alleles and fertilization: In a genetic cross, the probability of the dominant trait being expressed is dependent upon its frequency. In this case, both parents possessed a dominant and a recessive gene for the trait of flower color. The dominant trait is expressed in 3/4 of the offspring and the recessive trait is expressed in 1/4.

The Sum Rule

The sum rule is applied when considering two mutually-exclusive outcomes that can result from more than one pathway. It states that the probability of the occurrence of one event or the other, of two mutually-exclusive events, is the sum of their individual probabilities. The word "or" indicates that you should apply the sum rule. Let's imagine you are flipping a penny (P) and a quarter (Q). What is the probability of one coin coming up heads and one coming up tails? This can be achieved by two cases: the penny is heads (P_H) and the quarter is tails (Q_T), or the quarter is heads (Q_H) and the penny is tails (P_T). Either case fulfills the outcome. We calculate the probability of obtaining one head and one tail as $[(P_H) \times (Q_T)] + [(Q_H) \times (P_T)] = [(1/2) \times (1/2)] + [(1/2) \times (1/2)] = 1/2$. You should also notice that we used the product rule to calculate the probability of P_H and Q_T and also the probability of P_T and Q_H, before we summed them. The sum rule can be applied to show the probability of having just one dominant trait in the F_2 generation of a dihybrid cross.

To use probability laws in practice, it is necessary to work with large sample sizes because small sample sizes are prone to deviations caused by chance. The large quantities of pea plants that Mendel examined allowed him to calculate the probabilities of the traits appearing in his F_2 generation. This discovery meant that when parental traits were known, the offspring's traits could be predicted accurately even before fertilization.

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Key Points

- The Product Rule is used to determine the outcome of an event with two independent events; the probability of the event is the product of the probabilities of each individual event.
- The Sum Rule is used to determine the outcome of an event with two mutually exclusive events from multiple pathways; the probability of the event is the sum of the probabilities of each individual event.
- The Product Rule of probability is used to determine the probability of having both dominant traits in the F_2progeny; it is the product of the probabilities of having the dominant trait for each characteristic.
- The Sum Rule of probability is used to determine the probability of having one dominant trait in the F2 generation of a dihybrid cross; it is the sum of the probabilities of each individual with that trait.

Key Terms

- **sum rule**: the probability of the occurrence of one event or the other event, of two mutually exclusive events, is the sum of their individual probabilities
- **product rule**: the probability of two independent events occurring together can be calculated by multiplying the individual probabilities of each event occurring alone

- **probability**: a number, between 0 and 1, expressing the precise likelihood of an event happening

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12.5: Crossing Techniques Revealing Unknown Genotypes

Classical Genetics

Not only did Mendel solve the mystery of inheritance as units (genes), he also invented several testing and analysis techniques still used today. **Classical genetics** is the science of solving biological questions using controlled matings of model organisms. It began with Mendel in 1865 but did not take off until Thomas Morgan began working with fruit flies in 1908. Later, starting with Watson and Crick's structure of DNA in 1953, classical genetics was joined by **molecular genetics**, the science of solving biological questions using DNA, RNA, and proteins isolated from organisms. The genetics of **DNA cloning** began in 1970 with the discovery of restriction enzymes.

True Breeding Lines

Geneticists make use of **true breeding lines** just as Mendel did (Figure 12.5.6a). These are in-bred populations of plants or animals in which all parents and their offspring (over many generations) have the same phenotypes with respect to a particular trait. True breeding lines are useful, because they are typically assumed to be homozygous for the alleles that affect the trait of interest. When two individuals that are homozygous for the same alleles are crossed, all of their offspring will all also be homozygous. The continuation of such crosses constitutes a true breeding line or strain. A large variety of different strains, each with a different, true breeding character, can be collected and maintained for genetic research.

Monohybrid Crosses

A **monohybrid cross** is one in which both parents are heterozygous (or a hybrid) for a single (mono) trait. The trait might be petal colour in pea plants (Figure 12.5.6b). Recall from chapter 1 that the generations in a cross are named P (parental), F_1 (first filial), F_2 (second filial), and so on.

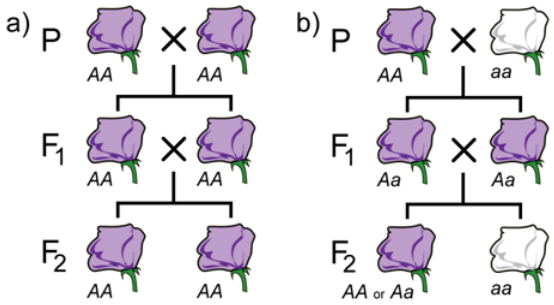


Figure 12.5.6: (a) A true-breeding line **(b)** A monohybrid cross produced by mating two different pure-breeding lines. (Original-Deholos-CC:AN)

Punnett Squares

Given the genotypes of any two parents, we can predict all of the possible genotypes of the offspring. Furthermore, if we also know the dominance relationships for all of the alleles, we can predict the phenotypes of the offspring. A convenient method for calculating the expected genotypic and phenotypic ratios from a cross was invented by Reginald Punnett. A **Punnett square** is a matrix in which all of the possible gametes produced by one parent are listed along one axis, and the gametes from the other parent are listed along the other axis. Each possible combination of gametes is listed at the intersection of each row and column. The F_1 cross from Figure 12.5.6b would be drawn as in Figure 12.5.7. Punnett squares can also be used to calculate the frequency of offspring. The frequency of each offspring is the frequency of the male gametes multiplied by the frequency of the female gamete.

	A	***a***
A	*AA*	*Aa*
a	*Aa*	*aa*

Figure 12.5.7: *A Punnett square showing a monohybrid cross.* (Original-Deholos (Fireworks)-CC:AN)

Test Crosses

Knowing the genotypes of an individual is usually an important part of a genetic experiment. However, genotypes cannot be observed directly; they must be inferred based on phenotypes. Because of dominance, it is often not possible to distinguish between a heterozygote and a homozgyote based on phenotype alone (e.g. see the purple-flowered F_2 plants in Figure **12.5.6**b). To determine the genotype of a specific individual, a **test cross** can be performed, in which the individual with an uncertain genotype is crossed with an individual that is homozygous recessive for all of the loci being tested.

For example, if you were given a pea plant with purple flowers it might be a homozygote (*AA*) or a heterozygote (*Aa*). You could cross this purple-flowered plant to a white-flowered plant as a **tester**, since you know the genotype of the tester is *aa*. Depending on the genotype of the purple-flowered parent (Figure **12.5.8**), you will observe different phenotypic ratios in the F_1 generation. If the purple-flowered parent was a homozgyote, all of the F_1 progeny will be purple. If the purple-flowered parent was a heterozygote, the F_1 progeny should segregate purple-flowered and white-flowered plants in a 1:1 ratio.

	A	***A***
a	*Aa*	*Aa*
a	*Aa*	*Aa*

	A	***a***
a	*Aa*	*aa*
a	*Aa*	*aa*

Figure* 12.5.8*: *Punnett Squares showing the two possible outcomes of a test cross.* (Original-Deholos (Fireworks)-CC:AN)

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SECTION OVERVIEW

12.6: Extensions to Mendel

12.6.1: Complex Inheritance

12.6.2: Quantitative Trait Loci

12.6.3: Pleiotropy

12.6.4: Alternatives to Dominance and Recessiveness

12.6.5: Epistasis

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12.6.1: COMPLEX INHERITANCE

FAMILY PORTRAIT

This photo of a South African family shows some of the variations that exist in human skin color. The color of human skin can range from very light to very dark with every possible gradation in between. As you might expect, the skin color trait has a more complex genetic basis than just one gene with two alleles, which is the type of simple trait that Mendel studied in pea plants. Like skin color, many other human traits have more complicated modes of inheritance than Mendelian traits. Such modes of inheritance are called **non-Mendelian inheritance,** and they include inheritance of multiple allele traits, traits with codominance or incomplete dominance, and polygenic traits, among others, all of which are described below.



Figure **12.6.1.1**: Family

MULTIPLE ALLELE TRAITS

The majority of human genes are thought to have more than two normal versions or alleles. Traits controlled by a single gene with more than two alleles are called **multiple allele traits**. An example is ABO blood type. Your blood type refers to which of certain proteins called antigens are found on your red blood cells. There are three common alleles for this trait, which are represented by the letters I^A, I^B, and i.

Table **12.6.1.1**: ABO Blood Group

Genotype	Phenotype (blood type)
I^AI^A	A
I^Ai	A
I^BI^B	B
I^Bi	B
ii	O
I^AI^B	AB

As shown in the table below, there are six possible ABO genotypes because the three alleles, taken two at a time, result in six possible combinations. The IA and IB alleles are dominant to the i allele. As a result, both I^AI_A and I^Ai genotypes have the same phenotype, with the A antigen in their blood (type A blood). Similarly, both I^BI^B and I^Bi genotypes have the same phenotype, with the B antigen in their blood (type B blood). No antigen is associated with the i allele, so people with the ii genotype have no antigens for ABO blood type in their blood (type O blood).

CODOMINANCE

Look at the genotype I^AI^B in the ABO blood group table. Alleles I^A and I^B for ABO blood type are neither dominant nor recessive to one another. Instead, they are codominant to each other. **Codominance** occurs when two alleles for a gene are expressed equally in the phenotype of heterozygotes. In the case of ABO blood type, I^AI^B heterozygotes have a unique phenotype, with both A and B antigens in their blood (type AB blood).

INCOMPLETE DOMINANCE

Another relationship that may occur between alleles for the same gene is **incomplete dominance.** This occurs when the dominant allele is not completely dominant, so an intermediate phenotype results in heterozygotes who inherit both alleles. Generally, this happens when the two alleles for a given gene both produce proteins but one protein is not functional. As a result, the heterozygote individual produces only half the amount of normal protein as is produced by an individual who is homozygous for the normal allele.

An example of incomplete dominance in humans is Tay Sachs disease. The normal allele for the gene, in this case, produces an enzyme that is responsible for breaking down lipids. A defective allele for the gene results in the production of a nonfunctional enzyme. Heterozygotes who have one normal and one defective allele produce half as much functional enzyme as the normal homozygote, and this is enough for normal development. However, homozygotes who have only defective alleles produce only the nonfunctional enzyme. This leads to the accumulation of lipids in the brain beginning *in utero*, which causes significant brain damage. Most individuals with Tay Sachs disease die at a young age, typically by the age of five years.

POLYGENIC TRAITS

Many human traits are controlled by more than one gene. These traits are called **polygenic traits**. The alleles of each gene have a minor additive effect on the phenotype. There are many possible combinations of alleles, especially if each gene has multiple alleles. Therefore, a whole continuum of phenotypes is possible.

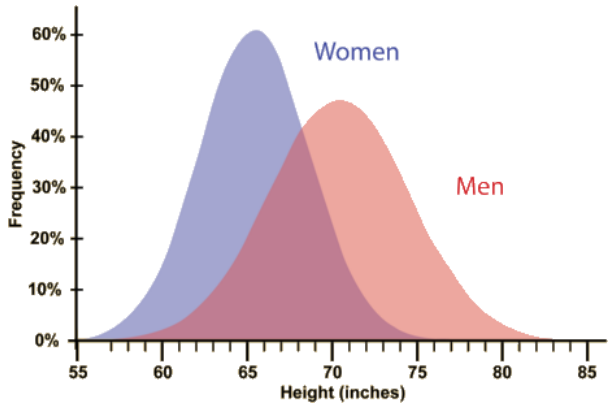


Figure **12.6.1.2**. Human Adult Height. Like many other polygenic traits, adult height has a bell-shaped distribution.

An example of a human polygenic trait is adult height. Several genes, each with more than one allele, contribute to this trait, so there are many possible adult heights. For example, one adult's height might be 1.655 m (5.430 feet), and another adult's height might be 1.656 m (5.433 feet). Adult height ranges from less than 5 feet to more than 6 feet, with males being somewhat taller than females on average. The majority of people fall near the middle of the range of heights for their sex, as shown in the graph in Figure **12.6.1.2**.

ENVIRONMENTAL EFFECTS ON PHENOTYPE

Many traits are affected by the environment as well as by genes. This may be especially true for polygenic traits. For example, adult height might be negatively impacted by poor diet or illness during childhood. Skin color is another polygenic trait. There is a wide range of skin colors in people worldwide. In addition to differences in skin color genes, differences in exposure to ultraviolet (UV) light cause some of the variations. As shown in *Figure* **12.6.1.3**, exposure to UV light darkens the skin.

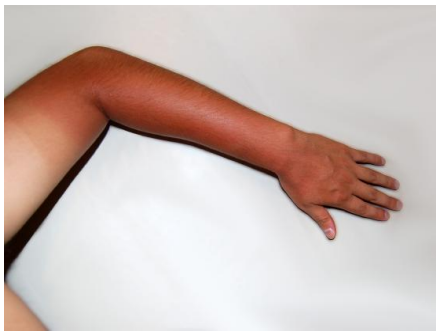


Figure **12.6.1.3**: Skin on the lower part of the arm is much darker in color than protected skin near the top due to the effects of UV radiation.

PLEIOTROPY

Some genes affect more than one phenotypic trait. This is called **pleiotropy**. There are numerous examples of pleiotropy in humans. They generally involve important proteins that are needed for the normal development or functioning of more than one organ system. An example of pleiotropy in humans occurs with the gene that codes for the main protein in collagen, a substance that helps form bones. This protein is also important in the ears and eyes. Mutations in the gene result in problems not only in bones but also in these sensory organs, which is how the gene's pleiotropic effects were discovered.

Another example of pleiotropy occurs with sickle cell anemia. This recessive genetic disorder occurs when there is a mutation in the gene that normally encodes the red blood cell protein called hemoglobin. People with the disorder have two alleles for sickle-cell hemoglobin, so named for the sickle shape (Figure **12.6.1.4**) that their red blood cells take on under certain conditions such as physical exertion. The sickle-shaped red blood cells clog small blood vessels, causing multiple phenotypic effects, including stunting of physical growth, certain bone deformities, kidney failure, and strokes.

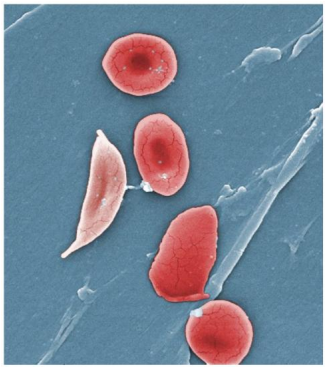


Figure **12.6.1.4**: The sickle-shaped red blood cell on the left is shown next to several normal red blood cells for comparison.

EPISTASIS

Some genes affect the expression of other genes. This is called **epistasis**. Epistasis is similar to dominance, except that it occurs between different genes rather than between different alleles for the same gene.

Albinism is an example of epistasis. A person with albinism has virtually no pigment in the skin. The condition occurs due to an entirely different gene than the genes that encode skin color. Albinism occurs because a protein called tyrosinase, which is needed for the production of normal skin pigment, is not produced due to a gene mutation. If an individual has albinism mutation, he or she will not have any skin pigment, regardless of the skin color genes that were inherited.

FEATURE: MY HUMAN BODY

Do you know your ABO blood type? In an emergency, knowing this valuable piece of information could possibly save your life. If you ever need a blood transfusion, it is vital that you receive blood that matches your own blood type. Why? If the blood transfused into your body contains an antigen that your own blood does not contain, antibodies in your blood plasma (the liquid part of your blood) will recognize the antigen as foreign to your body and cause a reaction called agglutination. In this reaction, the transfused red blood cells will clump together, as shown in the image below. The agglutination reaction is serious and potentially fatal.

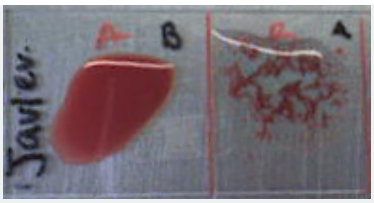
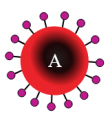
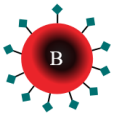
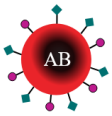


Figure **12.6.1.5**: Two samples of the same blood are shown here. The sample on the left is mixed with anti-B antibodies; the sample on the right is mixed with anti-A antibodies. Agglutination by the anti-A antibodies on the right shows that the sample is type A blood.

Knowing the antigens and antibodies present in each of the ABO blood types will help you understand which type(s) of blood you can safely receive if you ever need a transfusion. This information is shown in the table below for all of the ABO blood types. For example, if you have blood type A, this means that your red blood cells have the A antigen and that your blood plasma contains anti-B antibodies. If you were to receive a transfusion of type B or type AB blood, both of which have the B antigen, your anti-B antibodies would attack the transfused red blood cells, causing agglutination.

Table **12.6.1.2**: Antigens and antibodies in ABO blood types

Characteristics	Type A	Type B	Type AB	Type O
Red Blood Cell				
Antibodies in Plasma	 Anti-B	 Anti-A	None	 Anti-A and Anti-B
Antigens in Red Blood Cells	 A antigen	 B antigens	 A and B antigens	None

You may have heard that people with blood type O are called universal donors and that people with blood type AB are called universal recipients. People with type O blood have neither A nor B antigens in their blood, so if their blood is transfused into someone with a different ABO blood type, it causes no immune reaction. In other words, they can donate blood to anyone. On the other hand, people with type AB blood have no anti-A or anti-B antibodies in their blood, so they can receive a transfusion of blood from anyone. Which blood type(s) can safely receive a transfusion of type AB blood, and which blood type(s) can be safely received by those with type O blood?

REVIEW

1. What is non-Mendelian inheritance?
2. Explain why the human ABO blood group is an example of a multiple allele trait with codominance.
3. What is incomplete dominance? Give an example of this type of non-Mendelian inheritance in humans.
4. Explain the genetic basis of human skin color.
5. How may the human trait of adult height be influenced by the environment?
6. Define pleiotropy, and give a human example.
7. What is the difference between pleiotropy and epistasis?
8. Which of the following terms best matches each trait description? Choose only the one term that best fits each trait. (codominance; multiple allele trait; Mendelian trait; polygenic trait)
   A. A trait controlled by four genes.
   B. A trait where each allele of a heterozygote makes an equal contribution to the phenotype.
   C. A trait controlled by a single gene that has three different versions.
   D. A trait controlled by a single gene where one allele is fully dominant to the only other allele.
9. People with type AB blood have:
   A. anti-O antibodies
   B. anti-A and anti-B antibodies
   C. A and B antigens
10. *True or False*. People with type O blood cannot receive a blood transfusion from anyone besides others with type O blood.
11. *True or False*. People with type O blood can be heterozygous for this trait.

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12.6.2: Quantitative Trait Loci

The rules of inheritance discovered by Mendel depended on his wisely choosing traits that varied in a clear-cut, easily distinguishable, **qualitative** way. But humans are not either tall or short nor are they either heavy or light. Many traits differ in a continuous, **quantitative** way throughout a population.

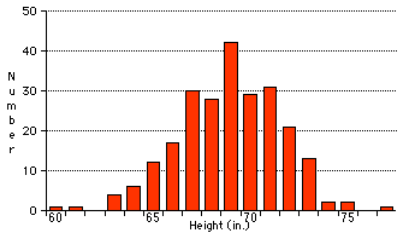


Figure 8.6.1: Distribution of heights among group of male secondary-school seniors

This histogram shows the distribution of heights among a group of male secondary-school seniors. As you can see, the plot resembles a bell-shaped curve. Such distributions are typical of quantitative traits. Some of the variation can be explained by differences in diet and perhaps other factors in the environment. Environment alone is not, however, sufficient to explain the full range of heights or weights.

An understanding of how genes can control quantitative traits emerged in 1908 from the work of the Swedish geneticist Nilsson-Ehle who studied quantitative traits in wheat. Using Mendel's methods, he mated pure-breeding red-kernel strains with pure-breeding white-kernel strains. The offspring were all red, but the intensity of color was much less that in the red parent. It seemed as though the effect of the red allele in the F_1 generation was being modified by the presence of the white allele.

Nilsson-Ehle: Genetics of Two Crosses

When Nilsson-Ehle mated two F_1 plants, he produced an F_2 generation in which red-kerneled plants outnumbered white-kerneled plants 15:1. But the red kernels were not all alike. They could quite easily be sorted into four categories. One sixteenth of them were deep red, like the P type. Four sixteenths were medium dark red, six sixteenths were medium red (like the F_1 generation), and four sixteenths were light red. The genetics of the two crosses is shown here. The alleles at one locus are indicated with prime marks; at the other, without.

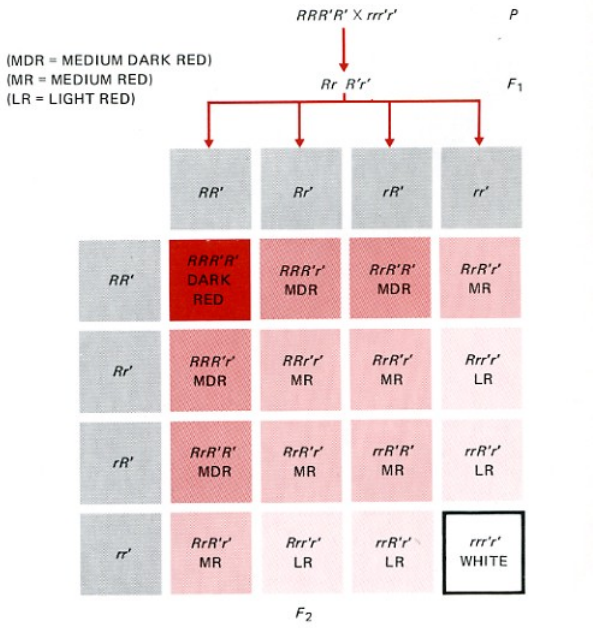


Figure 8.6.2: Genetics of the two crosses by Nilsson-Ehle

These results could be explained by assuming that kernel color in wheat is controlled by not one, but two pairs of genes, the effects of which add up without distinct dominance. Each pair is located on a different chromosome or so far apart on the same chromosome that there is no linkage. Four alleles for red produce a deep red kernel. Four alleles for white produce a white kernel. Just one red allele out of four produces a light red kernel. Any two out of the four produce a medium red kernel. Any three of the four produce a medium dark red kernel. If one plots the numbers of the different colored offspring in the F_2 generation against color intensity, one gets a graph like Figure 8.6.3.

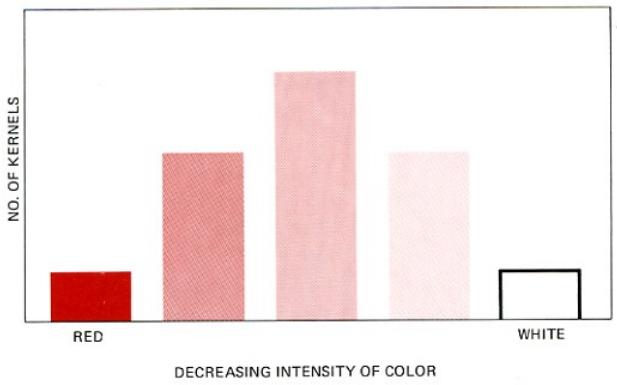


Figure 8.6.3: Genetics of the two crosses results interpretation by Nilsson-Ehle,

In other wheat varieties, Nilsson-Ehle found F_2 generations with a ratio of red kernels to white of 63:1. These could be explained by assuming that three pairs of alleles were involved. In these cases, six different shades of red could be detected, but the color differences were very slight. Environmental influences also caused alterations in intensity so that in practice the collection of kernels displayed a continuous range of hues all the way from deep red to white.

So the occurrence of continuous variation of a trait in a population can be explained by assuming it is controlled by several pairs of genes — called **quantitative trait loci** (**QTL**) — the effects of which are added together. This is called **polygenic inheritance** or the **multiple-factor hypothesis**. At first the study of quantitative traits was mostly confined to animal husbandry and the breeding of agricultural crops. It was based on the premise that

- When two extreme types ae mated (e.g., *AABB* and *aabb*). the offspring are intermediate in type.
- When two intermediate types are mated, most of their offspring are also intermediate, but some extreme types will be produced.
- The results of random matings in a large population will be a large range of types with the greatest number in the middle range and the fewest at the extremes.

In more recent times, the search for quantitative trait loci has turned to humans. A number of diseases, cancers for example, are thought to be caused by the additive effects of genes at different loci. Pedigree analysis has provided some insights, but the use of microarrays promises to provide more.

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12.6.3: Pleiotropy

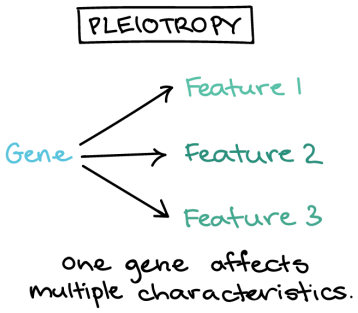
Based on Mendel's experiments, you might imagine that all genes control a single characteristic, are present in two copies, and affect some harmless aspect of an organism's appearance (such as color, height, or shape). Although those predictions are accurate in many cases, there are also some important exceptions. For instance, how can we explain observations like the following?

- The genetic disorder Marfan syndrome is caused by a mutation in one gene, yet it affects many aspects of growth and development, including height, vision, and heart function.

To understand observations like these, we need to look more deeply at what genes are. Rather than abstract "heritable factors," genes are stretches of DNA found on chromosomes, and most of them encode (specify the sequence of) proteins that do a certain job in the cell or body. In this article, we'll look in more detail at genes affecting multiple characteristics (pleiotropy).

Pleiotropy

When we discussed Mendel's experiments with purple-flowered and white-flowered plants, we didn't mention any other phenotypes associated with the two flower colors. However, Mendel noticed that the flower colors were always correlated with two other features: the color of the seed coat (covering of the seed) and the color of the axils (junctions where the leaves met the main stem)[1]. In plants with white flowers, the seed coats and axils were colorless, while in plants with purple flowers, the seed coats were brown-gray and the axils were reddish. Thus, rather than affecting just one characteristic, the flower color gene actually affected three.



Based on similar diagram by Ingrid Lobo

Genes like this, which affect multiple, seemingly unrelated aspects of an organism's phenotype, are said to be **pleiotropic** (*pleio–* = many, *–tropic* = effects)[2]. We now know that Mendel's flower color gene encodes a regulator protein that activates pigment biosynthesis, and that it works in several different parts of the pea plant (flowers, seed coat, and leaf axils). Thus, the seemingly unrelated phenotypes can all be traced back to a defect in a single gene with several jobs.

Alleles of pleiotropic genes are transmitted in the same way as alleles of genes that affect single traits. In these cases, the difference is that the phenotype contains multiple elements. These elements are specified as a package, and there would be both a dominant and recessive version of this package of traits.

Pleiotropy in Human Genetic Disorders

Genes affected in human genetic disorders are often pleiotropic. For example, people with the hereditary disorder Marfan syndrome may have a constellation of seemingly unrelated symptoms[3]:

- Unusually tall height
- Thin fingers and toes
- Dislocation of the lens of the eye
- Heart problems (in which the aorta, the large blood vessel carrying blood away from the heart, bulges or ruptures).

These symptoms don't appear directly related to one another, but as it turns out, they can all be traced back to the mutation of a single gene. This gene encodes a protein that assembles into chains, making elastic fibrils that give strength and flexibility to the body's connective tissues[4]. Disease-causing mutations in the Marfan syndrome reduce the amount of functional protein produced,

resulting in fewer fibrils. The eye and the aorta normally contain many fibrils that help maintain structure, explaining why these two organs are strongly affected in Marfan syndrome[5]. In addition, the fibrils serve as “storage shelves” for growth factors. When there are fewer of them in Marfan syndrome, the growth factors cannot be shelved and thus cause excess growth (leading to the characteristic tall, thin Marfan build)[6].

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12.6.4: Alternatives to Dominance and Recessiveness

Learning Objectives

- Discuss incomplete dominance, codominance, and multiple alleles as alternatives to dominance and recessiveness

Alternatives to Dominance and Recessiveness

Mendel's experiments with pea plants suggested that: (1) two "units" or alleles exist for every gene; (2) alleles maintain their integrity in each generation (no blending); and (3) in the presence of the dominant allele, the recessive allele is hidden and makes no contribution to the phenotype. Therefore, recessive alleles can be "carried" and not expressed by individuals. Such heterozygous individuals are sometimes referred to as "carriers." Further genetic studies in other plants and animals have shown that much more complexity exists, but that the fundamental principles of Mendelian genetics still hold true.

Mendel's results, that traits are inherited as dominant and recessive pairs, contradicted the view at that time that offspring exhibited a blend of their parents' traits. However, the heterozygote phenotype occasionally does appear to be intermediate between the two parents. For example, in the snapdragon, *Antirrhinum majus*, a cross between a homozygous parent with white flowers (C^WC^W) and a homozygous parent with red flowers (C^RC^R) will produce offspring with pink flowers (C^RC^W). This pattern of inheritance is described as incomplete dominance, denoting the expression of two contrasting alleles such that the individual displays an intermediate phenotype. The allele for red flowers is incompletely dominant over the allele for white flowers. However, the results of a heterozygote self-cross can still be predicted, just as with Mendelian dominant and recessive crosses. In this case, the genotypic ratio would be 1 C^RC^R:2 C^RC^W:1 C^WC^W, and the phenotypic ratio would be 1:2:1 for red:pink:white.



Figure **12.6.4.1**: Example of incomplete dominance: These pink flowers of a heterozygote snapdragon result from incomplete dominance.

A variation on incomplete dominance is codominance, in which both alleles for the same characteristic are simultaneously expressed in the heterozygote. An example of codominance is the MN blood groups of humans. The M and N alleles are expressed in the form of an M or N antigen present on the surface of red blood cells. Homozygotes ($L^ML^M$and L^NL^N) express either the M or the N allele, and heterozygotes (L^ML^N) express both alleles equally. In a self-cross between heterozygotes expressing a codominant trait, the three possible offspring genotypes are phenotypically distinct. However, the 1:2:1 genotypic ratio characteristic of a Mendelian monohybrid cross still applies.

Mendel implied that only two alleles, one dominant and one recessive, could exist for a given gene. We now know that this is an oversimplification. Although individual humans (and all diploid organisms) can only have two alleles for a given gene, multiple alleles may exist at the population level such that many combinations of two alleles are observed. Note that when many alleles exist for the same gene, the convention is to denote the most common phenotype or genotype among wild animals as the wild type (often

abbreviated "+"); this is considered the standard or norm. All other phenotypes or genotypes are considered variants of this standard, meaning that they deviate from the wild type. The variant may be recessive or dominant to the wild-type allele. An example of multiple alleles is coat color in rabbits. Here, four alleles exist for the c gene. The wild-type version, C^+C^+, is expressed as brown fur. The chinchilla phenotype, $c^{ch}c^{ch}$, is expressed as black-tipped white fur. The Himalayan phenotype, c^hc^h, has black fur on the extremities and white fur elsewhere. Finally, the albino, or "colorless" phenotype, cc, is expressed as white fur. In cases of multiple alleles, dominance hierarchies can exist. In this case, the wild-type allele is dominant over all the others, chinchilla is incompletely dominant over Himalayan and albino, and Himalayan is dominant over albino. This hierarchy, or allelic series, was revealed by observing the phenotypes of each possible heterozygote offspring.

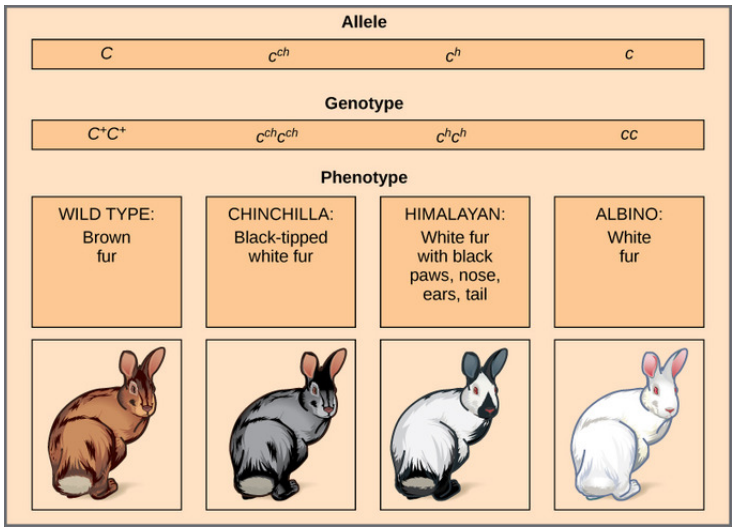


Figure **12.6.4.1**: Example of multiple alleles for rabbit coat color: Four different alleles exist for the rabbit coat color (C) gene.

The complete dominance of a wild-type phenotype over all other mutants often occurs as an effect of "dosage" of a specific gene product, such that the wild-type allele supplies the correct amount of gene product whereas the mutant alleles cannot. For the allelic series in rabbits, the wild-type allele may supply a given dosage of fur pigment, whereas the mutants supply a lesser dosage or none at all. Alternatively, one mutant allele can be dominant over all other phenotypes, including the wild type. This may occur when the mutant allele somehow interferes with the genetic message so that even a heterozygote with one wild-type allele copy expresses the mutant phenotype. One way in which the mutant allele can interfere is by enhancing the function of the wild-type gene product or changing its distribution in the body. One example of this is the Antennapedia mutation in *Drosophila*. In this case, the mutant allele expands the distribution of the gene product; as a result, the Antennapedia heterozygote develops legs on its head where its antennae should be.



Figure **12.6.4.1**: Example of a mutant allele interfering with the function of a wild-type gene: As seen in comparing the wild-type *Drosophila*(left) and the Antennapedia mutant (right), the Antennapedia mutant has legs on its head in place of antennae.

Key Points

- Incomplete dominance is the expression of two contrasting alleles such that the individual displays an intermediate phenotype.
- Codominance is a variation on incomplete dominance in which both alleles for the same characteristic are simultaneously expressed in the heterozygote.
- Diploid organisms can only have two alleles for a given gene; however, multiple alleles may exist at the population level such that many combinations of two alleles are observed.
- The complete dominance of a wild-type phenotype over all other mutants often occurs as an effect of “dosage” of a specific gene product: the wild-type allele supplies the correct amount of gene product whereas the mutant alleles cannot.
- One mutant allele can also be dominant over all other phenotypes, including the wild type.

Key Terms

- **allele**: one of a number of alternative forms of the same gene occupying a given position on a chromosome
- **incomplete dominance**: a condition in which the phenotype of the heterozygous genotype is distinct from and often intermediate to the phenotypes of the homozygous genotypes
- **codominance**: a condition in which both alleles of a gene pair in a heterozygote are fully expressed, with neither one being dominant or recessive to the other

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12.6.5: Epistasis

Learning Objectives

- Explain the phenotypic outcomes of epistatic effects between genes

Epistasis

Mendel's studies in pea plants implied that the sum of an individual's phenotype was controlled by genes (or as he called them, unit factors): every characteristic was distinctly and completely controlled by a single gene. In fact, single observable characteristics are almost always under the influence of multiple genes (each with two or more alleles) acting in unison. For example, at least eight genes contribute to eye color in humans.

In some cases, several genes can contribute to aspects of a common phenotype without their gene products ever directly interacting. In the case of organ development, for instance, genes may be expressed sequentially, with each gene adding to the complexity and specificity of the organ. Genes may function in complementary or synergistic fashions: two or more genes need to be expressed simultaneously to affect a phenotype. Genes may also oppose each other with one gene modifying the expression of another.

In epistasis, the interaction between genes is antagonistic: one gene masks or interferes with the expression of another. "Epistasis" is a word composed of Greek roots that mean "standing upon." The alleles that are being masked or silenced are said to be hypostatic to the epistatic alleles that are doing the masking. Often the biochemical basis of epistasis is a gene pathway in which the expression of one gene is dependent on the function of a gene that precedes or follows it in the pathway.

An example of epistasis is pigmentation in mice. The wild-type coat color, agouti (AA), is dominant to solid-colored fur (aa). However, a separate gene (C) is necessary for pigment production. A mouse with a recessive c allele at this locus is unable to produce pigment and is albino regardless of the allele present at locus A. Therefore, the genotypes AAcc, Aacc, and aacc all produce the same albino phenotype. A cross between heterozygotes for both genes (AaCc x AaCc) would generate offspring with a phenotypic ratio of 9 agouti:3 solid color:4 albino. In this case, the C gene is epistatic to the A gene.

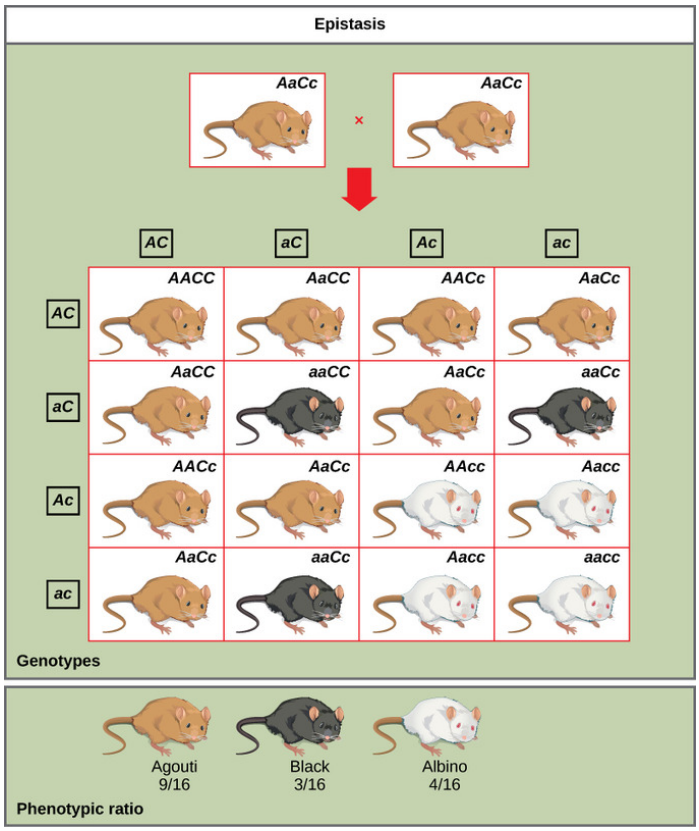


Figure **12.6.5.1**: Epistasis in mouse coat color: In mice, the mottled agouti coat color (A) is dominant to a solid coloration, such as black or gray. A gene at a separate locus (C) is responsible for pigment production. The recessive c allele does not produce pigmentnand a mouse with the homozygous recessive cc genotype is albino regardless of the allele present at the A locus. Thus, the C gene is epistatic to the A gene.

Epistasis can also occur when a dominant allele masks expression at a separate gene. Fruit color in summer squash is expressed in this way. Homozygous recessive expression of the W gene (ww) coupled with homozygous dominant or heterozygous expression of the Y gene (YY or Yy) generates yellow fruit, while the wwyy genotype produces green fruit. However, if a dominant copy of the W gene is present in the homozygous or heterozygous form, the summer squash will produce white fruit regardless of the Y alleles. A cross between white heterozygotes for both genes (WwYy × WwYy) would produce offspring with a phenotypic ratio of 12 white:3 yellow:1 green.

Finally, epistasis can be reciprocal: either gene, when present in the dominant (or recessive) form, expresses the same phenotype. In the shepherd's purse plant (*Capsella bursa-pastoris*), the characteristic of seed shape is controlled by two genes in a dominant epistatic relationship. When the genes A and B are both homozygous recessive (aabb), the seeds are ovoid. If the dominant allele for either of these genes is present, the result is triangular seeds. That is, every possible genotype other than aabb results in triangular seeds; a cross between heterozygotes for both genes (AaBb x AaBb) would yield offspring with a phenotypic ratio of 15 triangular:1 ovoid.

Keep in mind that any single characteristic that results in a phenotypic ratio that totals 16 is typical of a two-gene interaction. Recall the phenotypic inheritance pattern for Mendel's dihybrid cross, which considered two non-interacting genes: 9:3:3:1. Similarly, we would expect interacting gene pairs to also exhibit ratios expressed as 16 parts. Note that we are assuming the interacting genes are not linked; they are still assorting independently into gametes.

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Key Points

- In many cases, several genes may contribute to a particular phenotype; when the actions of one gene masks the effects of another, this gene is said to be epistatic to the second.
- Epistasis can occur when a recessive genotype masks the actions of another gene, or when a dominant allele masks the effects of another gene.
- Epistasis can be reciprocal: either gene, when present in the dominant (or recessive) form, expresses the same phenotype.
- Any single characteristic that results in a phenotypic ratio that totals 16 (such as 12:3:1, 9:3:4, or others) is typical of a two-gene interaction.

Key Terms

- **epistasis**: the modification of the expression of a gene by another unrelated one

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CHAPTER OVERVIEW

13: Chromosomes, Mapping, and the Meiosis-Inheritance Connection

13.1: Sex Linkage and the Chromosomal Theory of Inheritance

13.2: Sex Chromosomes and Sex Determination

13.2.1: Sex Chromosomes

13.2.2: Inferring the Mode of Inheritance

13.3: Exceptions to Chromosomal Theory of Inheritance

13.3.1: Organellar Inheritance

13.4: Genetic Mapping

13.4.1: Classification and Detection of Molecular Markers

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13.5.1: Imprinted Genes

13.5.2: Prenatal Screening

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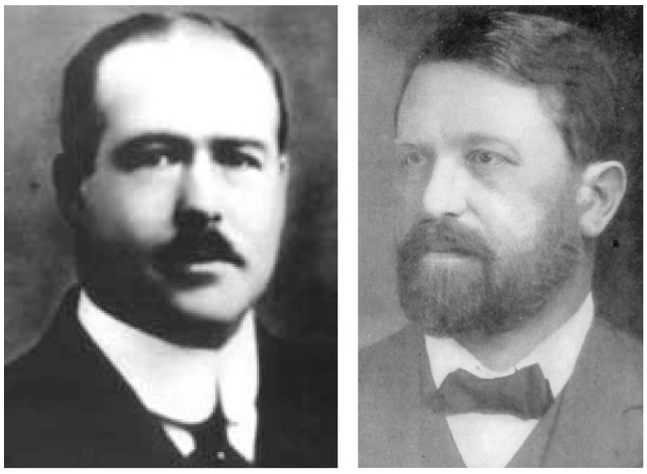
13.1: Sex Linkage and the Chromosomal Theory of Inheritance

Learning Objectives

- List the reasons that fruit flies are excellent model organisms for genetic research

Chromosomal Theory of Inheritance

The speculation that chromosomes might be the key to understanding heredity led several scientists to examine Mendel's publications and re-evaluate his model in terms of the behavior of chromosomes during mitosis and meiosis. In 1902, Theodor Boveri observed that proper embryonic development of sea urchins does not occur unless chromosomes are present. That same year, Walter Sutton observed the separation of chromosomes into daughter cells during meiosis. Together, these observations led to the development of the Chromosomal Theory of Inheritance, which identified chromosomes as the genetic material responsible for Mendelian inheritance.



(a) (b)

Figure **13.1.1**: Sutton and Boveri: (a) Walter Sutton and (b) Theodor Boveri are credited with developing the Chromosomal Theory of Inheritance, which states that chromosomes carry the unit of heredity (genes).

The Chromosomal Theory of Inheritance was consistent with Mendel's laws and was supported by the following observations:

- During meiosis, homologous chromosome pairs migrate as discrete structures that are independent of other chromosome pairs.
- The sorting of chromosomes from each homologous pair into pre-gametes appears to be random.
- Each parent synthesizes gametes that contain only half of their chromosomal complement.
- Even though male and female gametes (sperm and egg) differ in size and morphology, they have the same number of chromosomes, suggesting equal genetic contributions from each parent.
- The gametic chromosomes combine during fertilization to produce offspring with the same chromosome number as their parents.

Despite compelling correlations between the behavior of chromosomes during meiosis and Mendel's abstract laws, the Chromosomal Theory of Inheritance was proposed long before there was any direct evidence that traits were carried on chromosomes. Critics pointed out that individuals had far more independently segregating traits than they had chromosomes. It was only after several years of carrying out crosses with the fruit fly, *Drosophila melanogaster*, that Thomas Hunt Morgan provided experimental evidence to support the Chromosomal Theory of Inheritance.

In 1910, Thomas Hunt Morgan started his work with *Drosophila melanogaster*, a fruit fly. He chose fruit flies because they can be cultured easily, are present in large numbers, have a short generation time, and have only four pair of chromosomes that can be easily identified under the microscope. They have three pair of autosomes and a pair of sex chromosomes. At that time, he already knew that X and Y have to do with gender. He used normal flies with red eyes and mutated flies with white eyes and cross bred them. In flies, the wild type eye color is red (XW) and is dominant to white eye color (Xw). He was able to conclude that the gene

for eye color was on the X chromosome. This trait was thus determined to be X-linked and was the first X-linked trait to be identified. Males are said to be hemizygous, in that they have only one allele for any X-linked characteristic.



Figure **13.1.1**: Eye Color in Fruit Flies: In Drosophila, the gene for eye color is located on the X chromosome. Red eye color is wild type and is dominant to white eye color.

Key Points

- Homologous chromosome pairs are independent of other chromosome pairs.
- Chromosomes from each homologous pair are sorted randomly into pre- gametes.
- Parents synthesize gametes that contain only half of their chromosomes; eggs and sperm have the same number of chromosomes.
- Gametic chromosomes combine during fertilization to produce offspring with the same chromosome number as their parents.
- Eye color in fruit flies was the first X-linked trait to be discovered; thus, Morgan's experiments with fruit flies solidified the Chromosomal Theory of Inheritance.

Key Terms

- **autosome**: any chromosome other than sex chromosomes
- **hemizygous**: having some single copies of genes in an otherwise diploid cell or organism
- **wild type**: the typical form of an organism, strain, gene or characteristic as it occurs in nature

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SECTION OVERVIEW

13.2: Sex Chromosomes and Sex Determination

13.2.1: Sex Chromosomes

13.2.2: Inferring the Mode of Inheritance

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13.2.1: Sex Chromosomes

The nuclei of human cells contain 22 autosomes and 2 sex chromosomes. In females, the sex chromosomes are the 2 **X chromosomes**. Males have one X chromosome and one **Y chromosome**. The presence of the Y chromosome is decisive for unleashing the developmental program that leads to a baby boy.

The Y Chromosome

In making sperm by meiosis, the X and Y chromosomes must separate in anaphase just as homologous autosomes do. This occurs without a problem because, like homologous autosomes, the X and Y chromosome synapse during prophase of meiosis I. There is a small region of homology shared by the X and Y chromosome and synapsis occurs at that region.

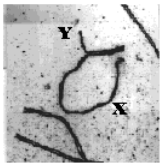


Figure 7.6.1 Synapsis of the X and Y chromosomes courtesy of C. Tease

This image, shows synapsis of the X and Y chromosomes of a mouse during prophase of meiosis I. Crossing over occurs in two regions of pairing, called the **pseudoautosomal regions**. These are located at opposite ends of the chromosome.

The Pseudoautosomal Regions

The **pseudoautosomal regions** get their name because any genes located within them (so far only 9 have been found) are inherited just like any autosomal genes. Males have two copies of these genes: one in the pseudoautosomal region of their Y, the other in the corresponding portion of their X chromosome. So males can inherit an allele originally present on the X chromosome of their father and females can inherit an allele originally present on the Y chromosome of their father.

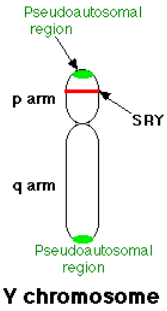


Figure 7.6.2 Human Y Chromosome

Genes outside the pseudoautosomal regions

Although 95% of the Y chromosome lies between the pseudoautosomal regions, only 27 different functional genes have been found here. Over half of this region is genetically-barren heterochromatin. Of the 27 genes found in the euchromatin, some encode proteins used by all cells. The others encode proteins that appear to function only in the testes. A key player in this latter group is ***SRY***.

SRY

SRY (for **s**ex-determining **r**egion **Y**) is a gene located on the short (p) arm just outside the pseudoautosomal region. It is the master switch that triggers the events that converts the embryo into a male. Without this gene, you get a female instead.

What is the evidence?

1. On very rare occasions aneuploid humans are born with such karyotypes as XXY, XXXY, and even XXXXY. Despite their extra X chromosomes, all these cases are male.
2. This image shows two mice with an **XX karyotype** (and thus they should be female). However, as you may be able to see, they have a male phenotype. This is because they are transgenic for ***SRY***. Fertilized XX eggs were injected with DNA carrying the

SRY gene.

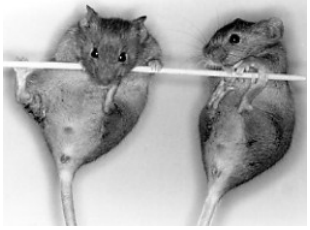


Figure 7.6.3 Transgenic mice courtesy of Robin Lovell-Badge from Nature 351:117, 1991

Although these mice have testes, male sex hormones, and normal mating behavior, they are sterile.

3. Another rarity: XX humans with testicular tissue because a translocation has placed the *SRY* gene on one of the X chromosomes
4. Still another rarity that demonstrates the case: women with an XY karyotype who, despite their Y chromosome, are female because of a destructive mutation in *SRY*.

In 1996, a test based on a molecular probe for *SRY* was used to ensure that potential competitors for the women's Olympic events in Atlanta had no *SRY* gene. But because of possibilities like that in case 4, this testing is no longer used to screen female Olympic athletes.

The X Chromosome

The X chromosome carries nearly 1,000 genes but few, if any, of these have anything to do directly with sex. However, the inheritance of these genes follows special rules. These arise because:

- males have only a single X chromosome
- almost all the genes on the X have no counterpart on the Y; thus
- any gene on the X, **even if recessive in females**, will be expressed in males.

Genes inherited in this fashion are described as sex-linked or, more precisely, **X-linked**.

X-Linkage example

Hemophilia is a blood clotting disorder caused by a mutant gene encoding either

- clotting **factor VIII**, causing hemophilia A or
- clotting **factor IX**, causing hemophilia B.

Both genes are located on the X chromosome (shown here in red). With only a single X chromosome, males who inherit the defective gene (always from their mother) will be unable to produce the clotting factor and suffer from difficult-to-control episodes of bleeding. In heterozygous females, the unmutated copy of the gene will provide all the clotting factor they need. Heterozygous females are called **"carriers"** because although they show no symptoms, they pass the gene on to approximately half their sons, who develop the disease, and half their daughters, who also become carriers.

	X	Y
X	XX	XY
X^h	X^hX	X^hY

Women rarely suffer from hemophilia because to do so they would have to inherit a defective gene from their father as well as their mother. Until recently, few hemophiliacs ever became fathers.

X-chromosome Inactivation (XCI)

Human females inherit two copies of every gene on the X chromosome, whereas males inherit only one (with some exceptions: the 9 pseudoautosomal genes and the small number of "housekeeping" genes found on the Y). But for the hundreds of other genes on the X, are males at a disadvantage in the amount of gene product their cells produce? The answer is no, because females have only a single **active** X chromosome in each cell.

During interphase, chromosomes are too tenuous to be stained and seen by light microscopy. However, a dense, stainable structure, called a **Barr body** (after its discoverer) is seen in the interphase nuclei of female mammals. The Barr body is one of the X chromosomes. Its compact appearance reflects its inactivity. So, the cells of females have only one functioning copy of each X-linked gene — the same as males.

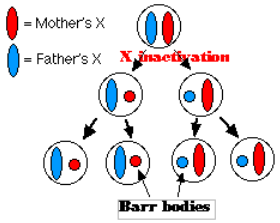


Figure 7.6.4 Genetic Mosaic due to XChromosome Inactivation

X-chromosome inactivation occurs early in embryonic development. In a given cell, which of a female's X chromosomes becomes inactivated and converted into a Barr body is a matter of chance (except in marsupials like the kangaroo, where it is always the father's X chromosome that is inactivated). After inactivation has occurred, all the descendants of that cell will have the same chromosome inactivated. Thus X-chromosome inactivation creates clones with differing effective gene content. An organism whose cells vary in effective gene content and hence in the expression of a trait, is called a **genetic mosaic**.

Mechanism of X-chromosome inactivation

Inactivation of an X chromosome requires a gene on that chromosome called ***XIST***.

- *XIST* is transcribed into a **long noncoding RNA**.
- XIST RNA accumulates along the X chromosome containing the active *XIST* gene and proceeds to inactivate all (or almost all) of the hundreds of other genes on that chromosome.
- **Barr bodies** are inactive X chromosomes "painted" with XIST RNA.

The Sequence of Events in Mice

- During the first cell divisions of the female mouse zygote, the *XIST* locus on the father's X chromosome is expressed so most of his X-linked genes are silent.
- By the time the blastocyst has formed, the silencing of the paternal X chromosome still continues in the trophoblast (which will go on to form the placenta) but
- in the inner cell mass (the ICM, which will go on to form the embryo) transcription of *XIST* **ceases** on the paternal X chromosome allowing its hundreds of other genes to be expressed. The shut-down of the *XIST* locus is done by methylating *XIST* regulatory sequences. So the pluripotent stem cells of the ICM express both X chromosomes.
- However, as embryonic development proceeds, X-chromosome inactivation begins again. But this time it is entirely random. There is no predicting whether it will be the **maternal X** or the **paternal X** that is inactivated in a given cell.

Some genes on the X chromosome escape inactivation

What about those 18 genes that are found on the Y as well as the X? There should be no need for females to inactivate one copy of these to keep in balance with the situation in males. And, as it turns out, these genes escape inactivation in females. Just how they manage this is still under investigation.

X-chromosome Abnormalities

As we saw above, people are sometimes found with abnormal numbers of X chromosomes. Unlike most cases of aneuploidy, which are lethal, the phenotypic effects of aneuploidy of the X chromosome are usually not severe.

Examples:

- Females with but a single intact X chromosome (usually the one she got from her mother) in some (thus a genetic mosaic) or all of her cells show a variable constellation of phenotypic traits called **Turner syndrome**. For those girls that survive to birth, the phenotypic effects are generally mild because each cell has a single functioning X chromosome like those of XX females. Number of Barr bodies = zero.

- **XXX**, **XXXX**, **XXXXX** karyotypes: all females with mild phenotypic effects because in each cell all the extra X chromosomes are inactivated. Number of Barr bodies = number of X chromosomes minus one.
- **Klinefelter's syndrome**: people with XXY or XXXY karyotypes are males (because of their Y chromosome). But again, the phenotypic effects of the extra X chromosomes are mild because, just as in females, the extra Xs are inactivated and converted into Barr bodies.

Sex Determination in Other Animals

Although the male fruit fly, *Drosophila melanogaster*, is X-Y, the Y chromosome does not dictate its maleness but rather the absence of a second X. Furthermore, instead of females shutting down one X to balance the single X of the males — as we do — male flies double the output of their single X relative to that of females.

In birds, moths, schistosomes, and some lizards, the male has two of the same chromosome (designated ZZ), whereas the female has "heterogametic" chromosomes (designated Z and W). In chickens, a single gene on the Z chromosome (designated *DMRT1*), when present in a double dose (ZZ), produces males while the presence of only one copy of the gene produces females (ZW).

Environmental Sex Determination

In some cold-blooded vertebrates such as

- fishes
- reptiles (e.g. certain snakes, lizards, turtles, and all crocodiles and alligators)
- invertebrates (e.g. certain crustaceans),

sex is determined **after fertilization** — not by sex chromosomes deposited in the egg.

The choice is usually determined by the **temperature** at which early embryonic development takes place.

- In some cases (e.g. many turtles and lizards), a higher temperature during incubation favors the production of females.
- In other cases (e.g., alligators), a higher temperature favors the production of males.

Even in cases (e.g. some lizards) where there are sex chromosomes, a high temperature can convert a genotypic male (ZZ) into a female.

Hermaphrodites

Hermaphrodites have both male and female sex organs. Many species of fish are hermaphroditic.

Some start out as one sex and then, in response to stimuli in their environment, switch to the other.

Other species have both testes and ovaries at the same time (but seldom fertilize themselves). However, populations of C. elegans consist mostly of hermaphrodites and these only fertilize themselves.

Hermaphroditic fishes have no sex chromosomes.

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13.2.2: Inferring the Mode of Inheritance

Given a pedigree of an uncharacterized disease or trait, one of the first tasks is to determine which modes of inheritance are possible and then which mode of inheritance is most likely. This information is essential in calculating the probability that the trait will be inherited in any future offspring. We will mostly consider five major types of inheritance: autosomal dominant (AD), autosomal recessive (AR), X-linked dominant (XD), X-linked recessive (XR), and Y-linked (Y).

Autosomal Dominant (AD)

When a disease is caused by a dominant allele of a gene, every person with that allele will show symptoms of the disease (assuming complete penetrance), and only one disease allele needs to be inherited for an individual to be affected. Thus, every affected individual must have an affected parent. A pedigree with affected individuals in every generation is typical of AD diseases. However, beware that other modes of inheritance can also show the disease in every generation, as described below. It is also possible for an affected individual with an AD disease to have a family without any affected children, if the affected parent is a heterozygote. This is particularly true in small families, where the probability of every child inheriting the normal, rather than disease allele is not extremely small. Note that AD diseases are usually rare in populations, therefore affected individuals with AD diseases tend to be heterozygotes (otherwise, both parents would have had to been affected with the same rare disease). Achondroplastic dwarfism, and polydactyly are both examples of human conditions that may follow an AD mode of inheritance.

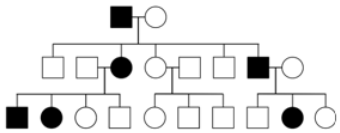


Figure **13.2.2.3**: A pedigree consistent with AD inheritance. (Original-Deyholos-CC:AN)

X-linked dominant (XD)

In X-linked dominant inheritance, the gene responsible for the disease is located on the X-chromosome, and the allele that causes the disease is dominant to the normal allele in females. Because females have twice as many X-chromosomes as males, females tend to be more frequently affected than males in the population. However, not all pedigrees provide sufficient information to distinguish XD and AD. One definitive indication that a trait is inherited as AD, and not XD, is that an affected father passes the disease to a son; this type of transmission is not possible with XD, since males inherit their X chromosome from their mothers.

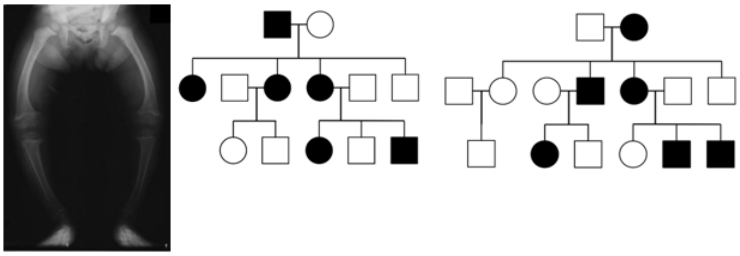


Figure **13.2.2.5**: Some types of rickets may follow an XD mode of inheritance. (Wikipedia-Mrish-CC:AS) (middle and left) Two pedigrees consistent with XD inheritance. (Original-Deyholos_CC:AN)

Autosomal recessive (AR)

Diseases that are inherited in an autosomal recessive pattern require that both parents of an affected individual carry at least one copy of the disease allele. With AR traits, many individuals in a pedigree can be carriers, probably without knowing it. Compared to pedigrees of dominant traits, AR pedigrees tend to show fewer affected individuals and are more likely than AD or XD to “skip a generation”. Thus, the major feature that distinguishes AR from AD or XD is that unaffected individuals can have affected offspring.



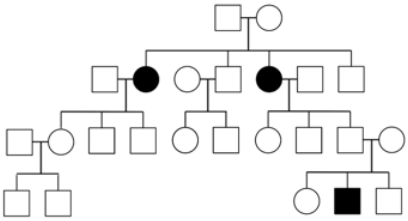
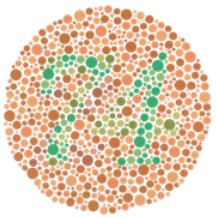


Figure **13.2.2.6**: (left) Many inborn errors of metabolism, such as phenylketonuria (PKU) are inherited as AR. Newborns are often tested for a few of the most common metabolic diseases. (Wikipedia-U.S. Air Force photo/Staff Sgt. Eric T. Sheler-PD) (right) A pedigree consistent with AR inheritance. (Original-Deyholos_CC:AN)

X-linked recessive (XR)

Because males have only one X-chromosome, any male that inherits an X-linked recessive disease allele will be affected by it (assuming complete penetrance). Therefore, in XR modes of inheritance, males tend to be affected more frequently than females in a population. This is in contrast to AR and AD, where both sexes tend to be affected equally, and XD, in which females are affected more frequently. Note, however, in the small sample sizes typical of human families, it is usually not possible to accurately determine whether one sex is affected more frequently than others. On the other hand, one feature of a pedigree that can be used to definitively establish that an inheritance pattern is not XR is the presence of an affected daughter from unaffected parents; because she would have had to inherit one X-chromosome from her father, he would also have been affected in XR.



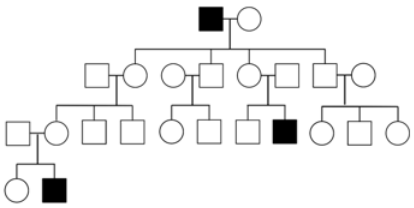


Figure **13.2.2.8**: Some forms of colour blindness are inherited as XR-traits. Colour blindness is diagnosed using tests such as this. Ishihara Test. (Wikipedia-unknown-PD) (right) A pedigree consistent with XR inheritance. (Original-Deyholos-CC:AN)

Y-linked and Mitochondrial Inheritance.

Two additional modes are **Y-linked** and **Mitochondrial inheritance**.

Only males are affected in human Y-linked inheritance (and other species with the X/Y sex determining system). There is only father to son transmission. This is the easiest mode of inheritance to identify, but it is one of the rarest because there are so few genes located on the Y-chromosome. An example of Y-linked inheritance is the **hairy-ear-rim** phenotype seen in some Indian families. As expected this trait is passed on from father to all sons and no daughters. Y-chromosome DNA polymorphisms can be used to follow the male lineage in large families or through ancient ancestral lineages. For example, the Y-chromosome of Mongolian ruler Genghis Khan (1162-1227 CE), and his male relatives, accounts for ~8% of the Y-chromosome lineage of men in Asia (0.5% world wide).

Mutations in Mitochondrial DNA are inherited through the maternal line (from your mother). There are some human diseases associated with mutations in mitochondria genes. These mutations can affect both males and females, but males cannot pass them on as the mitochondria are inherited via the egg, not the sperm. Mitochondrial DNA polymorphisms are also used to investigate evolutionary lineages, both ancient and recent. Because of the relative similarity of sequence mtDNA is also used in species identification in ecology studies.

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SECTION OVERVIEW

13.3: Exceptions to Chromosomal Theory of Inheritance

13.3.1: Organellar Inheritance

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13.3.1: Organellar Inheritance

Learning Objectives

- Explain why genetic information in organelles is passed independently of nuclear DNA.

In eukaryotes, DNA and genes also exist outside of the nuclear chromosomes. Both the **chloroplast** and **mitochondrion** have circular chromosomes (Figure **13.3.1.1**). These organellar genomes are often present in multiple copies within each organelle. In most sexually-reproducing species, **organellar chromosomes** are inherited from only one parent, usually the one that produces the largest gamete. Thus, in mammals, angiosperms, and many other organisms, mitochondria and chloroplasts are inherited only through the oocyte.

These organelles are likely the remnants of prokaryotic endosymbionts that entered the cytoplasm of ancient progenitors of today's eukaryotes (**endosymbiont theory**). These endosymbionts had their own, circular chromosomes, like most bacteria that exist today. Chloroplasts and mitochondria typically have circular chromosomes that behave more like bacterial chromosomes than eukaryotic chromosomes, i.e. these organellar genomes do not undergo mitosis or meiosis.

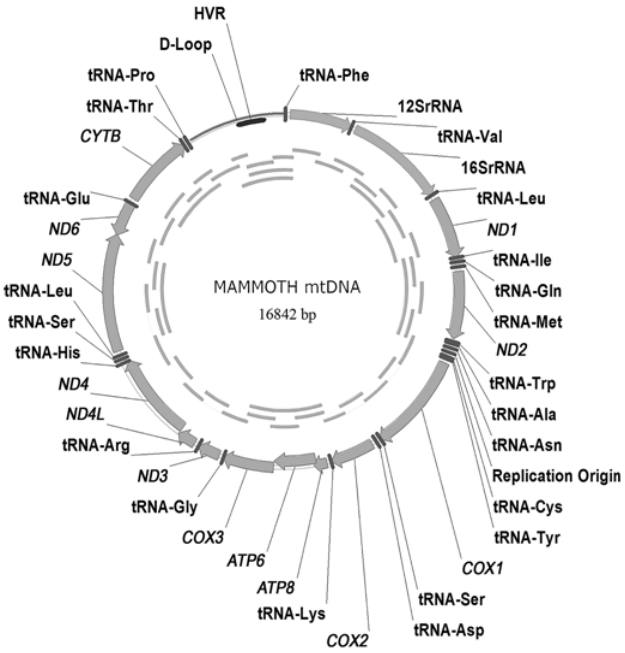


Figure **13.3.1.1**: A map of the complete mitochondrial chromosome of the woolly mammoth (*Mammuthus primigenius*). The mtDNA that was used to produce this map was obtained from tissue of a mammoth that lived approximately 32,000 years ago. The map shows the position of enzymes encoded on the chromosome including components of the NADH dehydrogenase (ND) complex and cytochrome oxidases (COX), all of which function during energy metabolism in the mitochondrion. The mitochondrial chromosome also encodes various tRNAs and rRNAs used in translation of the genes encoded on this chromosome. Other proteins required by the mitochondrion are encoded in the nuclear genome, and are translated in the cytoplasm and imported into the organelle. (From Rogaev et al, 2006). mtDNA work indicates that mammoths are more closely related to Indian elephants than to either of the African species (Rohland et al, 2010).

Implications of mitochondrial inheritance

As with nuclear DNA, organellar DNA can be mutated. Cells can have a mixture of hundreds to thousands of organelles with different alleles for genes. Because there are not simply one or two organelles in a cell, terms like heterozygous and homozygous do not apply to this situation and patterns of inheritance can be unpredictable. Some patterns of inheritance that are usually observed for mitochondrial inheritance are:

- Traits can be passed via egg to offspring

- Traits are not passed via sperm to offspring
- Variable penetrance and expressivity are often observed are often due to different proportions of wild type and mutant organelles in the organism of even differing proportions between different tissues in the same organism.

Mitochondrial DNA polymorphisms are also used to investigate evolutionary lineages, both ancient and recent.

Current Research in Plant Genetics:

Although organelles are most often inherited through oocytes, exceptions have been identified. Recent studies of cucumber plants (*Cucumis sativus* var. *sativus)* identified SNPs in true-breeding lines and performed reciprocal crosses. The results showed that the chloroplasts were inherited from the maternal parent but that mitochondria are inherited from the male parent.

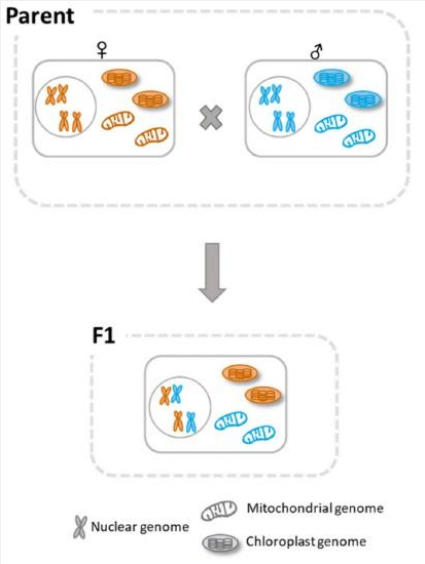


Figure **13.3.1.2**: Inheritance of organelles and nuclear chromosomes in cucumbers. (CC BY (http://creativecommons.org/licenses/by/4.0/) Park et al. (2021) via https://doi.org/10.1038/s41598-021-81988-w)

Reference: Park, HS., Lee, W.K., Lee, SC. *et al.* Inheritance of chloroplast and mitochondrial genomes in cucumber revealed by four reciprocal F_1 hybrid combinations. *Sci Rep* **11,** 2506 (2021). https://doi.org/10.1038/s41598-021-81988-w

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SECTION OVERVIEW

13.4: Genetic Mapping

13.4.1: Classification and Detection of Molecular Markers

13.4.2: Genetic Linkage and Distances

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13.4.1: Classification and Detection of Molecular Markers

Regardless of their origins, molecular markers can be classified as polymorphisms that either vary in the length of a DNA sequence, or vary only in the identity of nucleotides at a particular position on a chromosome (Figure **13.4.1.1**). In both cases, because two or more alternative versions of the DNA sequence exist, we can treat each variant as a different allele of a single locus. Each allele gives a different **molecular phenotype**. For example, polymorphisms of **SSRs** (short sequence repeats) can be distinguished based on the length of PCR products: one allele of a particular SSR locus might produce a 100bp band, while the same primers used with a different allele as a template might produce a 120bp band (Figure **13.4.1.2**). A different type of marker, called a **SNP** (single nucleotide polymorphism), is an example of polymorphism that varies in nucleotide identity, but not length. SNPs are the most common of any molecular markers, and the genotypes of thousands of SNP loci can be determined in parallel, using new, hybridization based instruments. Note that the alleles of most molecular markers are co-dominant, since it is possible to distinguish the molecular phenotype of a heterozygote from either homozygote.

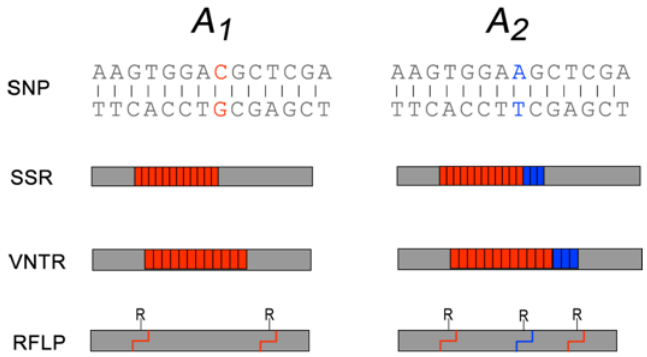


Figure **13.4.1.1**: Some examples of DNA polymorphisms. The variant region is marked in blue, and each variant sequence is arbitrarily assigned one of two allele labels. Abbreviations: SNP (Single Nucleotide Polymorphism); SSR (Simple Sequence Repeat) = SSLP (Simple Sequence Length Polymorphism); **VNTR** (Variable Number of Tandem Repeats); **RFLP** (Restriction Fragment Length Polymorphisms. VNTRs and SSRs differ in the size of the repeat unit; VNTRs are larger than SSRs. (Original-Deyholos-CC:AN)

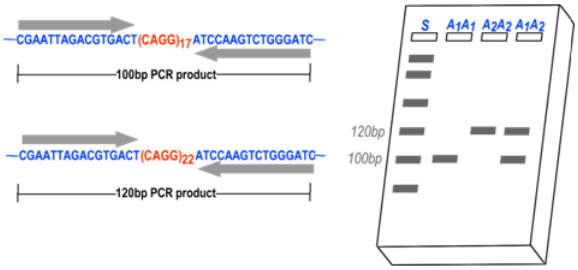


Figure **13.4.1.2**: Determining the genotype of an individual at a single SSR locus using a specific pair of PCR primers and agarose gel electrophoresis. S= size standard (Original-Deyholos-CC:AN)

Mutations that do not affect the function of protein sequences or gene expression are likely to persist in a population as polymorphisms, since there will be no selection either in favor or against them (i.e. they are **neutral**). Note that the although the rate of spontaneous mutation in natural populations is sufficiently high so as to generate millions of polymorphisms that accumulate over thousands of generations, the rate of mutation is on the other hand sufficiently low that existing polymorphisms are stable throughout the few generations we study in a typical genetic experiment.

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13.4.2: Genetic Linkage and Distances

Learning Objectives

- Discuss how linked genes can be inherited separately

Genetic Linkage and Distances

Mendel's work suggested that traits are inherited independently of each other. Morgan identified a 1:1 ratio between a segregating trait and the X chromosome, suggesting that the random segregation of chromosomes was the physical basis of Mendel's model. This also demonstrated that linked genes disrupt Mendel's predicted outcomes. The fact that each chromosome can carry many linked genes explains how individuals can have many more traits than they have chromosomes. However, observations by researchers in Morgan's laboratory suggested that alleles positioned on the same chromosome were not always inherited together. During meiosis, linked genes somehow became unlinked.

Homologous Recombination

In 1909, Frans Janssen observed chiasmata (the point at which chromatids are in contact with each other and may exchange segments) prior to the first division of meiosis. He suggested that alleles become unlinked when chromosomes physically exchange segments. As chromosomes condensed and paired with their homologs, they appeared to interact at distinct points. Janssen suggested that these points corresponded to regions in which chromosome segments were exchanged. It is now known that the pairing and interaction between homologous chromosomes, known as synapsis, does more than simply organize the homologs for migration to separate daughter cells. When synapsed, homologous chromosomes undergo reciprocal physical exchanges of DNA at their arms in a process called homologous recombination, or more simply, "crossing over."

Genetic Maps

In 1913, Alfred Sturtevant, a student in Morgan's laboratory, created the first "chromosome map," a linear representation of gene order and relative distance on a chromosome.To construct a chromosome map, Sturtevant assumed that genes were ordered serially on threadlike chromosomes. He also assumed that the incidence of recombination between two homologous chromosomes could occur with equal likelihood anywhere along the length of the chromosome. Operating under these assumptions, Sturtevant hypothesized alleles that were far apart on a chromosome were more likely to dissociate during meiosis simply because there was a larger region over which recombination could occur. Conversely, alleles that were close to each other on the chromosome were likely to be inherited together. The average number of crossovers between two alleles, or their recombination frequency, correlated with their genetic distance from each other, relative to the locations of other genes on that chromosome. Sturtevant divided his genetic map into map units, or centimorgans (cM), in which a recombination frequency of 0.01 corresponds to 1 cM.

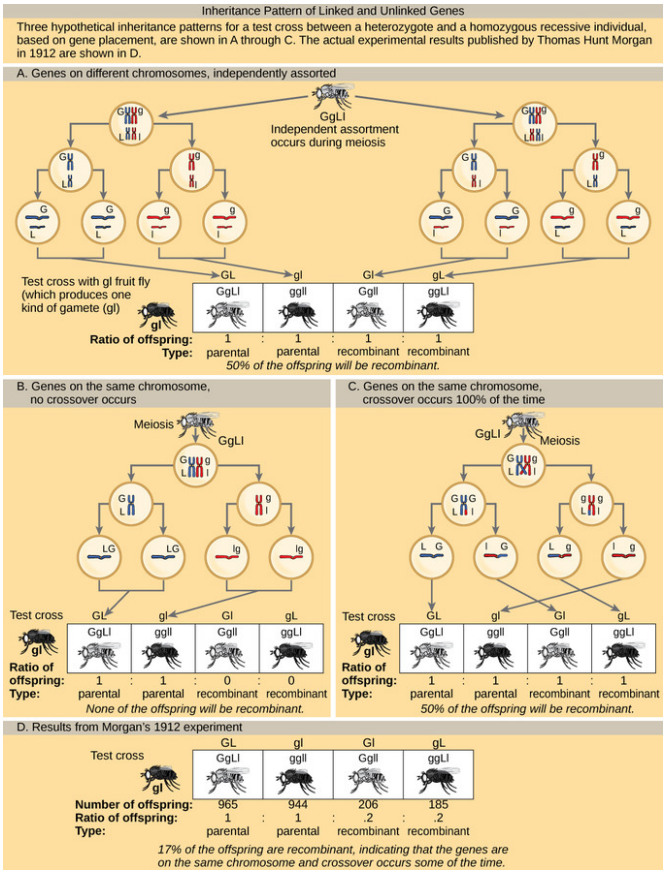


Figure 13.4.2.1: Inheritance Patterns of Unlinked and Linked Genes: In (a), two genes are located on different chromosomes so independent assortment occurs during meiosis. The offspring have an equal chance of being the parental type (inheriting the same combination of traits as the parents) or a nonparental type (inheriting a different combination of traits than the parents). In (b), two genes are very close together on the same chromosome so that no crossing over occurs between them. The genes are, therefore, always inherited together and all of the offspring are the parental type. In (c), two genes are far apart on the chromosome such that crossing over occurs during every meiotic event. The recombination frequency will be the same as if the genes were on separate chromosomes. (d) The actual recombination frequency of fruit fly wing length and body color that Thomas Morgan observed in 1912 was 17 percent. A crossover frequency between 0 percent and 50 percent indicates that the genes are on the same chromosome and crossover occurs some of the time.

Genetic Map Based on Recombination Frequencies in *Drosophila*

MUTANT		WILD TYPE
Short aristae	0	Long aristae
Black body	48.5	Gray body
Cinnabar eyes	57.5	Red eyes
Vestigial wings	65.5	Normal wings
Brown eyes	104.5	Red eyes

Values in centimorgan (cM) map units; recombination frequency of 0.01 = 1 cM

Figure 13.4.2.1: Genetic Maps: This genetic map orders Drosophila genes on the basis of recombination frequency.

By representing alleles in a linear map, Sturtevant suggested that genes can range from being perfectly linked (recombination frequency = 0) to being perfectly unlinked (recombination frequency = 0.5) when genes are on different chromosomes or genes are separated very far apart on the same chromosome. Perfectly unlinked genes correspond to the frequencies predicted by Mendel to

assort independently in a dihybrid cross. A recombination frequency of 0.5 indicates that 50 percent of offspring are recombinants and the other 50 percent are parental types. That is, every type of allele combination is represented with equal frequency. This allowed Sturtevant to calculate distances between several genes on the same chromosome.

Key Points

- Alleles positioned on the same chromosome are not always inherited together because during meiosis linked genes can became unlinked.
- Frans Janssen suggested chromosomes become unlinked during homologous recombination, a process where homologous chromosomes exchange segments of DNA.
- Alfred Sturtevant hypothesized that alleles that were closer together on a gene were more likely to be inherited together rather than alleles that were farther apart and used measurements of recombination between genes to create the first genetic map.
- When genes are perfectly linked, they have a recombination frequency of 0.
- When genes are unlinked, they have a recombination frequency of 0.5, which means 50 percent of offspring are recombinants and the other 50 percent are parental types.

Key Terms

- **homologous recombination**: a type of genetic recombination in which nucleotide sequences are exchanged between two similar or identical molecules of DNA
- **linkage**: the property of genes of being inherited together
- **synapsis**: the association of homologous maternal and paternal chromosomes during the initial part of meiosis

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SECTION OVERVIEW

13.5: Human Genetic Disorders



Is being short-statured inherited?

It can be. Achondroplasia is the most common form of dwarfism in humans, and it is caused by a dominant mutation. The mutation can be passed from one generation to the next.

Genetic Disorders

Many **genetic disorders** are caused by mutations in one or a few genes. Other genetic disorders are caused by abnormal numbers of chromosomes.

Genetic Disorders Caused by Mutations

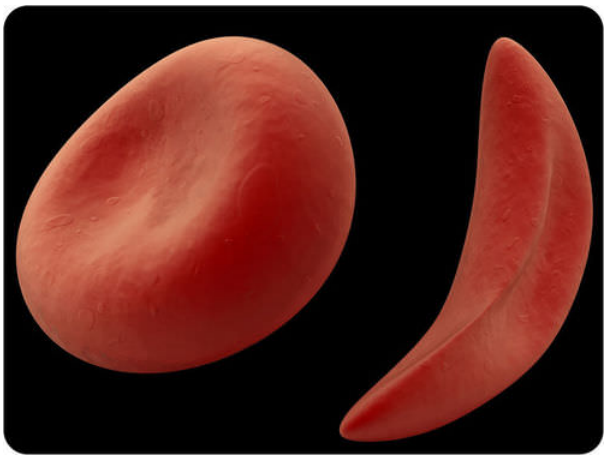
The **Table** below lists several genetic disorders caused by mutations in just one gene. Some of the disorders are caused by mutations in autosomal genes, others by mutations in X-linked genes. Which disorder would you expect to be more common in males than females? You can watch a video about the human genome, genetic disorders, and mutations at this link:http://www.pbs.org/wgbh/nova/programs/ht/rv/2809_03.html.

You can click on any human chromosome at this link to see the genetic disorders associated with it:http://www.ornl.gov/sci/techresource.../chooser.shtml.

Genetic Disorder	Direct Effect of Mutation	Signs and Symptoms of the Disorder	Mode of Inheritance
Marfan syndrome	defective protein in connective tissue	heart and bone defects and unusually long, slender limbs and fingers	autosomal dominant
Sickle cell anemia	abnormal hemoglobin protein in red blood cells	sickle-shaped red blood cells that clog tinyblood vessels, causing pain and damaging organs and joints	autosomal recessive
Vitamin D-resistant rickets	lack of a substance needed for bones to absorb minerals	soft bones that easily become deformed, leading to bowed legs and other skeletal deformities	X-linked dominant
Hemophilia A	reduced activity of a protein needed for blood clotting	internal and external bleeding that occurs easily and is difficult to control	X-linked recessive

Few genetic disorders are controlled by dominant alleles. A mutant dominant allele is expressed in every individual who inherits even one copy of it. If it causes a serious disorder, affected people may die young and fail to reproduce. Therefore, the mutant dominant allele is likely to die out of the population.

A mutant recessive allele, such as the allele that causes sickle cell anemia (see **Figure** belowand the link that follows), is not expressed in people who inherit just one copy of it. These people are called **carriers**. They do not have the disorder themselves, but they carry the mutant allele and can pass it to their offspring. Thus, the allele is likely to pass on to the next generation rather than die out. http://www.dnalc.org/resources/3d/17-sickle-cell.html



Sickle-Shaped and Normal Red Blood Cells. Sickle cell anemia is an autosomal recessive disorder. The mutation that causes the disorder affects just one amino acid in a single protein, but it has serious consequences for the affected person. This photo shows the sickle shape of red blood cells in people with sickle cell anemia.

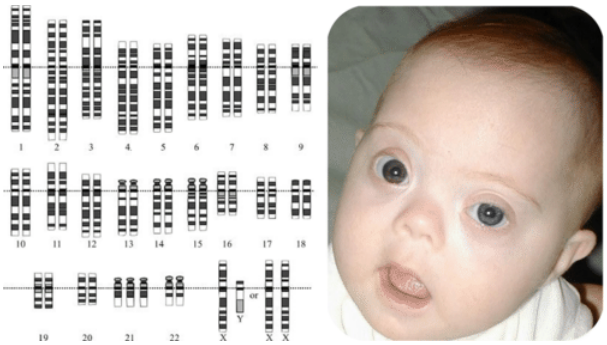
Cystic Fibrosis and Tay-Sachs disease are two additional severe genetic disorders. They are discussed in the following video: http://www.youtube.com/watch?v=8s4he3wLgkM (9:31). Tay-Sachs is further discussed at http://www.youtube.com/watch?v=1RO0LOgHbIo (3:13) andhttp://www.youtube.com/watch?v=6zNj5LdDuTA (2:01).

Chromosomal Disorders

Mistakes may occur during meiosis that result in **nondisjunction**. This is the failure of replicated chromosomes to separate during meiosis (the animation at the link below shows how this happens). Some of the resulting gametes will be missing a chromosome,

while others will have an extra copy of the chromosome. If such gametes are fertilized and form zygotes, they usually do not survive. If they do survive, the individuals are likely to have serious genetic disorders. **Table** below lists several genetic disorders that are caused by abnormal numbers of chromosomes. Most chromosomal disorders involve the X chromosome. Look back at the X and Y chromosomes and you will see why. The X and Y chromosomes are very different in size, so nondisjunction of the sex chromosomes occurs relatively often. learn.genetics.utah.edu/conte...der/index.html

Genetic Disorder	Genotype	Phenotypic Effects
Down syndrome	extra copy (complete or partial) of chromosome 21 (see **Figure** below)	developmental delays, distinctive facial appearance, and other abnormalities (see **Figure**below)
Turner's syndrome	one X chromosome but no other sex chromosome (XO)	female with short height and infertility (inability to reproduce)
Triple X syndrome	three X chromosomes (XXX)	female with mild developmental delays and menstrual irregularities
Klinefelter's syndrome	one Y chromosome and two or more X chromosomes (XXY, XXXY)	male with problems in sexual development and reduced levels of the male hormone testosterone



(left) Trisomy 21 (Down Syndrome) Karyotype. A **karyotype** is a picture of a cell's chromosomes. Note the extra chromosome 21. (right) Child with Down syndrome, exhibiting characteristic facial appearance.

Diagnosing Genetic Disorders

A genetic disorder that is caused by a mutation can be inherited. Therefore, people with a genetic disorder in their family may be concerned about having children with the disorder. Professionals known as **genetic counselors** can help them understand the risks of their children being affected. If they decide to have children, they may be advised to have **prenatal**("before birth") testing to see if the fetus has any genetic abnormalities. One method of prenatal testing is **amniocentesis**. In this procedure, a few fetal cells are extracted from the fluid surrounding the fetus, and the fetal chromosomes are examined.

Treating Genetic Disorders

The symptoms of genetic disorders can sometimes be treated, but cures for genetic disorders are still in the early stages of development. One potential cure that has already been used with some success is **gene therapy**. This involves inserting normal genes into cells with mutant genes. At the following link, you can watch the video ''Sickle Cell Anemia: Hope fromGene Therapy'', to learn how scientists are trying to cure sickle-cell anemia with gene therapy. www.pubinfo.vcu.edu/secretsof...list_frame.asp

If you could learn your risk of getting cancer or another genetic disease, would you? Though this is a personal decision, it is a possibility. A number of companies now makes it easy to order medical genetic tests through the Web. See *Genetic Testing through the Web* athttp://www.kqed.org/quest/televisi...hrough-the-web.

Summary

- Many genetic disorders are caused by mutations in one or a few genes.
- Other genetic disorders are caused by abnormal numbers of chromosomes.

Explore More

Use this resource to answer the questions that follow.

- **Genetic Disorders** at http://www.nlm.nih.gov/medlineplus/g...disorders.html.

1. How do mutations affect proteins?
2. What is a single-gene disorder?
3. What is a chromosomal disorder?
4. What is a complex disorder?
5. Give an example of a chromosomal disorder.

Review

1. Describe a genetic disorder caused by a mutation in a single gene.
2. What causes Down syndrome?
3. What is nondisjunction?
4. What is gene therapy?
5. Explain why genetic disorders caused by abnormal numbers of chromosomes most often involve the X chromosome.

13.5.1: Imprinted Genes

13.5.2: Prenatal Screening

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13.5.1: Imprinted Genes

Imprinted genes are genes whose expression is determined by the parent that contributed them. Imprinted genes violate the usual rule of inheritance that both alleles in a heterozygote are equally expressed.

Examples of the **usual rule**:

- If a child inherits the gene for **blood group A** from either parent and the gene for **group B** from the other parent, the child's blood group will be **AB**.
- If a child inherits the gene encoding **hemoglobin A** from either parent and the gene encoding **hemoglobin S** from the other parent, the child's red blood cells will contain roughly equal amounts of the two types of hemoglobin.

But there are a few exceptions to this rule. A small number of genes in mammals (~80 of them at a recent count) and in angiosperms have been found to be **imprinted**. Because most imprinted genes are repressed, either

- the **maternal** (inherited from the mother) allele is expressed exclusively because the **paternal** (inherited from the father) allele is imprinted or
- vice versa.

The process begins during gamete formation when

- in males certain genes are imprinted in developing sperm and
- in females, others are imprinted in the developing egg.

All the cells in a resulting child will have the same set of imprinted genes from both its father and its mother EXCEPT for those cells ("germplasm") that are destined to go on to make gametes. All imprints — both maternal and paternal — are erased in them.

Examples

IGF2

— the gene encoding the **insulin-like growth factor-2**

In humans (and other mammals like mice and pigs) the *IGF2* allele inherited from the father (paternal) is expressed; the allele inherited from the mother is not.

If both alleles should begin to be expressed in a cell, that cell may develop into a cancer.

IGF2r

— the gene encoding the cell **receptor for Igf-2**

In mice the *IGF2r* allele inherited from the mother is expressed; that from the father is not. Differential imprinting accounts for this, and the mechanism is described below.

XIST

— the gene encoding the RNA that converts one of the X chromosomes in a female cell into an inactive **Barr body**. This process is random in the cells of the female **fetus** and thus is NOT an example of imprinting. However, all the cells of her extraembryonic membranes (which form the amnion, placenta, and umbilical cord) have the father's X chromosome inactivated. Imprinting of the *XIST* locus accounts for this.

Mechanism of parental imprinting

The process of imprinting starts in the gametes where the allele destined to be inactive in the new embryo (either the father's or the mother's as the case may be) is "marked". The mark appears to be **methylation** of the DNA in the promoter(s) of the gene.

Methyl groups are added to cytosines (Cs) in the DNA. When this occurs at stretches of alternating Cs and Gs called **CpG sites** in a promoter, it prevents binding of transcription factors to the promoter thus shutting down expression of the gene.



Although methylation seems to be the imprinting **signal**, keeping the gene shut down may require the production of **RNA**.

Methylation — and thus inactivation — of the promoters of tumor suppressor genes is frequently found in cancer cells.

The *IGF2r* gene

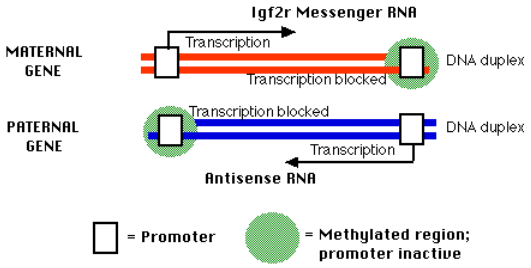


Figure 9.12.1 the IGF2r gene

A report in **Nature** (16 October 1997) by Wutz et al, reveals that:

In the mother's (**maternal**) copy of the gene,

- there is an upstream (left) promoter that is unmethylated and active
- binding of transcription factors to this upstream promoter enables transcription of the sense strand of the gene to produce **Igf2r messenger RNA**.
- There is also a downstream set of CpG sites that are methylated

In the father's (**paternal**) copy of the *IGF2r* gene (the imprinted version)

- the promoter for *IGF2r* transcription is methylated (and inactive),
- but the downstream promoter is unmethylated and active.
- Transcription of the antisense strand from the downstream promoter produces an **antisense RNA** (a long noncoding RNA) that participates in shutting his gene down.

XIST

The *XIST* locus on the X chromosome encodes a **long noncoding RNA** that shuts down all (or almost all) of the other genes on the chromosome, converting it into an inactive **Barr body**.

Is imprinting important?

Yes.

- Deliberate (in mice) or accidental (in humans) inheritance of two copies of a particular chromosome from one parent and none from the other parent is usually fatal (even though a complete genome is present).
- Inheritance of two copies of one of mother's genes and no copy of the father's (or vice versa) can produce serious developmental defects.
  - Failure to inherit several nonimprinted genes on the father's chromosome #15 causes a human congenital disorder called **Prader-Willi syndrome**.
  - Absence or mutation of a nonimprinted gene (*UBE3A*) on the mother's chromosome #15 causes **Angelman syndrome**.
- Failure of imprinting in somatic cells may lead to **cancer**.
  - The cancerous cells in some cases of a malignancy called **Wilms´ tumor** and many cases of colon cancer have both copies of the ***IGF2*** gene expressed (where only one, the father's, should be).
  - **Reduced methylation** — and hence increased expression — of **proto-oncogenes** can lead to cancer, while
  - **increased methylation** — and hence decreased expression — of **tumor suppressor genes** can also do so.

Imprinting and Parthenogenesis

Imprinting is the reason that parthenogenesis ("virgin birth") does not occur in mammals. Two complete female genomes cannot produce viable young because of the imprinted genes. For example, the embryo needs the father's *Igf2* gene because the mother's copy has been imprinted and is inactive.

- An insulator — with a bound protein designated CTCF ("CCCTC binding factor") (named for a nucleotide sequence found in all insulators) — prevents her *Igf2* gene from interacting with the enhancers needed to turn it ON.
- The father's copy of the gene can be turned on because methylation of his insulator prevents binding by CTCF so the enhancers can interact with the gene.

However, two healthy laboratory mice have been produced by parthenogenesis; that is, containing two female (haploid) genomes. (See Kono, T. *et al*., **Nature**, 22 April 2004.)

This was done by fusing two oocytes (thus each cell haploid):

- a normal oocyte with its imprinted (inactivated) *Igf2* gene
- an immature oocyte
  - harvested before imprinting occurs and
  - containing a deletion of the insulator that blocks enhancer activation of the *Igf2* gene. Thus the *Igf2* gene from this oocyte could be expressed in the developing embryo.

Out of several hundred attempts, two resulting blastocysts not only implanted successfully in a surrogate mother but went on to be born normally. One even grew up and had babies of her own.

Imprinting in Plants

Some genes in the endosperm of angiosperms are imprinted by the addition of methyl groups. For some, both maternal copies (endosperm is **3n**) are expressed (demethylated) while the male allele remains shut down. For other genes, it is the female alleles that are imprinted and thus not expressed while the male allele is functional.

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13.5.2: Prenatal Screening

Many tests are now available to detect genetic diseases such as sickle cell disease, cystic fibrosis and phenylketonuria (PKU). Most of these tests can not only be performed on cells removed from adults but also on cells removed from the fetus and even from a pre-implantation embryo.

Amniocentesis

During its development, the fetus sheds cells into the amniotic fluid. After 14–22 weeks of pregnancy, a small volume of this fluid can be removed (using a needle inserted through the abdominal wall).

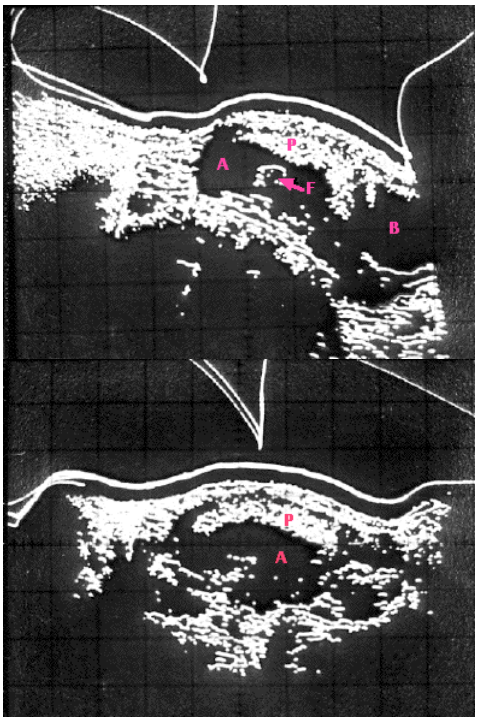


Figure 15.7.4.1 Ultrasound prior to amniocentesis

Using ultrasound to locate the position of the placenta prior to amniocentesis. These sonograms are made by recording the echoes received from structures within the abdomen. A, amniotic cavity; B, urinary bladder; F, part of the fetus; P, placenta. Both longitudinal (left) and transverse (right) scans are needed for accurate localization of the placenta. (Courtesy of the Downstate Medical Center of the State University of New York.)

Separating the cells and culturing them enables the clinician to look for

- chromosome abnormalities (e.g., the three number 21 chromosomes of Down syndrome)
- certain enzymatic defects (e.g., an inability to metabolize galactose, hence milk)
- the sex of the fetus

Over 100 genetic abnormalities can be diagnosed by amniocentesis and the pregnancy deliberately ended if the parents wish it.

Chorionic Villus Sampling (CVS)

This is an alternate method of prenatal diagnosis. A small amount of placental tissue is sucked out by a tube inserted through the abdominal wall or through the vagina (the latter avoiding the need for an incision). For some tests the fetal cells can be examined immediately without the need to culture them. Another advantage of CVS is that it can be performed earlier in pregnancy (after only 10–12 weeks) than amniocentesis. If an abortion is to be performed, it is a simpler process early in pregnancy.

Non-Invasive Prenatal Genetic Testing (NIPT)

Although the blood vessels of the placenta are in close contact with the mother's blood vessels in the uterus, intermingling of their blood does not normally occur. However some of cells of the fetus do manage to get into the mother's circulation where they may represent 1 in a million of her white blood cells (so only some 2–6 cells per ml of blood). Fragments of fetal DNA (~ 300 bp long) from apoptotic cells of the placenta are also found in the mother's plasma as early as 5 weeks after implantation. This raises the possibility of using genetic tests (e.g., PCR) to identify mutations or chromosomal abnormalities in the fetus using a small (~10 ml) sample of blood drawn from the mother.

Two home blood test kits for determining the sex of the fetus are already on the market. The collected drops of blood are sent to a laboratory to determine whether any Y-chromosome-specific DNA (e.g., *SRY*) is present. Tests of fetal DNA for Down syndrome (trisomy 21), as well as for trisomy 13 and 18, have both higher sensitivity (false negatives <0.1%) and specificity (false positives <0.2%) than amniocentesis and CVS.

In several European countries, Rh-negative mothers can now have their blood screened for the presence of an Rh-positive fetus. The time will surely come when such NIPT screening will become available for many genetic disorders. The procedure is also called non-invasive prenatal diagnosis - NIPD.

The level of fetal DNA in the mother's blood rises to a peak at the time of birth and some evidence suggests that this rise may be a trigger to start the birth process.

Preimplantation Genetic Diagnosis (PGD)

Genetic Analysis of Blastomeres

One of the remarkable facts about mammalian development is that all the cells in the early (e.g., 8-cell) embryo are not needed to produce a healthy fetus (which is why a single fertilized egg can on occasions produce identical twins, triplets, etc.). So couples using in vitro fertilization (IVF) also can take advantage of genetic screening. While the embryo is in culture, one or two cells can safely be removed and tested for their genotype. For example:

- The sex of the embryo can be determined with a probe for Y-specific DNA. This permits prospective mothers carrying a severe X-linked trait like hemophilia A to choose a female rather than a male embryo for attempted implantation.
- Fluorescent probes specific for the DNA of particular chromosomes can detect (by FISH) if there is an abnormal number (aneuploidy) such as the three #21 chromosomes of Down syndrome.
- In fact the entire karyotype of the embryo can be determined. Random fragments of DNA prepared by the polymerase chain reaction (PCR) of all the DNA of a cell from the **embryo** can be
  - given a fluorescent label
  - applied to the metaphase **chromosomes** of a standard reference cell that has a normal karyotype along with
  - DNA fragments from the reference cell labelled with a different color.

  Comparing the intensity of the two colors from each chromosome shows whether the embryo has the normal amount of DNA for that chromosome or is aneuploid containing either:
  - too much (e.g. 3 copies of #21 — trisomy)
  - too little (only a single copy of #14 — monosomy)

Genetic Analysis of Polar Bodies

As meiosis I is completed, one set of duplicated chromosomes (dyads) is extruded into the first polar body. The DNA of the polar body can be amplified by the polymerase chain reaction (PCR) and tested.

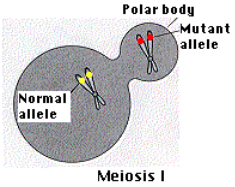


Figure 15.7.4.2 Polar body screening

If the mother is heterozygous for a trait, **and no crossover** has occurred, and the polar body contains the mutant alleles (see figure), the egg can be safely fertilized. (For simplicity, the figure shows only the pair of homologues carrying the locus of concern.)

However, if crossing over has occurred, the first polar body would contain one mutant and one healthy allele. In that case, there is a 50:50 chance that, after fertilization, the other copy of the mutant allele will end up in the egg (instead of in the second polar body). So the second polar body should also be tested to see if it also contains the mutant allele. Only if it does can the egg be safely used.

Contributors and Attributions

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CHAPTER OVERVIEW

14: DNA- The Genetic Material

14.1: The Nature of Genetic Material

14.2: DNA Structure

14.3: Basic Characteristics of DNA Replication

14.4: Prokaryotic Replication

14.4.1: DNA Replication in Prokaryotes

14.5: Eukaryotic Replication

14.6: DNA Repair

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14.1: The Nature of Genetic Material



The spiral structure in the picture is a large organic molecule. What type of organic molecule is it?

Here's a hint: molecules like this one determine who you are. They contain genetic information that controls your characteristics. They determine your eye color, facial features, and other physical attributes. What molecule is it?

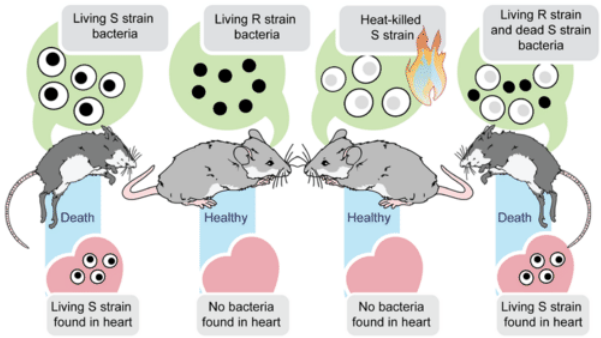
You probably answered "DNA." Today, it is commonly known that DNA is the genetic material. For a long time, scientists knew such molecules existed. They were aware that genetic information was contained within organic molecules. However, they didn't know which type of molecules play this role. In fact, for many decades, scientists thought that proteins were the molecules that carry genetic information. In this section, you will learn how scientists discovered that DNA carries the code of life.

DNA, the Genetic Material

DNA, deoxyribonucleic acid, is the genetic material in your cells. It was passed on to you from your parents and determines your characteristics. The discovery that DNA is the genetic material was another important milestone in molecular biology.

Griffith Searches for the Genetic Material

Many scientists contributed to the identification of DNA as the genetic material. In the 1920s, Frederick Griffith made an important discovery. He was studying two different strains of a bacterium, called R (rough) strain and S (smooth) strain. He injected the two strains into mice. The S strain killed (virulent) the mice, but the R strain did not (non-virulent) (see **Figure** below). Griffith also injected mice with S-strain bacteria that had been killed by heat. As expected, the killed bacteria did not harm the mice. However, when the dead S-strain bacteria were mixed with live R-strain bacteria and injected, the mice died.



Griffith's Experimental Results. Griffith showed that a substance could be transferred to harmless bacteria and make them deadly.

Based on his observations, Griffith deduced that something in the killed S strain was transferred to the previously harmless R strain, making the R strain deadly. He called this process **transformation**, as something was "transforming" the bacteria from one strain into another strain. What was that something? What type of substance could change the characteristics of the organism that received it?

Avery's Team Makes a Major Contribution

In the early 1940s, a team of scientists led by Oswald Avery tried to answer the question raised by Griffith's results. They inactivated various substances in the S-strain bacteria. They then killed the S-strain bacteria and mixed the remains with live R-

strain bacteria. (Keep in mind, the R-strain bacteria usually did not harm the mice.) When they inactivated proteins, the R-strain was deadly to the injected mice. This ruled out proteins as the genetic material. Why? Even without the S-strain proteins, the R strain was changed, or transformed, into the deadly strain. However, when the researchers inactivated DNA in the S strain, the R strain remained harmless. This led to the conclusion that DNA is the substance that controls the characteristics of organisms. In other words, DNA is the genetic material. You can watch an animation about the research of both Griffith and Avery at this link:http://www.dnalc.org/view/16375-Animation-17-A-gene-is-made-of-DNA-.html.

Hershey and Chase Seal the Deal

The conclusion that DNA is the genetic material was not widely accepted at first. It had to be confirmed by other research. In the 1950s, Alfred Hershey and Martha Chase did experiments with viruses and bacteria. **Viruses** are not made of cells. They are basically DNA inside a protein coat. To reproduce, a virus must insert its own genetic material into a cell (such as a bacterium). Then it uses the cell's machinery to make more viruses. The researchers used different radioactive elements to label the DNA and proteins in viruses. This allowed them to identify which molecule the viruses inserted into bacteria. DNA was the molecule they identified. This confirmed that DNA is the genetic material.

Summary

- The work of several researchers led to the discovery that DNA is the genetic material.
- Along the way, Griffith discovered the process of transformation.

Explore More

Use this resource to answer the questions that follow.

I) Bacteria and viruses have DNA too at

www.dnalc.org/resources/nobel/hershey.html

1. What is a bacteriophage?
2. How do phages reproduce?
3. Why was DNA labeled with radioactive phosphorus?
4. After the experiment, where was the radioactive phosphorus found?
5. What is the genetic material? Why?

II) A gene is made of DNA at

http://www.dnaftb.org/17/animation.html and http://www.dnaftb.org/17/problem.html.

Review

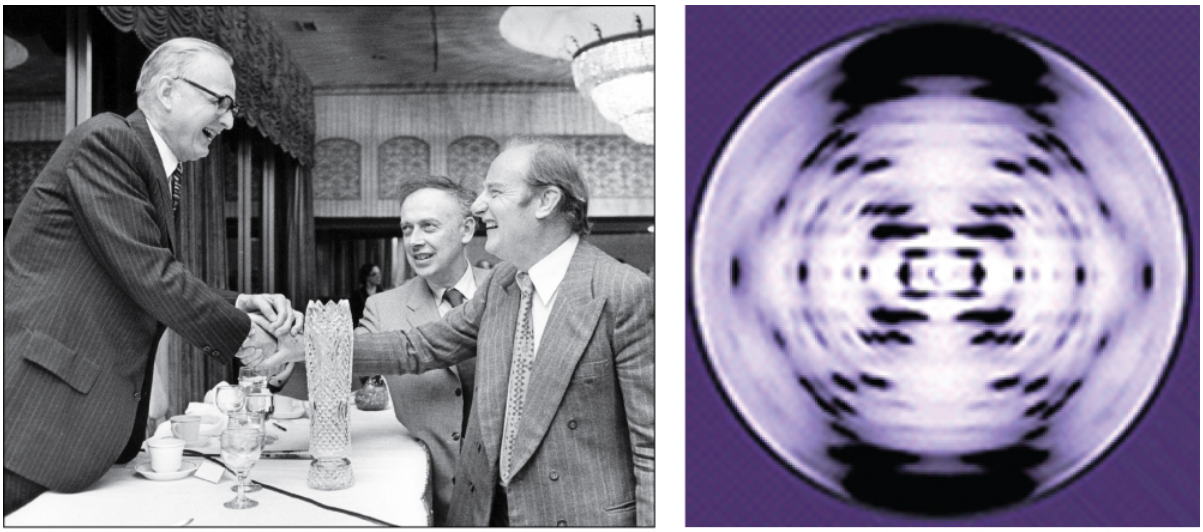
1. List the research that determined that DNA is the genetic material.
2. What is transformation?
3. What happened to the R-strain bacteria when Avery and his colleagues inactivated DNA in the S strain bacteria?

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14.2: DNA Structure

In the 1950s, Francis Crick and James Watson worked together at the University of Cambridge, England, to determine the structure of DNA. Other scientists, such as Linus Pauling and Maurice Wilkins, were also actively exploring this field. Pauling had discovered the secondary structure of proteins using X-ray crystallography. X-ray crystallography is a method for investigating molecular structure by observing the patterns formed by X-rays shot through a crystal of the substance. The patterns give important information about the structure of the molecule of interest. In Wilkins' lab, researcher Rosalind Franklin was using X-ray crystallography to understand the structure of DNA. Watson and Crick were able to piece together the puzzle of the DNA molecule using Franklin's data (Figure **14.2.1**). Watson and Crick also had key pieces of information available from other researchers such as Chargaff's rules. Chargaff had shown that of the four kinds of monomers (nucleotides) present in a DNA molecule, two types were always present in equal amounts and the remaining two types were also always present in equal amounts. This meant they were always paired in some way. In 1962, James Watson, Francis Crick, and Maurice Wilkins were awarded the Nobel Prize in Medicine for their work in determining the structure of DNA.



(a) (b)

Figure 14.2.1: Pioneering scientists (a) James Watson and Francis Crick are pictured here with American geneticist Maclyn McCarty. Scientist Rosalind Franklin discovered (b) the X-ray diffraction pattern of DNA, which helped to elucidate its double helix structure. (credit a: modification of work by Marjorie McCarty; b: modification of work by NIH)

Now let's consider the structure of the two types of nucleic acids, deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). The building blocks of DNA are nucleotides, which are made up of three parts: a deoxyribose (5-carbon sugar), a phosphate group, and a nitrogenous base (Figure **14.2.2**). There are four types of nitrogenous bases in DNA. Adenine (A) and guanine (G) are double-ringed purines, and cytosine (C) and thymine (T) are smaller, single-ringed pyrimidines. The nucleotide is named according to the nitrogenous base it contains.

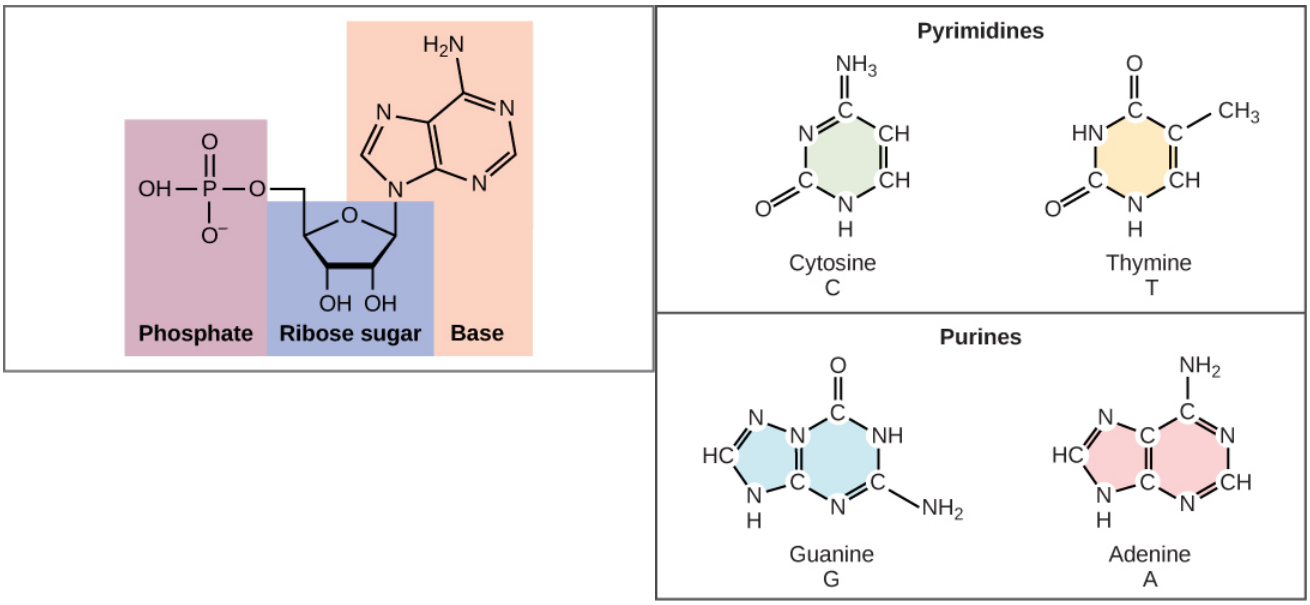


Figure 14.2.2: (a) Each DNA nucleotide is made up of a sugar, a phosphate group, and a base. (b) Cytosine and thymine are pyrimidines. Guanine and adenine are purines.

The phosphate group of one nucleotide bonds covalently with the sugar molecule of the next nucleotide, and so on, forming a long polymer of nucleotide monomers. The sugar–phosphate groups line up in a "backbone" for each single strand of DNA, and the nucleotide bases stick out from this backbone. The carbon atoms of the five-carbon sugar are numbered clockwise from the oxygen as 1', 2', 3', 4', and 5' (1' is read as "one prime"). The phosphate group is attached to the 5' carbon of one nucleotide and the 3' carbon of the next nucleotide. In its natural state, each DNA molecule is actually composed of two single strands held together along their length with hydrogen bonds between the bases.

Watson and Crick proposed that the DNA is made up of two strands that are twisted around each other to form a right-handed helix, called a double helix. Base-pairing takes place between a purine and pyrimidine: namely, A pairs with T, and G pairs with C. In other words, adenine and thymine are complementary base pairs, and cytosine and guanine are also complementary base pairs. This is the basis for Chargaff's rule; because of their complementarity, there is as much adenine as thymine in a DNA molecule and as much guanine as cytosine. Adenine and thymine are connected by two hydrogen bonds, and cytosine and guanine are connected by three hydrogen bonds. The two strands are anti-parallel in nature; that is, one strand will have the 3' carbon of the sugar in the "upward" position, whereas the other strand will have the 5' carbon in the upward position. The diameter of the DNA double helix is uniform throughout because a purine (two rings) always pairs with a pyrimidine (one ring) and their combined lengths are always equal (Figure **14.2.3**).

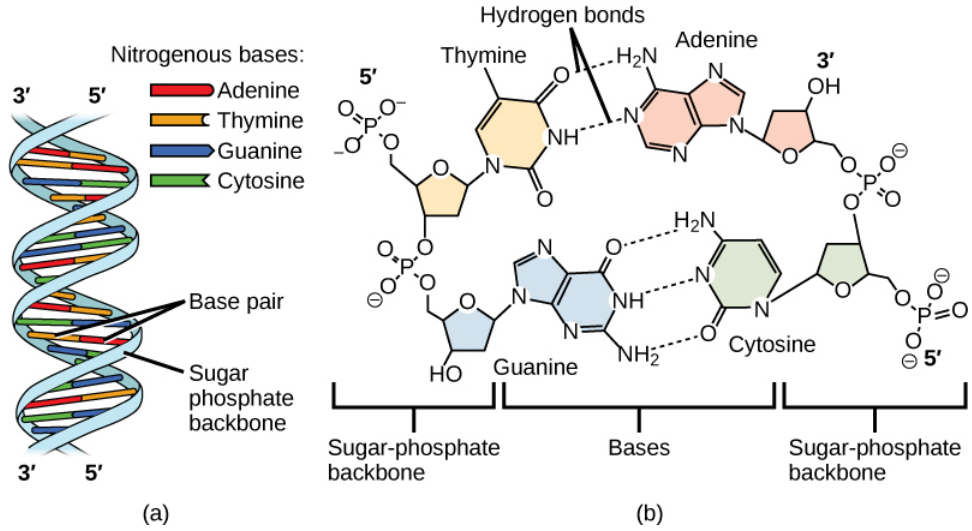


Figure 14.2.3: DNA (a) forms a double stranded helix, and (b) adenine pairs with thymine and cytosine pairs with guanine. (credit a: modification of work by Jerome Walker, Dennis Myts)

The Structure of RNA

There is a second nucleic acid in all cells called ribonucleic acid, or RNA. Like DNA, RNA is a polymer of nucleotides. Each of the nucleotides in RNA is made up of a nitrogenous base, a five-carbon sugar, and a phosphate group. In the case of RNA, the five-carbon sugar is ribose, not deoxyribose. Ribose has a hydroxyl group at the 2' carbon, unlike deoxyribose, which has only a hydrogen atom (Figure **14.2.4**).

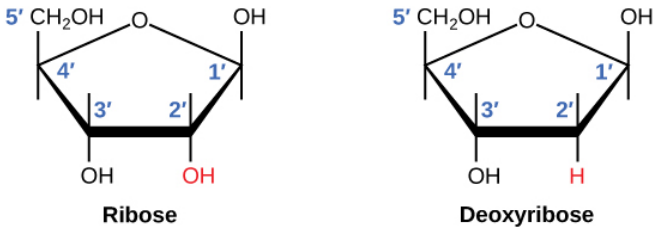


Figure 14.2.4: The difference between the ribose found in RNA and the deoxyribose found in DNA is that ribose has a hydroxyl group at the 2' carbon.

RNA nucleotides contain the nitrogenous bases adenine, cytosine, and guanine. However, they do not contain thymine, which is instead replaced by uracil, symbolized by a “U.” RNA exists as a single-stranded molecule rather than a double-stranded helix. Molecular biologists have named several kinds of RNA on the basis of their function. These include messenger RNA (mRNA), transfer RNA (tRNA), and ribosomal RNA (rRNA)—molecules that are involved in the production of proteins from the DNA code.

How DNA Is Arranged in the Cell

DNA is a working molecule; it must be replicated when a cell is ready to divide, and it must be “read” to produce the molecules, such as proteins, to carry out the functions of the cell. For this reason, the DNA is protected and packaged in very specific ways. In addition, DNA molecules can be very long. Stretched end-to-end, the DNA molecules in a single human cell would come to a length of about 2 meters. Thus, the DNA for a cell must be packaged in a very ordered way to fit and function within a structure (the cell) that is not visible to the naked eye. The chromosomes of prokaryotes are much simpler than those of eukaryotes in many of their features (Figure **14.2.5**). Most prokaryotes contain a single, circular chromosome that is found in an area in the cytoplasm called the nucleoid.

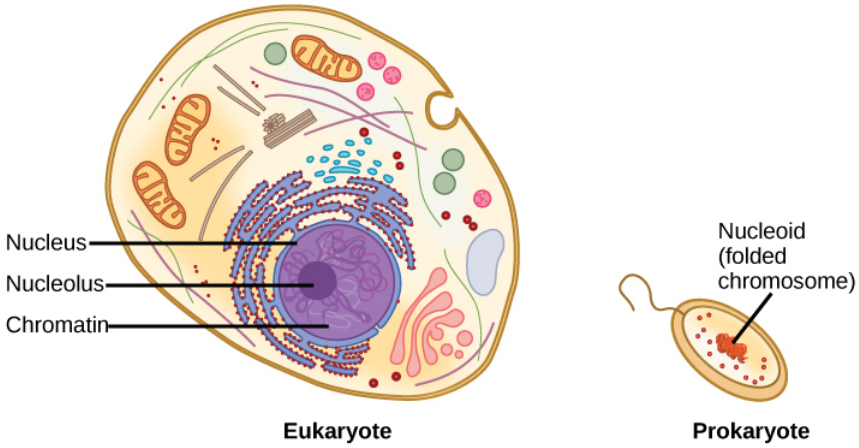


Figure 14.2.5: A eukaryote contains a well-defined nucleus, whereas in prokaryotes, the chromosome lies in the cytoplasm in an area called the nucleoid.

The size of the genome in one of the most well-studied prokaryotes, *Escherichia coli*, is 4.6 million base pairs, which would extend a distance of about 1.6 mm if stretched out. So how does this fit inside a small bacterial cell? The DNA is twisted beyond the double helix in what is known as supercoiling. Some proteins are known to be involved in the supercoiling; other proteins and enzymes help in maintaining the supercoiled structure.

Eukaryotes, whose chromosomes each consist of a linear DNA molecule, employ a different type of packing strategy to fit their DNA inside the nucleus (Figure 14.2.6). At the most basic level, DNA is wrapped around proteins known as histones to form structures called nucleosomes. The DNA is wrapped tightly around the histone core. This nucleosome is linked to the next one by a short strand of DNA that is free of histones. This is also known as the "beads on a string" structure; the nucleosomes are the "beads" and the short lengths of DNA between them are the "string." The nucleosomes, with their DNA coiled around them, stack compactly onto each other to form a 30-nm–wide fiber. This fiber is further coiled into a thicker and more compact structure. At the metaphase stage of mitosis, when the chromosomes are lined up in the center of the cell, the chromosomes are at their most compacted. They are approximately 700 nm in width, and are found in association with scaffold proteins.

In interphase, the phase of the cell cycle between mitoses at which the chromosomes are decondensed, eukaryotic chromosomes have two distinct regions that can be distinguished by staining. There is a tightly packaged region that stains darkly, and a less dense region. The darkly staining regions usually contain genes that are not active, and are found in the regions of the centromere and telomeres. The lightly staining regions usually contain genes that are active, with DNA packaged around nucleosomes but not further compacted.

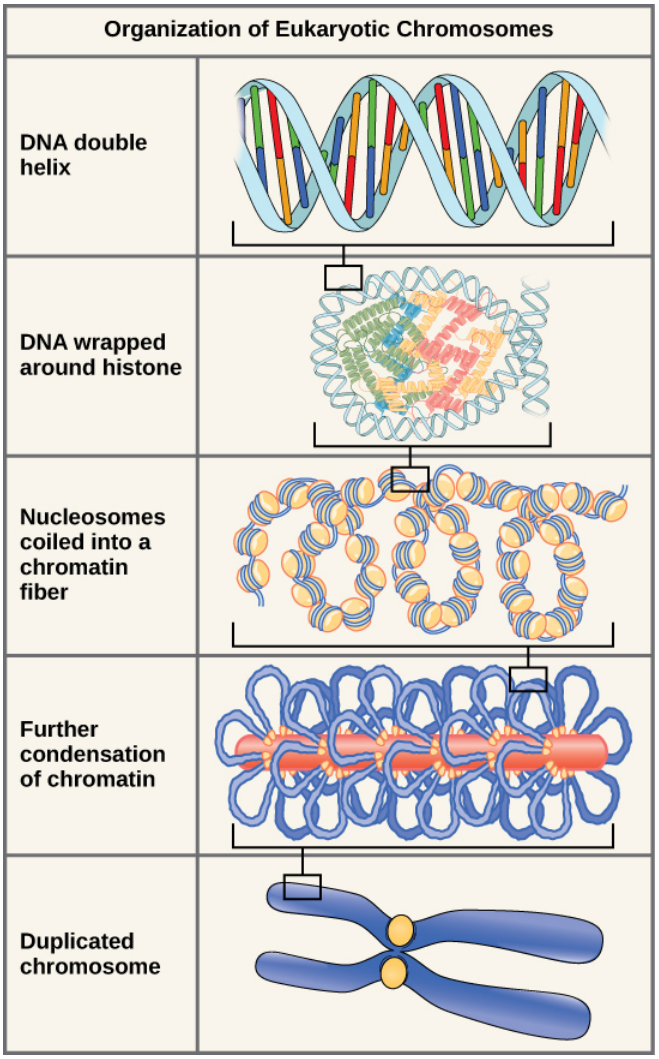


Figure 14.2.6: These figures illustrate the compaction of the eukaryotic chromosome.

CONCEPT IN ACTION



Watch this animation of DNA packaging.

Summary

The model of the double-helix structure of DNA was proposed by Watson and Crick. The DNA molecule is a polymer of nucleotides. Each nucleotide is composed of a nitrogenous base, a five-carbon sugar (deoxyribose), and a phosphate group. There

are four nitrogenous bases in DNA, two purines (adenine and guanine) and two pyrimidines (cytosine and thymine). A DNA molecule is composed of two strands. Each strand is composed of nucleotides bonded together covalently between the phosphate group of one and the deoxyribose sugar of the next. From this backbone extend the bases. The bases of one strand bond to the bases of the second strand with hydrogen bonds. Adenine always bonds with thymine, and cytosine always bonds with guanine. The bonding causes the two strands to spiral around each other in a shape called a double helix. Ribonucleic acid (RNA) is a second nucleic acid found in cells. RNA is a single-stranded polymer of nucleotides. It also differs from DNA in that it contains the sugar ribose, rather than deoxyribose, and the nucleotide uracil rather than thymine. Various RNA molecules function in the process of forming proteins from the genetic code in DNA.

Prokaryotes contain a single, double-stranded circular chromosome. Eukaryotes contain double-stranded linear DNA molecules packaged into chromosomes. The DNA helix is wrapped around proteins to form nucleosomes. The protein coils are further coiled, and during mitosis and meiosis, the chromosomes become even more greatly coiled to facilitate their movement. Chromosomes have two distinct regions which can be distinguished by staining, reflecting different degrees of packaging and determined by whether the DNA in a region is being expressed (euchromatin) or not (heterochromatin).

Glossary

deoxyribose
: a five-carbon sugar molecule with a hydrogen atom rather than a hydroxyl group in the 2' position; the sugar component of DNA nucleotides

double helix
: the molecular shape of DNA in which two strands of nucleotides wind around each other in a spiral shape

nitrogenous base
: a nitrogen-containing molecule that acts as a base; often referring to one of the purine or pyrimidine components of nucleic acids

phosphate group
: a molecular group consisting of a central phosphorus atom bound to four oxygen atoms

Contributors and Attributions

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14.3: Basic Characteristics of DNA Replication

Skills to Develop

- Explain how the structure of DNA reveals the replication process
- Describe the Meselson and Stahl experiments

The elucidation of the structure of the double helix provided a hint as to how DNA divides and makes copies of itself. This model suggests that the two strands of the double helix separate during replication, and each strand serves as a template from which the new complementary strand is copied. What was not clear was how the replication took place. There were three models suggested (Figure **14.3.1**): *conservative*, *semi-conservative*, *and dispersive*.

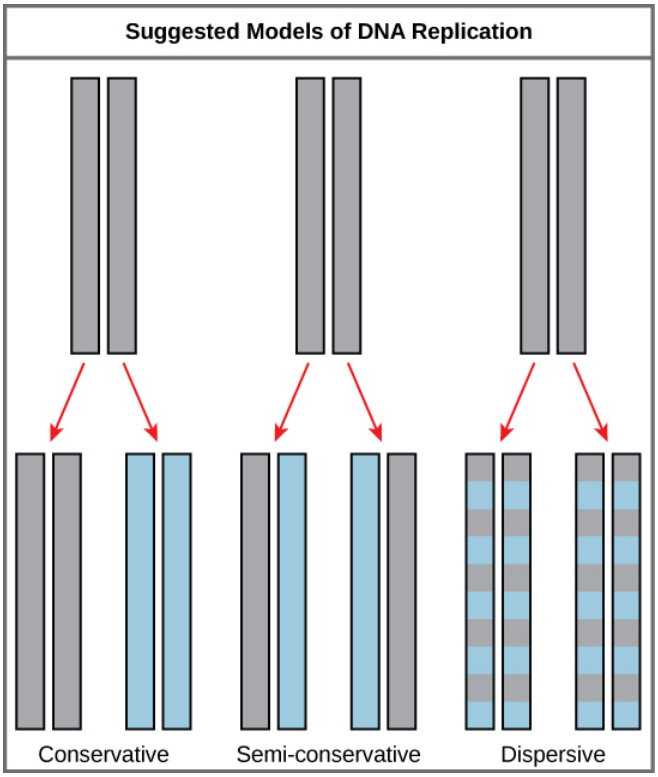


Figure **14.3.1**: The three suggested models of DNA replication. Grey indicates the original DNA strands, and blue indicates newly synthesized DNA

In conservative replication, the parental DNA remains together, and the newly formed daughter strands are together. The semi-conservative method suggests that each of the two parental DNA strands act as a template for new DNA to be synthesized; after replication, each double-stranded DNA includes one parental or “old” strand and one “new” strand. In the dispersive model, both copies of DNA have double-stranded segments of parental DNA and newly synthesized DNA interspersed.

Meselson and Stahl were interested in understanding how DNA replicates. They grew *E. coli* for several generations in a medium containing a “heavy” isotope of nitrogen (^{15}N) that gets incorporated into nitrogenous bases, and eventually into the DNA (Figure **14.3.2**).

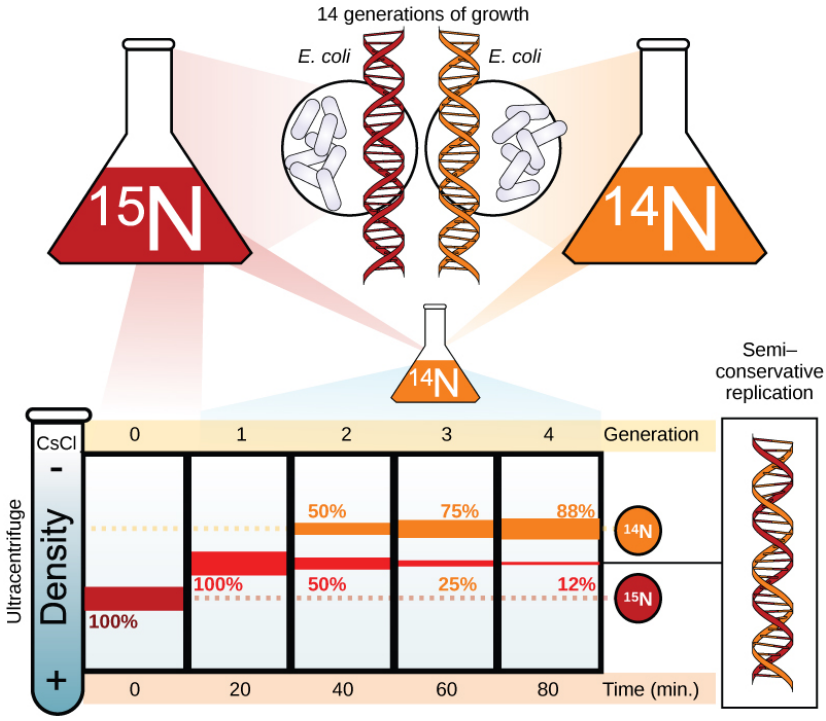
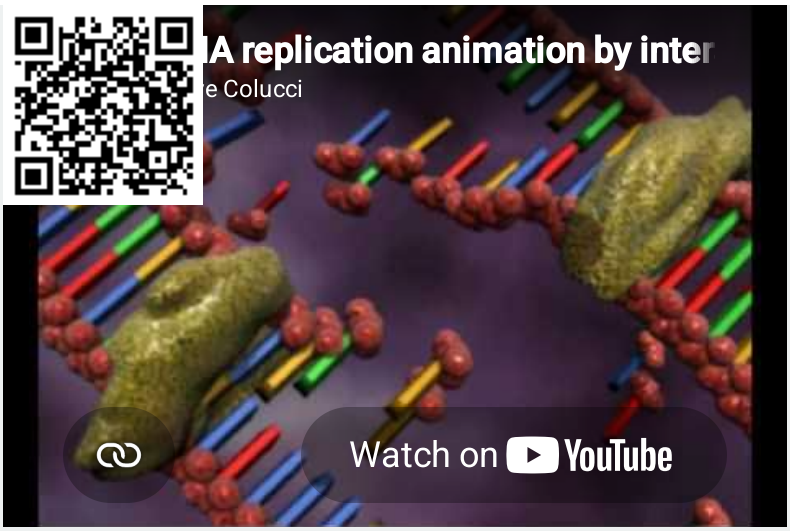


Figure **14.3.2**: Meselson and Stahl experimented with E. coli grown first in heavy nitrogen (^{15}N) then in ^{14}N. DNA grown in ^{15}N (red band) is heavier than DNA grown in ^{14}N (orange band), and sediments to a lower level in cesium chloride solution in an ultracentrifuge. When DNA grown in ^{15}N is switched to media containing ^{14}N, after one round of cell division the DNA sediments halfway between the ^{15}N and ^{14}N levels, indicating that it now contains fifty percent ^{14}N. In subsequent cell divisions, an increasing amount of DNA contains ^{14}N only. This data supports the semi-conservative replication model. (credit: modification of work by Mariana Ruiz Villareal)

The *E. coli* culture was then shifted into medium containing ^{14}N and allowed to grow for one generation. The cells were harvested and the DNA was isolated. The DNA was centrifuged at high speeds in an ultracentrifuge. Some cells were allowed to grow for one more life cycle in ^{14}N and spun again. During the density gradient centrifugation, the DNA is loaded into a gradient (typically a salt such as cesium chloride or sucrose) and spun at high speeds of 50,000 to 60,000 rpm. Under these circumstances, the DNA will form a band according to its density in the gradient. DNA grown in ^{15}N will band at a higher density position than that grown in ^{14}N. Meselson and Stahl noted that after one generation of growth in ^{14}N after they had been shifted from ^{15}N, the single band observed was intermediate in position in between DNA of cells grown exclusively in ^{15}N and ^{14}N. This suggested either a semi-conservative or dispersive mode of replication. The DNA harvested from cells grown for two generations in ^{14}N formed two bands: one DNA band was at the intermediate position between ^{15}N and ^{14}N, and the other corresponded to the band of ^{14}N DNA. These results could only be explained if DNA replicates in a semi-conservative manner. Therefore, the other two modes were ruled out.

During DNA replication, each of the two strands that make up the double helix serves as a template from which new strands are copied. The new strand will be complementary to the parental or “old” strand. When two daughter DNA copies are formed, they have the same sequence and are divided equally into the two daughter cells.

Link to Learning



Click through this tutorial on DNA replication.

Summary

The model for DNA replication suggests that the two strands of the double helix separate during replication, and each strand serves as a template from which the new complementary strand is copied. In conservative replication, the parental DNA is conserved, and the daughter DNA is newly synthesized. The semi-conservative method suggests that each of the two parental DNA strands acts as template for new DNA to be synthesized; after replication, each double-stranded DNA includes one parental or “old” strand and one “new” strand. The dispersive mode suggested that the two copies of the DNA would have segments of parental DNA and newly synthesized DNA.

Contributors and Attributions

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SECTION OVERVIEW

14.4: Prokaryotic Replication

Prokaryotes such as bacteria propagate by binary fission. For unicellular organisms, cell division is the only method to produce new individuals. In both prokaryotic and eukaryotic cells, the outcome of cell reproduction is a pair of daughter cells that are genetically identical to the parent cell. In unicellular organisms, daughter cells are individuals.

To achieve the outcome of identical daughter cells, some steps are essential. The genomic DNA must be replicated and then allocated into the daughter cells; the cytoplasmic contents must also be divided to give both new cells the machinery to sustain life. In bacterial cells, the genome consists of a single, circular DNA chromosome; therefore, the process of cell division is simplified. Mitosis is unnecessary because there is no nucleus or multiple chromosomes. This type of cell division is called binary fission.

Binary Fission

The cell division process of prokaryotes, called binary fission, is a less complicated and much quicker process than cell division in eukaryotes. Because of the speed of bacterial cell division, populations of bacteria can grow very rapidly. The single, circular DNA chromosome of bacteria is not enclosed in a nucleus, but instead occupies a specific location, the nucleoid, within the cell. As in eukaryotes, the DNA of the nucleoid is associated with proteins that aid in packaging the molecule into a compact size. The packing proteins of bacteria are, however, related to some of the proteins involved in the chromosome compaction of eukaryotes.

The starting point of replication, the origin, is close to the binding site of the chromosome to the plasma membrane (Figure **14.4.1**). Replication of the DNA is bidirectional—moving away from the origin on both strands of the DNA loop simultaneously. As the new double strands are formed, each origin point moves away from the cell-wall attachment toward opposite ends of the cell. As the cell elongates, the growing membrane aids in the transport of the chromosomes. After the chromosomes have cleared the midpoint of the elongated cell, cytoplasmic separation begins. A septum is formed between the nucleoids from the periphery toward the center of the cell. When the new cell walls are in place, the daughter cells separate.

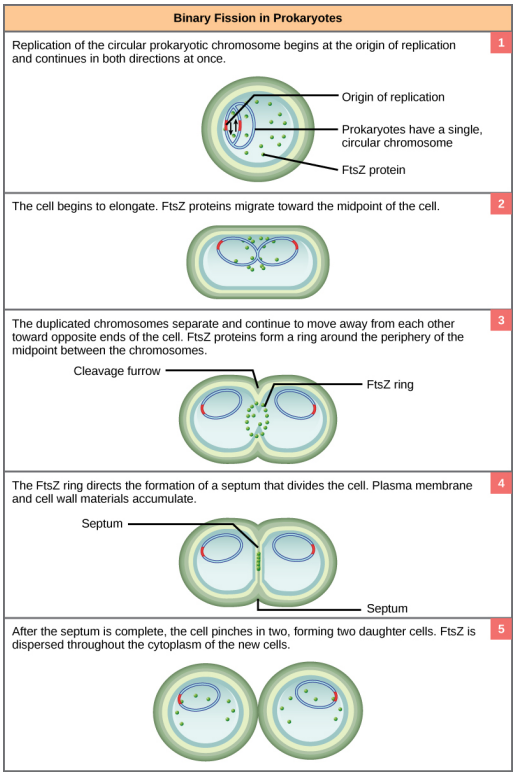


Figure 14.4.1: The binary fission of a bacterium is outlined in five steps. (credit: modification of work by "Mcstrother"/Wikimedia Commons)

EVOLUTION IN ACTION: Mitotic Spindle Apparatus

The precise timing and formation of the mitotic spindle is critical to the success of eukaryotic cell division. Prokaryotic cells, on the other hand, do not undergo mitosis and therefore have no need for a mitotic spindle. However, the FtsZ protein that plays such a vital role in prokaryotic cytokinesis is structurally and functionally very similar to tubulin, the building block of the microtubules that make up the mitotic spindle fibers that are necessary for eukaryotes. The formation of a ring composed of repeating units of a protein called FtsZ directs the partition between the nucleoids in prokaryotes. Formation of the FtsZ ring triggers the accumulation of other proteins that work together to recruit new membrane and cell-wall materials to the site. FtsZ proteins can form filaments, rings, and other three-dimensional structures resembling the way tubulin forms microtubules, centrioles, and various cytoskeleton components. In addition, both FtsZ and tubulin employ the same energy source, GTP (guanosine triphosphate), to rapidly assemble and disassemble complex structures.

FtsZ and tubulin are an example of homology, structures derived from the same evolutionary origins. In this example, FtsZ is presumed to be similar to the ancestor protein to both the modern FtsZ and tubulin. While both proteins are found in extant organisms, tubulin function has evolved and diversified tremendously since the evolution from its FtsZ-like prokaryotic origin. A survey of cell-division machinery in present-day unicellular eukaryotes reveals crucial intermediary steps to the complex mitotic machinery of multicellular eukaryotes (Table **14.4.1**).

Table 14.4.1: Mitotic Spindle Evolution

	Structure of genetic material	Division of nuclear material	Separation of daughter cells
Prokaryotes	There is no nucleus. The single, circular chromosome exists in a region of cytoplasm called the nucleoid.	Occurs through binary fission. As the chromosome is replicated, the two copies move to opposite ends of the cell by an unknown mechanism.	FtsZ proteins assemble into a ring that pinches the cell in two.
Some protists	Linear chromosomes exist in the nucleus.	Chromosomes attach to the nuclear envelope, which remains intact. The mitotic spindle passes through the envelope and elongates the cell. No centrioles exist.	Microfilaments form a cleavage furrow that pinches the cell in two.
Other protists	Linear chromosomes exist in the nucleus.	A mitotic spindle forms from the centrioles and passes through the nuclear membrane, which remains intact. Chromosomes attach to the mitotic spindle. The mitotic spindle separates the chromosomes and elongates the cell.	Microfilaments form a cleavage furrow that pinches the cell in two.
Animal cells	Linear chromosomes exist in the nucleus.	A mitotic spindle forms from the centrioles. The nuclear envelope dissolves. Chromosomes attach to the mitotic spindle, which separates them and elongates the cell.	Microfilaments form a cleavage furrow that pinches the cell in two.

Summary

In both prokaryotic and eukaryotic cell division, the genomic DNA is replicated and each copy is allocated into a daughter cell. The cytoplasmic contents are also divided evenly to the new cells. However, there are many differences between prokaryotic and eukaryotic cell division. Bacteria have a single, circular DNA chromosome and no nucleus. Therefore, mitosis is not necessary in bacterial cell division. Bacterial cytokinesis is directed by a ring composed of a protein called FtsZ. Ingrowth of membrane and cell-wall material from the periphery of the cells results in a septum that eventually forms the separate cell walls of the daughter cells.

Glossary

binary fission
: the process of prokaryotic cell division

FtsZ
: a tubulin-like protein component of the prokaryotic cytoskeleton that is important in prokaryotic cytokinesis (name origin: **F**ilamenting **t**emperature-**s**ensitive mutant **Z**)

origin
: the region of the prokaryotic chromosome at which replication begins

septum
: a wall formed between bacterial daughter cells as a precursor to cell separation

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14.4.1: DNA Replication in Prokaryotes

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14.4.1: DNA Replication in Prokaryotes

Skills to Develop

- Explain the process of DNA replication in prokaryotes
- Discuss the role of different enzymes and proteins in supporting this process

DNA replication has been extremely well studied in prokaryotes primarily because of the small size of the genome and the mutants that are available. *E. coli* has 4.6 million base pairs in a single circular chromosome and all of it gets replicated in approximately 42 minutes, starting from a single origin of replication and proceeding around the circle in both directions. This means that approximately 1000 nucleotides are added per second. The process is quite rapid and occurs without many mistakes.

DNA replication employs a large number of proteins and enzymes, each of which plays a critical role during the process. One of the key players is the enzyme DNA polymerase, also known as DNA pol, which adds nucleotides one by one to the growing DNA chain that are complementary to the template strand. The addition of nucleotides requires energy; this energy is obtained from the nucleotides that have three phosphates attached to them, similar to ATP which has three phosphate groups attached. When the bond between the phosphates is broken, the energy released is used to form the phosphodiester bond between the incoming nucleotide and the growing chain. In prokaryotes, three main types of polymerases are known: DNA pol I, DNA pol II, and DNA pol III. It is now known that DNA pol III is the enzyme required for DNA synthesis; DNA pol I and DNA pol II are primarily required for repair.

How does the replication machinery know where to begin? It turns out that there are specific nucleotide sequences called origins of replication where replication begins. In *E. coli*, which has a single origin of replication on its one chromosome (as do most prokaryotes), it is approximately 245 base pairs long and is rich in AT sequences. The origin of replication is recognized by certain proteins that bind to this site. An enzyme called helicase unwinds the DNA by breaking the hydrogen bonds between the nitrogenous base pairs. ATP hydrolysis is required for this process. As the DNA opens up, Y-shaped structures called replication forks are formed. Two replication forks are formed at the origin of replication and these get extended bi- directionally as replication proceeds. Single-strand binding proteins coat the single strands of DNA near the replication fork to prevent the single-stranded DNA from winding back into a double helix. DNA polymerase is able to add nucleotides only in the 5' to 3' direction (a new DNA strand can be only extended in this direction). It also requires a free 3'-OH group to which it can add nucleotides by forming a phosphodiester bond between the 3'-OH end and the 5' phosphate of the next nucleotide. This essentially means that it cannot add nucleotides if a free 3'-OH group is not available. Then how does it add the first nucleotide? The problem is solved with the help of a primer that provides the free 3'-OH end. Another enzyme, RNA primase, synthesizes an RNA primer that is about five to ten nucleotides long and complementary to the DNA. Because this sequence primes the DNA synthesis, it is appropriately called the primer. DNA polymerase can now extend this RNA primer, adding nucleotides one by one that are complementary to the template strand (Figure **14.4.1.1**).

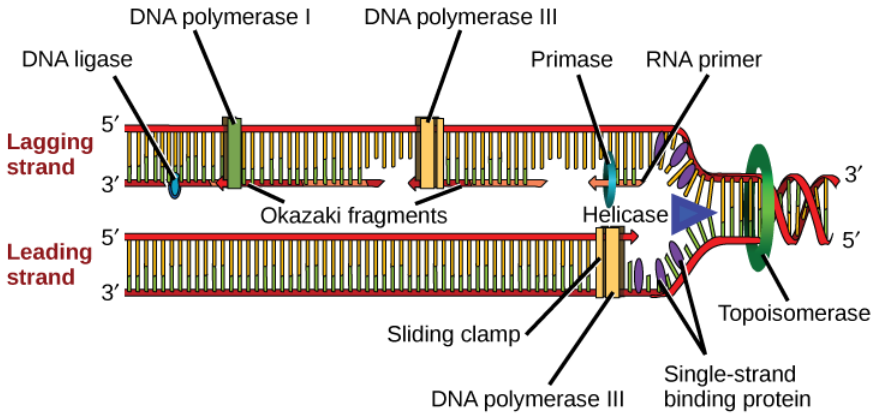


Figure **14.4.1.1**: A replication fork is formed when helicase separates the DNA strands at the origin of replication. The DNA tends to become more highly coiled ahead of the replication fork. Topoisomerase breaks and reforms DNA's phosphate backbone ahead of the replication fork, thereby relieving the pressure that results from this supercoiling. Single-strand binding proteins bind to the single-stranded DNA to prevent the helix from re-forming. Primase synthesizes an RNA primer. DNA polymerase III uses this primer to synthesize the daughter DNA strand. On the leading strand, DNA is synthesized continuously, whereas on the lagging strand, DNA is synthesized in short stretches called Okazaki fragments. DNA polymerase I replaces the RNA primer with DNA. DNA ligase seals the gaps between the Okazaki fragments, joining the fragments into a single DNA molecule. (credit: modification of work by Mariana Ruiz Villareal)

Exercise 14.4.1.1

You isolate a cell strain in which the joining together of Okazaki fragments is impaired and suspect that a mutation has occurred in an enzyme found at the replication fork. Which enzyme is most likely to be mutated?

Answer

DNA ligase, as this enzyme joins together Okazaki fragments.

The replication fork moves at the rate of 1000 nucleotides per second. DNA polymerase can only extend in the 5' to 3' direction, which poses a slight problem at the replication fork. As we know, the DNA double helix is anti-parallel; that is, one strand is in the 5' to 3' direction and the other is oriented in the 3' to 5' direction. One strand, which is complementary to the 3' to 5' parental DNA strand, is synthesized continuously towards the replication fork because the polymerase can add nucleotides in this direction. This continuously synthesized strand is known as the leading strand. The other strand, complementary to the 5' to 3' parental DNA, is extended away from the replication fork, in small fragments known as Okazaki fragments, each requiring a primer to start the synthesis. Okazaki fragments are named after the Japanese scientist who first discovered them. The strand with the Okazaki fragments is known as the lagging strand.

The leading strand can be extended by one primer alone, whereas the lagging strand needs a new primer for each of the short Okazaki fragments. The overall direction of the lagging strand will be 3' to 5', and that of the leading strand 5' to 3'. A protein called the sliding clamp holds the DNA polymerase in place as it continues to add nucleotides. The sliding clamp is a ring-shaped protein that binds to the DNA and holds the polymerase in place. Topoisomerase prevents the over-winding of the DNA double helix ahead of the replication fork as the DNA is opening up; it does so by causing temporary nicks in the DNA helix and then resealing it. As synthesis proceeds, the RNA primers are replaced by DNA. The primers are removed by the exonuclease activity of DNA pol I, and the gaps are filled in by deoxyribonucleotides. The nicks that remain between the newly synthesized DNA (that replaced the RNA primer) and the previously synthesized DNA are sealed by the enzyme DNA ligase that catalyzes the formation of phosphodiester linkage between the 3'-OH end of one nucleotide and the 5' phosphate end of the other fragment.

Once the chromosome has been completely replicated, the two DNA copies move into two different cells during cell division. The process of DNA replication can be summarized as follows.

DNA replication steps

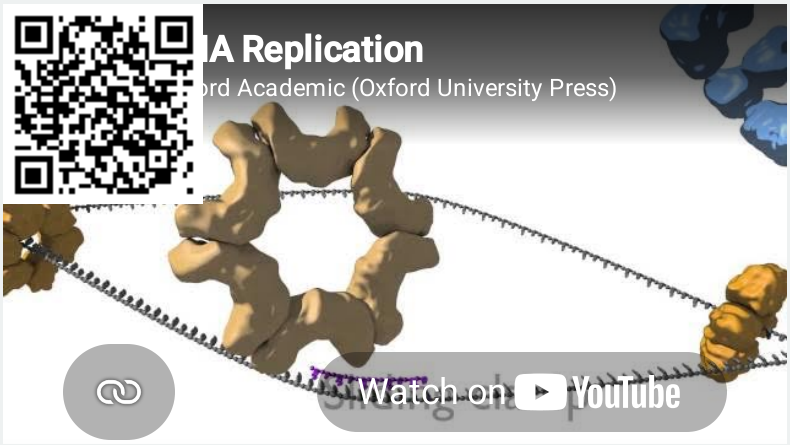
1. DNA unwinds at the origin of replication.
2. Helicase opens up the DNA-forming replication forks; these are extended bidirectionally.
3. Single-strand binding proteins coat the DNA around the replication fork to prevent rewinding of the DNA.
4. Topoisomerase binds at the region ahead of the replication fork to prevent supercoiling.
5. Primase synthesizes RNA primers complementary to the DNA strand.
6. DNA polymerase starts adding nucleotides to the 3'-OH end of the primer.
7. Elongation of both the lagging and the leading strand continues.
8. RNA primers are removed by exonuclease activity.
9. Gaps are filled by DNA pol by adding dNTPs.
10. The gap between the two DNA fragments is sealed by DNA ligase, which helps in the formation of phosphodiester bonds.

Table **14.4.1.1** summarizes the enzymes involved in prokaryotic DNA replication and the functions of each.

Table **14.4.1.1**: Prokaryotic DNA Replication: Enzymes and Their Function

Enzyme/protein	Specific Function
DNA pol I	Exonuclease activity removes RNA primer and replaces with newly synthesized DNA
DNA pol II	Repair function
DNA pol III	Main enzyme that adds nucleotides in the 5'-3' direction
Helicase	Opens the DNA helix by breaking hydrogen bonds between the nitrogenous bases
Ligase	Seals the gaps between the Okazaki fragments to create one continuous DNA strand
Primase	Synthesizes RNA primers needed to start replication
Sliding Clamp	Helps to hold the DNA polymerase in place when nucleotides are being added
Topoisomerase	Helps relieve the stress on DNA when unwinding by causing breaks and then resealing the DNA
Single-strand binding proteins (SSB)	Binds to single-stranded DNA to avoid DNA rewinding back.

Link to Learning



Review the full process of DNA replication here.

Summary

Replication in prokaryotes starts from a sequence found on the chromosome called the origin of replication—the point at which the DNA opens up. Helicase opens up the DNA double helix, resulting in the formation of the replication fork. Single-strand binding proteins bind to the single-stranded DNA near the replication fork to keep the fork open. Primase synthesizes an RNA primer to initiate synthesis by DNA polymerase, which can add nucleotides only in the 5' to 3' direction. One strand is synthesized continuously in the direction of the replication fork; this is called the leading strand. The other strand is synthesized in a direction away from the replication fork, in short stretches of DNA known as Okazaki fragments. This strand is known as the lagging strand. Once replication is completed, the RNA primers are replaced by DNA nucleotides and the DNA is sealed with DNA ligase, which creates phosphodiester bonds between the 3'-OH of one end and the 5' phosphate of the other strand.

Glossary

helicase
: during replication, this enzyme helps to open up the DNA helix by breaking the hydrogen bonds

lagging strand
: during replication, the strand that is replicated in short fragments and away from the replication fork

leading strand
: strand that is synthesized continuously in the 5'-3' direction which is synthesized in the direction of the replication fork

ligase
: enzyme that catalyzes the formation of a phosphodiester linkage between the 3' OH and 5' phosphate ends of the DNA

Okazaki fragment
: DNA fragment that is synthesized in short stretches on the lagging strand

primase
: enzyme that synthesizes the RNA primer; the primer is needed for DNA pol to start synthesis of a new DNA strand

primer
: short stretch of nucleotides that is required to initiate replication; in the case of replication, the primer has RNA nucleotides

replication fork
: Y-shaped structure formed during initiation of replication

single-strand binding protein
: during replication, protein that binds to the single-stranded DNA; this helps in keeping the two strands of DNA apart so that they may serve as templates

sliding clamp
: ring-shaped protein that holds the DNA pol on the DNA strand

topoisomerase
: enzyme that causes underwinding or overwinding of DNA when DNA replication is taking place

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14.5: Eukaryotic Replication

Skills to Develop

- Discuss the similarities and differences between DNA replication in eukaryotes and prokaryotes
- State the role of telomerase in DNA replication

Eukaryotic genomes are much more complex and larger in size than prokaryotic genomes. The human genome has three billion base pairs per haploid set of chromosomes, and 6 billion base pairs are replicated during the S phase of the cell cycle. There are multiple origins of replication on the eukaryotic chromosome; humans can have up to 100,000 origins of replication. The rate of replication is approximately 100 nucleotides per second, much slower than prokaryotic replication. In yeast, which is a eukaryote, special sequences known as Autonomously Replicating Sequences (ARS) are found on the chromosomes. These are equivalent to the origin of replication in *E. coli*.

The number of DNA polymerases in eukaryotes is much more than prokaryotes: 14 are known, of which five are known to have major roles during replication and have been well studied. They are known as pol α, pol β, pol γ, pol δ, and pol ε.

The essential steps of replication are the same as in prokaryotes. Before replication can start, the DNA has to be made available as template. Eukaryotic DNA is bound to basic proteins known as histones to form structures called nucleosomes. The chromatin (the complex between DNA and proteins) may undergo some chemical modifications, so that the DNA may be able to slide off the proteins or be accessible to the enzymes of the DNA replication machinery. At the origin of replication, a pre-replication complex is made with other initiator proteins. Other proteins are then recruited to start the replication process (Table **14.5.1**).

A helicase using the energy from ATP hydrolysis opens up the DNA helix. Replication forks are formed at each replication origin as the DNA unwinds. The opening of the double helix causes over-winding, or supercoiling, in the DNA ahead of the replication fork. These are resolved with the action of topoisomerases. Primers are formed by the enzyme primase, and using the primer, DNA pol can start synthesis. While the leading strand is continuously synthesized by the enzyme pol δ, the lagging strand is synthesized by pol ε. A sliding clamp protein known as PCNA (Proliferating Cell Nuclear Antigen) holds the DNA pol in place so that it does not slide off the DNA. RNase H removes the RNA primer, which is then replaced with DNA nucleotides. The Okazaki fragments in the lagging strand are joined together after the replacement of the RNA primers with DNA. The gaps that remain are sealed by DNA ligase, which forms the phosphodiester bond.

Telomere replication

Unlike prokaryotic chromosomes, eukaryotic chromosomes are linear. As you've learned, the enzyme DNA pol can add nucleotides only in the 5' to 3' direction. In the leading strand, synthesis continues until the end of the chromosome is reached. On the lagging strand, DNA is synthesized in short stretches, each of which is initiated by a separate primer. When the replication fork reaches the end of the linear chromosome, there is no place for a primer to be made for the DNA fragment to be copied at the end of the chromosome. These ends thus remain unpaired, and over time these ends may get progressively shorter as cells continue to divide.

The ends of the linear chromosomes are known as telomeres, which have repetitive sequences that code for no particular gene. In a way, these telomeres protect the genes from getting deleted as cells continue to divide. In humans, a six base pair sequence, TTAGGG, is repeated 100 to 1000 times. The discovery of the enzyme telomerase (Figure **14.5.1**) helped in the understanding of how chromosome ends are maintained. The telomerase enzyme contains a catalytic part and a built-in RNA template. It attaches to the end of the chromosome, and complementary bases to the RNA template are added on the 3' end of the DNA strand. Once the 3' end of the lagging strand template is sufficiently elongated, DNA polymerase can add the nucleotides complementary to the ends of the chromosomes. Thus, the ends of the chromosomes are replicated.

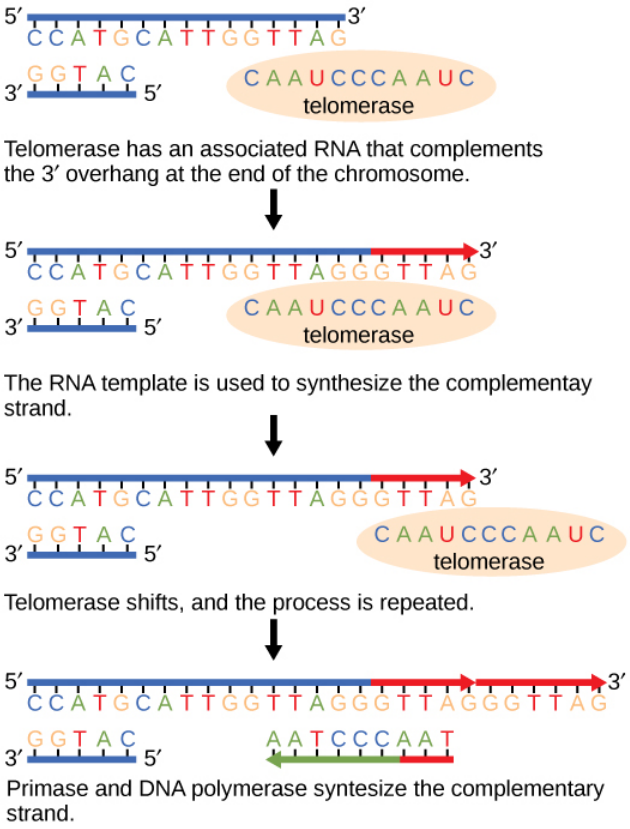


Figure **14.5.1**: The ends of linear chromosomes are maintained by the action of the telomerase enzyme.

Telomerase is typically active in germ cells and adult stem cells. It is not active in adult somatic cells. For her discovery of telomerase and its action, Elizabeth Blackburn (Figure **14.5.2**) received the Nobel Prize for Medicine and Physiology in 2009.



Figure **14.5.2**: Elizabeth Blackburn, 2009 Nobel Laureate, is the scientist who discovered how telomerase works. (credit: US Embassy Sweden)

Telomerase and Aging

Cells that undergo cell division continue to have their telomeres shortened because most somatic cells do not make telomerase. This essentially means that telomere shortening is associated with aging. With the advent of modern medicine, preventative health care, and healthier lifestyles, the human life span has increased, and there is an increasing demand for people to look younger and have a better quality of life as they grow older.

In 2010, scientists found that telomerase can reverse some age-related conditions in mice. This may have potential in regenerative medicine.[1] Telomerase-deficient mice were used in these studies; these mice have tissue atrophy, stem cell depletion, organ system failure, and impaired tissue injury responses. Telomerase reactivation in these mice caused extension of telomeres, reduced DNA damage, reversed neurodegeneration, and improved the function of the testes, spleen, and intestines. Thus, telomere reactivation may have potential for treating age-related diseases in humans.

Cancer is characterized by uncontrolled cell division of abnormal cells. The cells accumulate mutations, proliferate uncontrollably, and can migrate to different parts of the body through a process called metastasis. Scientists have observed that cancerous cells have considerably shortened telomeres and that telomerase is active in these cells. Interestingly, only after the telomeres were

shortened in the cancer cells did the telomerase become active. If the action of telomerase in these cells can be inhibited by drugs during cancer therapy, then the cancerous cells could potentially be stopped from further division.

Table **14.5.1**: Difference between Prokaryotic and Eukaryotic Replication

Property	Prokaryotes	Eukaryotes
Origin of replication	Single	Multiple
Rate of replication	1000 nucleotides/s	50 to 100 nucleotides/s
DNA polymerase types	5	14
Telomerase	Not present	Present
RNA primer removal	DNA pol I	RNase H
Strand elongation	DNA pol III	Pol δ, pol ε
Sliding clamp	Sliding clamp	PCNA

Summary

Replication in eukaryotes starts at multiple origins of replication. The mechanism is quite similar to prokaryotes. A primer is required to initiate synthesis, which is then extended by DNA polymerase as it adds nucleotides one by one to the growing chain. The leading strand is synthesized continuously, whereas the lagging strand is synthesized in short stretches called Okazaki fragments. The RNA primers are replaced with DNA nucleotides; the DNA remains one continuous strand by linking the DNA fragments with DNA ligase. The ends of the chromosomes pose a problem as polymerase is unable to extend them without a primer. Telomerase, an enzyme with an inbuilt RNA template, extends the ends by copying the RNA template and extending one end of the chromosome. DNA polymerase can then extend the DNA using the primer. In this way, the ends of the chromosomes are protected.

Footnotes

1. 1 Jaskelioff et al., “Telomerase reactivation reverses tissue degeneration in aged telomerase-deficient mice,” *Nature* 469 (2011): 102-7.

Glossary

telomerase
enzyme that contains a catalytic part and an inbuilt RNA template; it functions to maintain telomeres at chromosome ends

telomere
DNA at the end of linear chromosomes

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14.6: DNA Repair

Skills to Develop

- Discuss the different types of mutations in DNA
- Explain DNA repair mechanisms

DNA replication is a highly accurate process, but mistakes can occasionally occur, such as a DNA polymerase inserting a wrong base. Uncorrected mistakes may sometimes lead to serious consequences, such as cancer. Repair mechanisms correct the mistakes. In rare cases, mistakes are not corrected, leading to mutations; in other cases, repair enzymes are themselves mutated or defective.

Most of the mistakes during DNA replication are promptly corrected by DNA polymerase by proofreading the base that has been just added (Figure **14.6.1**). In proofreading, the DNA pol reads the newly added base before adding the next one, so a correction can be made. The polymerase checks whether the newly added base has paired correctly with the base in the template strand. If it is the right base, the next nucleotide is added. If an incorrect base has been added, the enzyme makes a cut at the phosphodiester bond and releases the wrong nucleotide. This is performed by the exonuclease action of DNA pol III. Once the incorrect nucleotide has been removed, a new one will be added again.

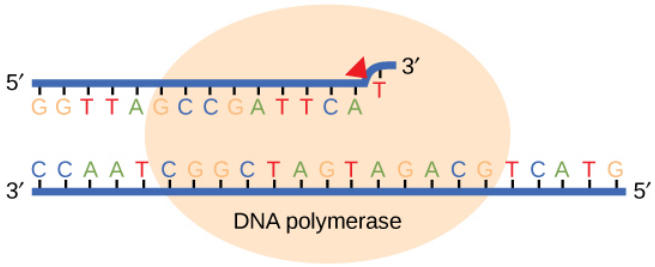


Figure **14.6.1**: Proofreading by DNA polymerase corrects errors during replication.

Some errors are not corrected during replication, but are instead corrected after replication is completed; this type of repair is known as mismatch repair (Figure **14.6.2**). The enzymes recognize the incorrectly added nucleotide and excise it; this is then replaced by the correct base. If this remains uncorrected, it may lead to more permanent damage. How do mismatch repair enzymes recognize which of the two bases is the incorrect one? In *E. coli*, after replication, the nitrogenous base adenine acquires a methyl group; the parental DNA strand will have methyl groups, whereas the newly synthesized strand lacks them. Thus, DNA polymerase is able to remove the wrongly incorporated bases from the newly synthesized, non-methylated strand. In eukaryotes, the mechanism is not very well understood, but it is believed to involve recognition of unsealed nicks in the new strand, as well as a short-term continuing association of some of the replication proteins with the new daughter strand after replication has completed.

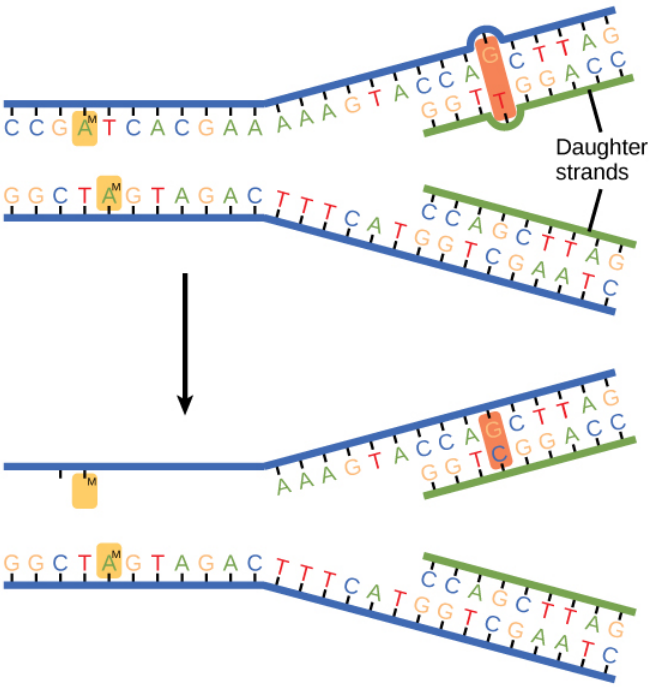


Figure **14.6.2**: In mismatch repair, the incorrectly added base is detected after replication. The mismatch repair proteins detect this base and remove it from the newly synthesized strand by nuclease action. The gap is now filled with the correctly paired base.

In another type of repair mechanism, nucleotide excision repair, enzymes replace incorrect bases by making a cut on both the 3' and 5' ends of the incorrect base (Figure **14.6.3**). The segment of DNA is removed and replaced with the correctly paired nucleotides by the action of DNA pol. Once the bases are filled in, the remaining gap is sealed with a phosphodiester linkage catalyzed by DNA ligase. This repair mechanism is often employed when UV exposure causes the formation of pyrimidine dimers.

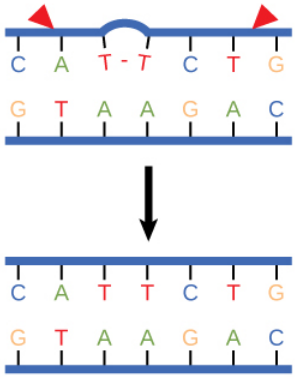


Figure **14.6.3**: Nucleotide excision repairs thymine dimers. When exposed to UV, thymines lying adjacent to each other can form thymine dimers. In normal cells, they are excised and replaced.

A well-studied example of mistakes not being corrected is seen in people suffering from xeroderma pigmentosa (Figure **14.6.4**). Affected individuals have skin that is highly sensitive to UV rays from the sun. When individuals are exposed to UV, pyrimidine dimers, especially those of thymine, are formed; people with xeroderma pigmentosa are not able to repair the damage. These are not repaired because of a defect in the nucleotide excision repair enzymes, whereas in normal individuals, the thymine dimers are excised and the defect is corrected. The thymine dimers distort the structure of the DNA double helix, and this may cause problems during DNA replication. People with xeroderma pigmentosa may have a higher risk of contracting skin cancer than those who dont have the condition.



Figure **14.6.4**: Xeroderma pigmentosa is a condition in which thymine dimerization from exposure to UV is not repaired. Exposure to sunlight results in skin lesions. (credit: James Halpern et al.)

Errors during DNA replication are not the only reason why mutations arise in DNA. Mutations, variations in the nucleotide sequence of a genome, can also occur because of damage to DNA. Such mutations may be of two types: induced or spontaneous. Induced mutations are those that result from an exposure to chemicals, UV rays, x-rays, or some other environmental agent. Spontaneous mutations occur without any exposure to any environmental agent; they are a result of natural reactions taking place within the body.

Mutations may have a wide range of effects. Some mutations are not expressed; these are known as silent mutations. Point mutations are those mutations that affect a single base pair. The most common nucleotide mutations are substitutions, in which one base is replaced by another. These can be of two types, either transitions or transversions. Transition substitution refers to a purine or pyrimidine being replaced by a base of the same kind; for example, a purine such as adenine may be replaced by the purine guanine. Transversion substitution refers to a purine being replaced by a pyrimidine, or vice versa; for example, cytosine, a pyrimidine, is replaced by adenine, a purine. Mutations can also be the result of the addition of a base, known as an insertion, or the removal of a base, also known as deletion. Sometimes a piece of DNA from one chromosome may get translocated to another chromosome or to another region of the same chromosome; this is also known as translocation. These mutation types are shown in Figure **14.6.5**.

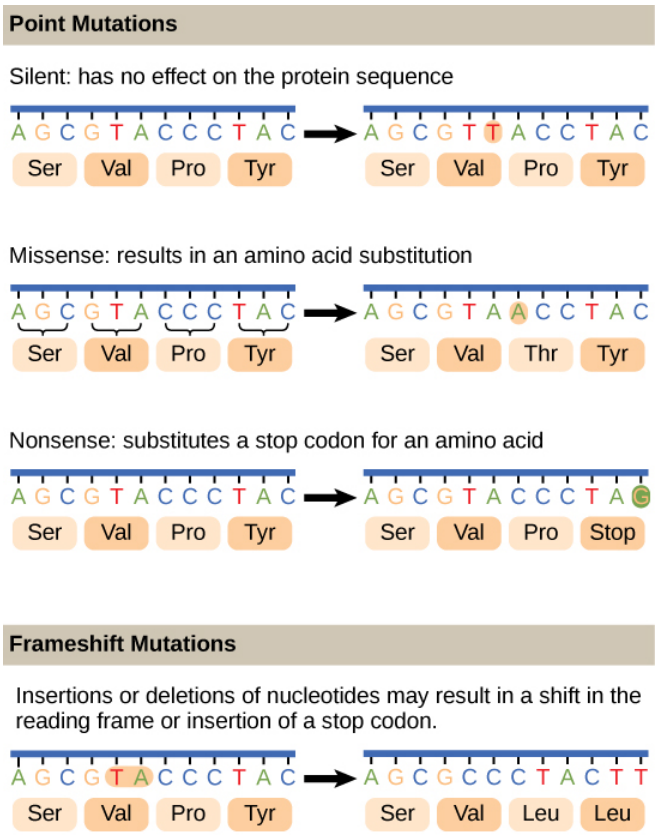


Figure **14.6.5**: Mutations can lead to changes in the protein sequence encoded by the DNA.

Exercise 14.6.1

A frameshift mutation that results in the insertion of three nucleotides is often less deleterious than a mutation that results in the insertion of one nucleotide. Why?

Answer

If three nucleotides are added, one additional amino acid will be incorporated into the protein chain, but the reading frame won't shift.

Mutations in repair genes have been known to cause cancer. Many mutated repair genes have been implicated in certain forms of pancreatic cancer, colon cancer, and colorectal cancer. Mutations can affect either somatic cells or germ cells. If many mutations accumulate in a somatic cell, they may lead to problems such as the uncontrolled cell division observed in cancer. If a mutation takes place in germ cells, the mutation will be passed on to the next generation, as in the case of hemophilia and xeroderma pigmentosa.

Summary

DNA polymerase can make mistakes while adding nucleotides. It edits the DNA by proofreading every newly added base. Incorrect bases are removed and replaced by the correct base, and then a new base is added. Most mistakes are corrected during replication, although when this does not happen, the mismatch repair mechanism is employed. Mismatch repair enzymes recognize the wrongly incorporated base and excise it from the DNA, replacing it with the correct base. In yet another type of repair, nucleotide excision repair, the incorrect base is removed along with a few bases on the 5' and 3' end, and these are replaced by copying the template with the help of DNA polymerase. The ends of the newly synthesized fragment are attached to the rest of the DNA using DNA ligase, which creates a phosphodiester bond.

Most mistakes are corrected, and if they are not, they may result in a mutation defined as a permanent change in the DNA sequence. Mutations can be of many types, such as substitution, deletion, insertion, and translocation. Mutations in repair genes

may lead to serious consequences such as cancer. Mutations can be induced or may occur spontaneously.

Glossary

induced mutation
mutation that results from exposure to chemicals or environmental agents

mutation
variation in the nucleotide sequence of a genome

mismatch repair
type of repair mechanism in which mismatched bases are removed after replication

nucleotide excision repair
type of DNA repair mechanism in which the wrong base, along with a few nucleotides upstream or downstream, are removed

proofreading
function of DNA pol in which it reads the newly added base before adding the next one

point mutation
mutation that affects a single base

silent mutation
mutation that is not expressed

spontaneous mutation
mutation that takes place in the cells as a result of chemical reactions taking place naturally without exposure to any external agent

transition substitution
when a purine is replaced with a purine or a pyrimidine is replaced with another pyrimidine

transversion substitution
when a purine is replaced by a pyrimidine or a pyrimidine is replaced by a purine

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CHAPTER OVERVIEW

15: Genes and How They Work

15.1: The Nature of Genes

15.1.1: The Function of Genes

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SECTION OVERVIEW

15.1: The Nature of Genes

15.1.1: The Function of Genes

15.1.2: Central Dogma- DNA to RNA to protein

15.1.3: Transcription and mRNA structure

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15.1.1: The Function of Genes

Beadle and Tatum: one gene, one enzyme hypothesis

Life depends on (bio)chemistry to supply energy and to produce the molecules to construct and regulate cells. In 1908, A. Garrod described "in born errors of metabolism" in humans using the congenital disorder, alkaptonuria (black urine disease), as an example of how "genetic defects" led to the lack of an enzyme in a biochemical pathway and caused a disease (phenotype). Over 40 years later, in 1941, **Beadle and Tatum** built on this connection between genes and metabolic pathways. Their research led to the "**one gene, one enzyme (or protein)**" hypothesis, which states that each of the enzymes that act in a biochemical pathway is encoded by a different gene. Although we now know of many exceptions to the "one gene, one enzyme (or protein)" principle, it is generally true that each different gene produces a protein that has a distinct catalytic, regulatory, or structural function.

Beadle and Tatum used the fungus ***Neurospora crassa*** (a mold) for their studies because it had practical advantages as a laboratory organism. They knew that Neurospora was **prototrophic**, meaning that it could synthesize its own amino acids when grown on **minimal medium**, which lacked most nutrients except for a few minerals, simple sugars, and one vitamin (biotin). They also knew that by exposing Neurospora spores to X-rays, they could randomly damage its DNA to create mutations in genes. Each different spore exposed to X-rays potentially contained a mutation in a different gene. After genetically screening many, many spores for growth, most appeared to still be prototrophic and still able to grow on minimal medium. However, some spores had mutations that changed them into **auxotrophic** strains that could no longer grow on minimal medium, but did grow on **complete medium** supplemented with nutrients (Figure **15.1.1.12**). In fact, some auxotrophic mutations could grow on minimal medium with only one, single nutrient supplied, such as arginine.

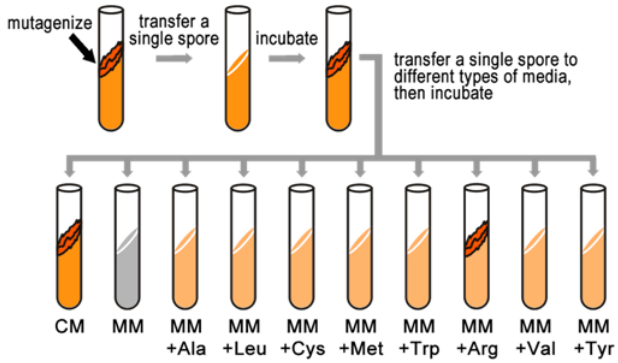


Figure **15.1.1.12**: A single mutagenized spore is used to establish a colony of genetically identical fungi, from which spores are tested for their ability to grow on different types of media. Because spores of this particular colony are able to grown only on complete medium (CM), or on miminal medium supplemented with arginine (MM+Arg), they are considered Arg auxotrophs and we infer that they have a mutation in a gene in the Arg biosynthetic pathway. This type of screen is repeated many times to identify other mutants in the Arg pathway and in other pathways. (Original-Deyholos-CC:AN)

B&T's 1 gene: 1 enzyme hypothesis led to Biochemical Pathway dissection using genetic screens and mutations

Beadle and Tatum's experiments are important not only for its conceptual advances in understanding genes, but also because they demonstrate the utility of **screening for genetic mutants** to investigate a biological process – **genetic analysis**. Beadle and Tatum's results were useful to investigate biological processes, specifically the metabolic pathways that produce amino acids. For example, Srb and Horowitz in 1944 tested the ability of the amino acids to **rescue** auxotrophic strains. They added one of each of the amino acids to minimal medium and recorded which of these restored growth to independent mutants. For example, if the progeny of a mutagenized spore could grow on minimal medium only when it was supplemented with arginine (Arg), then the auxotroph must bear a mutation in the Arg biosynthetic pathway and was called an "arginineless" strain (arg-).

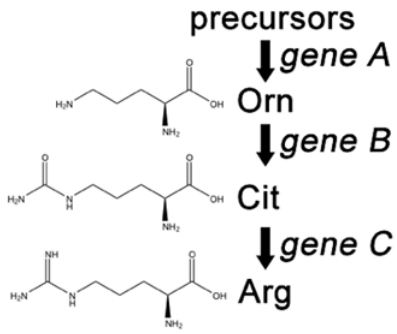


Figure **15.1.1.13**: A simplified version of the Arg biosynthetic pathway, showing citrulline (Cit) and ornithine (Orn) as intermediates in Arg metabolism. These chemical reactions depend on enzymes represented here as the products of three different genes. (Original-Deyholos-CC:AN)

Synthesis of even a relatively simple molecule such as arginine requires many steps, each with a different enzyme. Each enzyme works sequentially on a different intermediate in the pathway (Figure **15.1.1.13**). For arginine (Arg), two of the intermediates are ornithine (Orn) and citrulline (Cit). Thus, mutation of any one of the enzymes in this pathway could turn Neurospora into an Arg auxotroph (arg-). Srb and Horowitz extended their analysis of Arg auxotrophs by testing the intermediates of amino acid biosynthesis for the ability to restore growth of the mutants (Figure **15.1.1.14**).

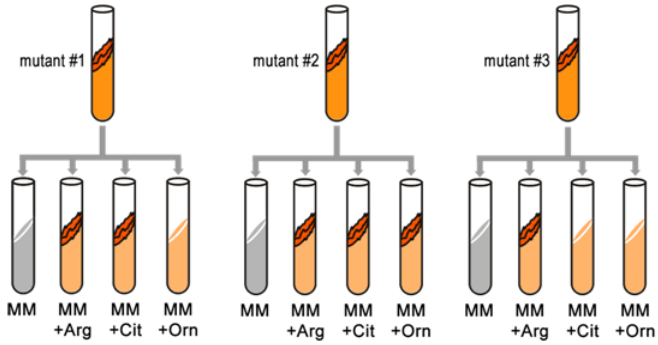


Figure **15.1.1.14**: Testing different Arg auxotrophs for their ability to grow on media supplemented with intermediates in the Arg biosynthetic pathway. (Original-Deyholos-CC:AN)

They found that some of the Arg auxotrophs could be rescued only by Arg, while others could be rescued by either Arg or Cit, and still other mutants could be rescued by Arg, Cit, or Orn (Table **15.1.1.1**). Based on these results, they deduced the location of each mutation in the Arg biochemical pathway, (i.e. which gene was responsible for the metabolism of which intermediate).

Table **15.1.1.1**: Ability of auxotrophic mutants of each of the three enzymes of the Arg biosynthetic pathways to grow on minimal medium (MM) supplemented with Arg or either of its precursors, Orn and Cit. Gene names refer to the labels used in Figure **15.1.1.14**

	MM + Orn	MM + Cit	MM + Arg
gene A mutants	**Yes**	**Yes**	**Yes**
gene B mutants	**No**	**Yes**	**Yes**
gene C mutants	**No**	**No**	**Yes**

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15.1.2: Central Dogma- DNA to RNA to protein

A few years after he and James Watson had proposed the double helical structure for DNA, Francis Crick (with other collaborators) proposed that a less stable nucleic acid, RNA, served as a messenger RNA that provided a transient copy of the genetic material that could be translated into the protein product encoded by the gene. Such mRNAs were indeed found. These and other studies led Francis Crick to formulate this “central dogma” of molecular biology (Figure 1.21).

This model states that **DNA serves as the repository of genetic information**. It can be **replicated** accurately and indefinitely. The **genetic information is expressed** by the DNA first serving as a template for the **synthesis of (messenger) RNA**; this occurs in a process called **transcription**. The mRNA then serves as a template, which is read by ribosomes and **translated**into **protein**. The protein products can be enzymes that catalyze the many metabolic transformations in the cell, or they can be structural proteins.

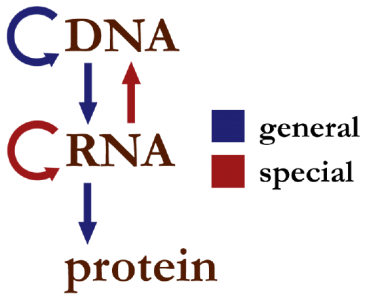


Figure 1.21.The central dogma of molecular biology. (Public Domain; Narayanese).

Although there have been some additional steps added since its formulation, the central dogma has stood the test of time and myriad experiments. It provides a strong unifying theme to molecular genetics and information flow in cell biology and biochemistry.

Although in many cases a gene encodes one polypeptide, other genes encode a **functional RNA**. Some genes encode **tRNAs** and **rRNAs** needed for translation, others encode other structural and catalytic RNAs. Genes encode some product that is used in the cell, i.e. that when altered generates an identifiable phenotype. More generally, genes encode RNAs, some of which are functional as transcribed (or with minor alterations via processing) such as tRNAs and rRNAs, and others are messengers that are then translated into proteins. These proteins can provide structural, catalytic and regulatory roles in the cell.

Note the **static role of DNA** in this process. Implicit in this model is the idea that DNA does not provide an active cellular function, but rather it encodes macromolecules that are functional. However, the expression of virtually all genes is highly regulated. The sites on the DNA where this control is exerted are indeed functional entities, such as promoters and enhancers. In this case, the DNA is directly functional (*cis*-regulatory sites), but the genes being regulated by these sites still encode some functional product (RNA or protein).

Studies of retroviruses lead Dulbecco to argue that the flow of information is not unidirectional, but in fact RNA can be converted into DNA (some viral RNA genomes are converted into DNA proviruses integrated into the genome). Subsequently Temin and Baltimore discovered the enzyme that can make a DNA copy of RNA, i.e. reverse transcriptase.

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15.1.3: Transcription and mRNA structure

Several aspects of the structure of genes can be illustrated by examining the general features of a bacterial gene as now understood.

A gene is a string of nucleotides in the duplex DNA that encodes a mRNA, which itself codes for protein. Only one strand of the duplex DNA is copied into mRNA (Figure 1.22). Sometimes genes overlap, and in some of those cases each strand of DNA is copied, but each for a different mRNA. The strand of DNA that reads the same as the sequence of mRNA is the **nontemplate strand**. The strand that reads as the reverse complement of the mRNA is the **template strand**.

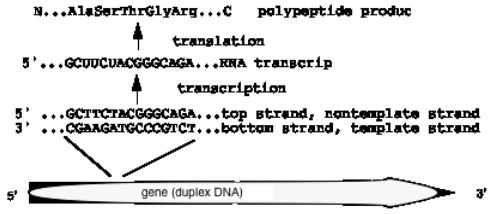


Figure 1.22.Only one strand of duplex DNA codes for a particular product.

Note

The term "sense strand" has two **opposite** uses (unfortunately). Sidney Brenner first used it to designate the strand that served as the template to make RNA (bottom strand above), and this is still used in many genetics texts. However, now many authors use the term to refer to the strand that reads the same as the mRNA (top strand above). The same confusion applies to the term "coding strand" which can refer to the strand encoding mRNA (bottom strand) or the strand "encoding" the protein (top strand). Interestingly, "antisense" is used exclusively to refer to the strand that is the reverse complement of the mRNA (bottom strand).

Figure 1.22 helps illustrate the origin of terms used in gene expression. Copying the information of DNA into RNA stays in the same "language" in that both of these polymers are nucleic acids, hence the process is called transcription. An analogy would be writing exercises where you had to copy, e.g. a poem, from a book onto your paper - you transcribed the poem, but it is still in English. Converting the information from RNA into DNA is equivalent to converting from one "language" to another, in this case from one type of polymer (the nucleic acid RNA) to a different one (a polypeptide or protein). Hence the process is called translation. This is analogous to translating a poem written in French into English.

Figure 1.23 illustrates the point that a gene may be longer than the region coding for the protein because of 5' and/or 3' **untranslated regions**.

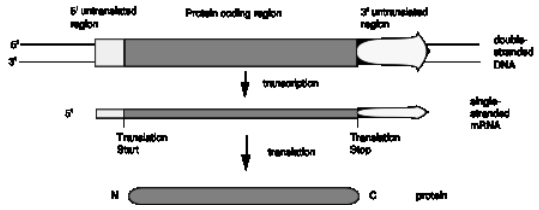


Figure 1.23: Genes and mRNA have untranslated sequences at both the 5’ and 3’ ends.

Eukaryotic mRNAs have covalent attachment of nucleotides at the 5' and 3' ends, and in some cases nucleotides are added internally (a process called *RNA editing*). Recent work shows that additional nucleotides are added post-transcriptionally to some bacterial mRNAs as well.

Regulatory signals can be considered parts of genes

In order to express a gene at the correct time, the DNA also carries signals to start transcription (e.g. promoters), signals for regulating the efficiency of starting transcription (e.g. operators, enhancers or silencers), and signals to stop transcription (e.g. terminators). Minimally, a gene includes the **transcription unit**, which is the segment of DNA that is copied into RNA in the primary transcript. The signals directing RNA polymerase to start at the correct site, and other DNA segments that influence the efficiency of this process are regulatory elements for the gene. One can also consider them to be part of the gene, along with the transcription unit.

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15.2: The Genetic Code

Skills to Develop

- Explain the “central dogma” of protein synthesis
- Describe the genetic code and how the nucleotide sequence prescribes the amino acid and the protein sequence

The cellular process of transcription generates messenger RNA (mRNA), a mobile molecular copy of one or more genes with an alphabet of A, C, G, and uracil (U). Translation of the mRNA template converts nucleotide-based genetic information into a protein product. Protein sequences consist of 20 commonly occurring amino acids; therefore, it can be said that the protein alphabet consists of 20 letters (Figure **15.2.1**). Each amino acid is defined by a three-nucleotide sequence called the triplet codon. Different amino acids have different chemistries (such as acidic versus basic, or polar and nonpolar) and different structural constraints. Variation in amino acid sequence gives rise to enormous variation in protein structure and function.

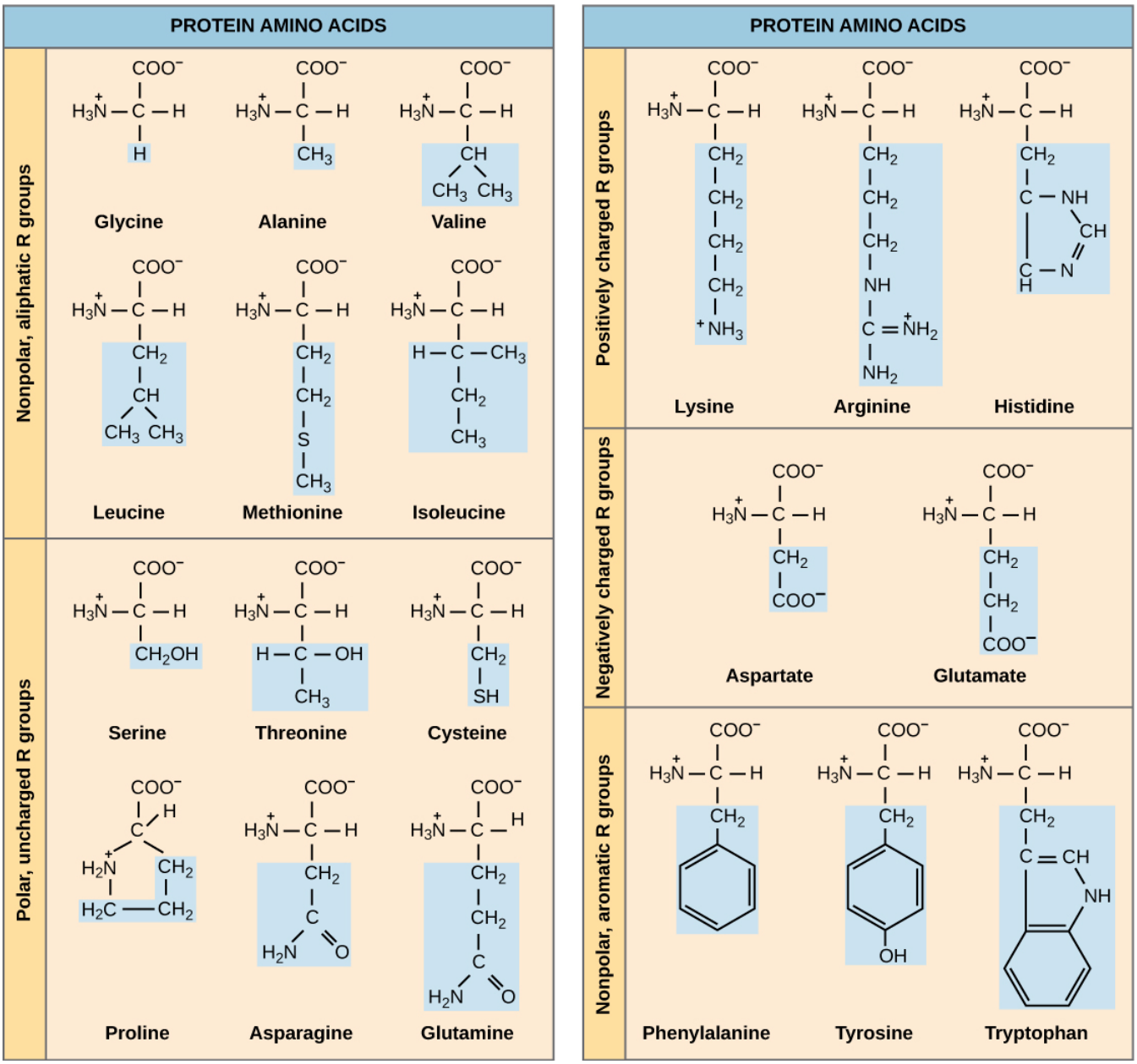


Figure 15.2.1: Structures of the 20 amino acids found in proteins are shown. Each amino acid is composed of an amino group (NH_3^+), a carboxyl group (COO^-), and a side chain (blue). The side chain may be nonpolar, polar, or charged, as well as large or small. It is the variety of amino acid side chains that gives rise to the incredible variation of protein structure and function.

The Central Dogma: DNA Encodes RNA; RNA Encodes Protein

The flow of genetic information in cells from DNA to mRNA to protein is described by the Central Dogma (Figure 15.2.2), which states that genes specify the sequence of mRNAs, which in turn specify the sequence of proteins. The decoding of one molecule to another is performed by specific proteins and RNAs. Because the information stored in DNA is so central to cellular function, it makes intuitive sense that the cell would make mRNA copies of this information for protein synthesis, while keeping the DNA itself intact and protected. The copying of DNA to RNA is relatively straightforward, with one nucleotide being added to the mRNA strand for every nucleotide read in the DNA strand. The translation to protein is a bit more complex because three mRNA nucleotides correspond to one amino acid in the polypeptide sequence. However, the translation to protein is still systematic and colinear, such that nucleotides 1 to 3 correspond to amino acid 1, nucleotides 4 to 6 correspond to amino acid 2, and so on.

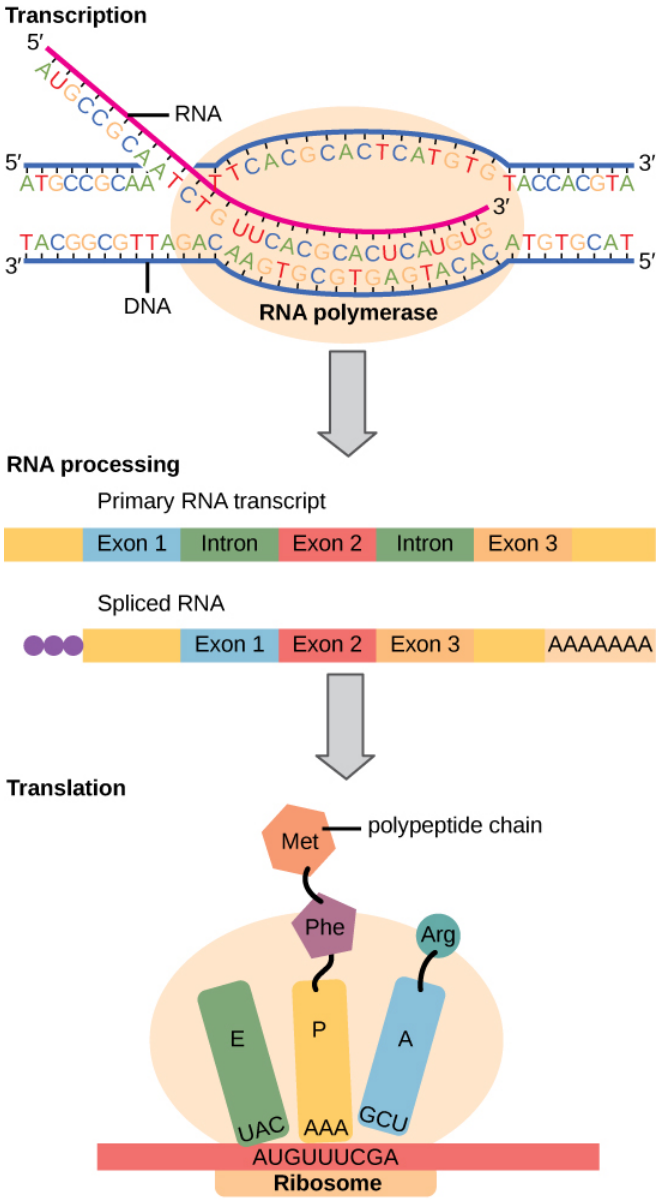


Figure **15.2.2**: Instructions on DNA are transcribed onto messenger RNA. Ribosomes are able to read the genetic information inscribed on a strand of messenger RNA and use this information to string amino acids together into a protein.

The Genetic Code Is Degenerate and Universal

Given the different numbers of "letters" in the mRNA and protein "alphabets," scientists theorized that combinations of nucleotides corresponded to single amino acids. Nucleotide doublets would not be sufficient to specify every amino acid because there are only 16 possible two-nucleotide combinations (4^2). In contrast, there are 64 possible nucleotide triplets (4^3), which is far more than the number of amino acids. Scientists theorized that amino acids were encoded by nucleotide triplets and that the genetic code was degenerate. In other words, a given amino acid could be encoded by more than one nucleotide triplet. This was later confirmed experimentally; Francis Crick and Sydney Brenner used the chemical mutagen proflavin to insert one, two, or three nucleotides into the gene of a virus. When one or two nucleotides were inserted, protein synthesis was completely abolished. When three nucleotides were inserted, the protein was synthesized and functional. This demonstrated that three nucleotides specify each amino acid. These nucleotide triplets are called codons. The insertion of one or two nucleotides completely changed the triplet reading frame, thereby altering the message for every subsequent amino acid (Figure **15.2.4**). Though insertion of three nucleotides caused an extra amino acid to be inserted during translation, the integrity of the rest of the protein was maintained.

Scientists painstakingly solved the genetic code by translating synthetic mRNAs in vitro and sequencing the proteins they specified (Figure 15.2.3).

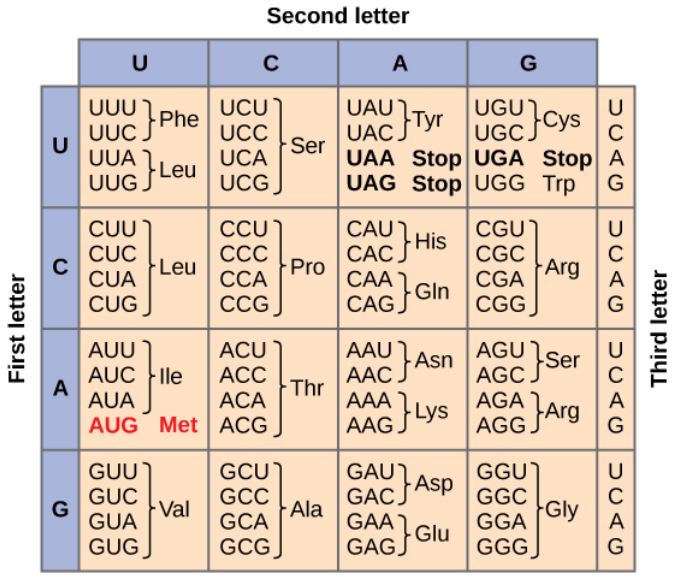


Figure 15.2.3: This figure shows the genetic code for translating each nucleotide triplet in mRNA into an amino acid or a termination signal in a nascent protein. (credit: modification of work by NIH)

In addition to instructing the addition of a specific amino acid to a polypeptide chain, three of the 64 codons terminate protein synthesis and release the polypeptide from the translation machinery. These triplets are called nonsense codons, or stop codons. Another codon, AUG, also has a special function. In addition to specifying the amino acid methionine, it also serves as the start codon to initiate translation. The reading frame for translation is set by the AUG start codon near the 5' end of the mRNA.

The genetic code is universal. With a few exceptions, virtually all species use the same genetic code for protein synthesis. Conservation of codons means that a purified mRNA encoding the globin protein in horses could be transferred to a tulip cell, and the tulip would synthesize horse globin. That there is only one genetic code is powerful evidence that all of life on Earth shares a common origin, especially considering that there are about 10^{84} possible combinations of 20 amino acids and 64 triplet codons.

Link to Learning

Transcribe a gene and translate it to protein using complementary pairing and the genetic code at this site.

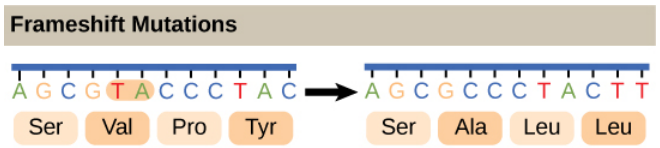


Figure 15.2.4: The deletion of two nucleotides shifts the reading frame of an mRNA and changes the entire protein message, creating a nonfunctional protein or terminating protein synthesis altogether.

Degeneracy is believed to be a cellular mechanism to reduce the negative impact of random mutations. Codons that specify the same amino acid typically only differ by one nucleotide. In addition, amino acids with chemically similar side chains are encoded by similar codons. This nuance of the genetic code ensures that a single-nucleotide substitution mutation might either specify the

same amino acid but have no effect or specify a similar amino acid, preventing the protein from being rendered completely nonfunctional.

Scientific Method Connection: Which Has More DNA: A Kiwi or a Strawberry?

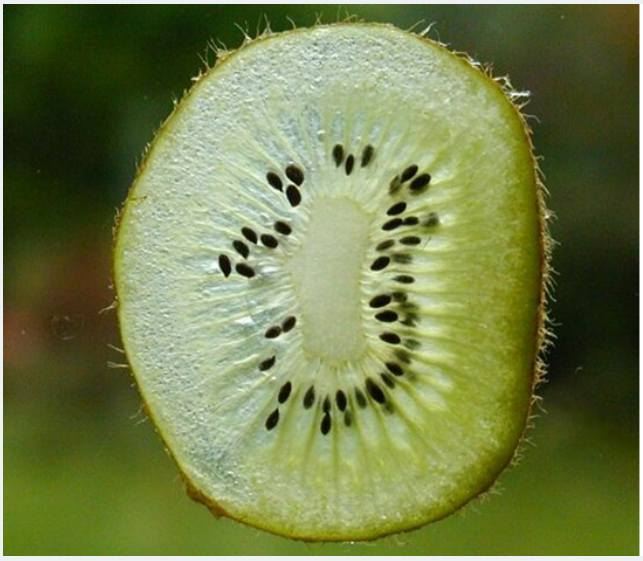



Figure **15.2.5**: Do you think that a kiwi or a strawberry has more DNA per fruit? (credit “kiwi”: "Kelbv"/Flickr; credit: “strawberry”: Alisdair McDiarmid)

Question: Would a kiwifruit and strawberry that are approximately the same size (Figure **15.2.5**) also have approximately the same amount of DNA?

Background: Genes are carried on chromosomes and are made of DNA. All mammals are diploid, meaning they have two copies of each chromosome. However, not all plants are diploid. The common strawberry is octoploid (8*n*) and the cultivated kiwi is hexaploid (6*n*). Research the total number of chromosomes in the cells of each of these fruits and think about how this might correspond to the amount of DNA in these fruits’ cell nuclei. Read about the technique of DNA isolation to understand how each step in the isolation protocol helps liberate and precipitate DNA.

Hypothesis: Hypothesize whether you would be able to detect a difference in DNA quantity from similarly sized strawberries and kiwis. Which fruit do you think would yield more DNA?

Test your hypothesis: Isolate the DNA from a strawberry and a kiwi that are similarly sized. Perform the experiment in at least triplicate for each fruit.

1. Prepare a bottle of DNA extraction buffer from 900 mL water, 50 mL dish detergent, and two teaspoons of table salt. Mix by inversion (cap it and turn it upside down a few times).
2. Grind a strawberry and a kiwifruit by hand in a plastic bag, or using a mortar and pestle, or with a metal bowl and the end of a blunt instrument. Grind for at least two minutes per fruit.
3. Add 10 mL of the DNA extraction buffer to each fruit, and mix well for at least one minute.
4. Remove cellular debris by filtering each fruit mixture through cheesecloth or porous cloth and into a funnel placed in a test tube or an appropriate container.
5. Pour ice-cold ethanol or isopropanol (rubbing alcohol) into the test tube. You should observe white, precipitated DNA.
6. Gather the DNA from each fruit by winding it around separate glass rods.

Record your observations: Because you are not quantitatively measuring DNA volume, you can record for each trial whether the two fruits produced the same or different amounts of DNA as observed by eye. If one or the other fruit produced noticeably more DNA, record this as well. Determine whether your observations are consistent with several pieces of each fruit.

Analyze your data: Did you notice an obvious difference in the amount of DNA produced by each fruit? Were your results reproducible?

> **Draw a conclusion:** Given what you know about the number of chromosomes in each fruit, can you conclude that chromosome number necessarily correlates to DNA amount? Can you identify any drawbacks to this procedure? If you had access to a laboratory, how could you standardize your comparison and make it more quantitative?

Summary

The genetic code refers to the DNA alphabet (A, T, C, G), the RNA alphabet (A, U, C, G), and the polypeptide alphabet (20 amino acids). The Central Dogma describes the flow of genetic information in the cell from genes to mRNA to proteins. Genes are used to make mRNA by the process of transcription; mRNA is used to synthesize proteins by the process of translation. The genetic code is degenerate because 64 triplet codons in mRNA specify only 20 amino acids and three nonsense codons. Almost every species on the planet uses the same genetic code.

Glossary

Central Dogma
: states that genes specify the sequence of mRNAs, which in turn specify the sequence of proteins

codon
: three consecutive nucleotides in mRNA that specify the insertion of an amino acid or the release of a polypeptide chain during translation

colinear
: in terms of RNA and protein, three “units” of RNA (nucleotides) specify one “unit” of protein (amino acid) in a consecutive fashion

degeneracy
: (of the genetic code) describes that a given amino acid can be encoded by more than one nucleotide triplet; the code is degenerate, but not ambiguous

nonsense codon
: one of the three mRNA codons that specifies termination of translation

reading frame
: sequence of triplet codons in mRNA that specify a particular protein; a ribosome shift of one or two nucleotides in either direction completely abolishes synthesis of that protein

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15.3: Prokaryotic Transcription

Skills to Develop

- List the different steps in prokaryotic transcription
- Discuss the role of promoters in prokaryotic transcription
- Describe how and when transcription is terminated

The prokaryotes, which include bacteria and archaea, are mostly single-celled organisms that, by definition, lack membrane-bound nuclei and other organelles. A bacterial chromosome is a covalently closed circle that, unlike eukaryotic chromosomes, is not organized around histone proteins. The central region of the cell in which prokaryotic DNA resides is called the nucleoid. In addition, prokaryotes often have abundant plasmids, which are shorter circular DNA molecules that may only contain one or a few genes. Plasmids can be transferred independently of the bacterial chromosome during cell division and often carry traits such as antibiotic resistance.

Transcription in prokaryotes (and in eukaryotes) requires the DNA double helix to partially unwind in the region of mRNA synthesis. The region of unwinding is called a transcription bubble. Transcription always proceeds from the same DNA strand for each gene, which is called the template strand. The mRNA product is complementary to the template strand and is almost identical to the other DNA strand, called the nontemplate strand. The only difference is that in mRNA, all of the T nucleotides are replaced with U nucleotides. In an RNA double helix, A can bind U via two hydrogen bonds, just as in A–T pairing in a DNA double helix.

The nucleotide pair in the DNA double helix that corresponds to the site from which the first 5' mRNA nucleotide is transcribed is called the +1 site, or the initiation site. Nucleotides preceding the initiation site are given negative numbers and are designated upstream. Conversely, nucleotides following the initiation site are denoted with "+" numbering and are called downstream nucleotides.

Initiation of Transcription in Prokaryotes

Prokaryotes do not have membrane-enclosed nuclei. Therefore, the processes of transcription, translation, and mRNA degradation can all occur simultaneously. The intracellular level of a bacterial protein can quickly be amplified by multiple transcription and translation events occurring concurrently on the same DNA template. Prokaryotic transcription often covers more than one gene and produces polycistronic mRNAs that specify more than one protein.

Our discussion here will exemplify transcription by describing this process in *Escherichia coli*, a well-studied bacterial species. Although some differences exist between transcription in *E. coli* and transcription in archaea, an understanding of *E. coli* transcription can be applied to virtually all bacterial species.

Prokaryotic RNA Polymerase

Prokaryotes use the same RNA polymerase to transcribe all of their genes. In *E. coli*, the polymerase is composed of five polypeptide subunits, two of which are identical. Four of these subunits, denoted α, α, β, and β' comprise the polymerase core enzyme. These subunits assemble every time a gene is transcribed, and they disassemble once transcription is complete. Each subunit has a unique role; the two α-subunits are necessary to assemble the polymerase on the DNA; the β-subunit binds to the ribonucleoside triphosphate that will become part of the nascent "recently born" mRNA molecule; and the β' binds the DNA template strand. The fifth subunit, σ, is involved only in transcription initiation. It confers transcriptional specificity such that the polymerase begins to synthesize mRNA from an appropriate initiation site. Without σ, the core enzyme would transcribe from random sites and would produce mRNA molecules that specified protein gibberish. The polymerase comprised of all five subunits is called the holoenzyme.

Prokaryotic Promoters

A promoter is a DNA sequence onto which the transcription machinery binds and initiates transcription. In most cases, promoters exist upstream of the genes they regulate. The specific sequence of a promoter is very important because it determines whether the corresponding gene is transcribed all the time, some of the time, or infrequently. Although promoters vary among prokaryotic genomes, a few elements are conserved. At the -10 and -35 regions upstream of the initiation site, there are two promoter consensus

sequences, or regions that are similar across all promoters and across various bacterial species (Figure 15.3.1). The -10 consensus sequence, called the -10 region, is TATAAT. The -35 sequence, TTGACA, is recognized and bound by σ. Once this interaction is made, the subunits of the core enzyme bind to the site. The A–T-rich -10 region facilitates unwinding of the DNA template, and several phosphodiester bonds are made. The transcription initiation phase ends with the production of abortive transcripts, which are polymers of approximately 10 nucleotides that are made and released.

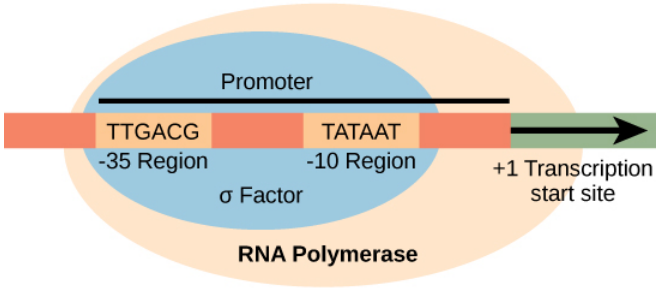
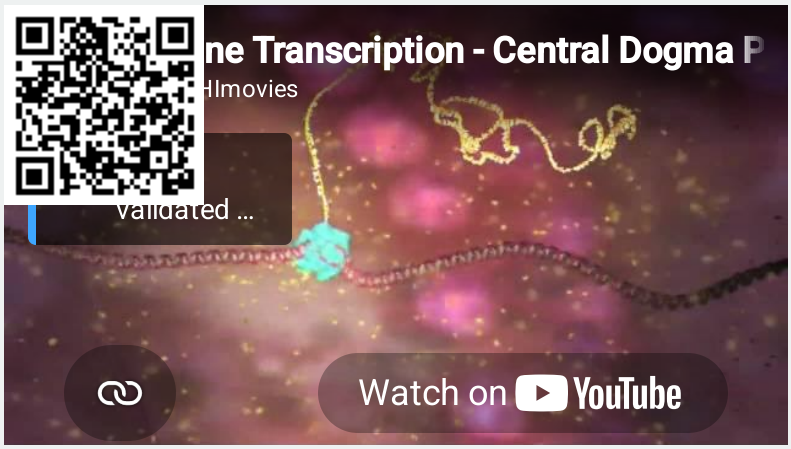


Figure 15.3.1: The σ subunit of prokaryotic RNA polymerase recognizes consensus sequences found in the promoter region upstream of the transcription start sight. The σ subunit dissociates from the polymerase after transcription has been initiated.

Link to Learning



View this MolecularMovies animation to see the first part of transcription and the base sequence repetition of the TATA box.

Elongation and Termination in Prokaryotes

The transcription elongation phase begins with the release of the σ subunit from the polymerase. The dissociation of σ allows the core enzyme to proceed along the DNA template, synthesizing mRNA in the 5' to 3' direction at a rate of approximately 40 nucleotides per second. As elongation proceeds, the DNA is continuously unwound ahead of the core enzyme and rewound behind it (Figure 15.3.2). The base pairing between DNA and RNA is not stable enough to maintain the stability of the mRNA synthesis components. Instead, the RNA polymerase acts as a stable linker between the DNA template and the nascent RNA strands to ensure that elongation is not interrupted prematurely.

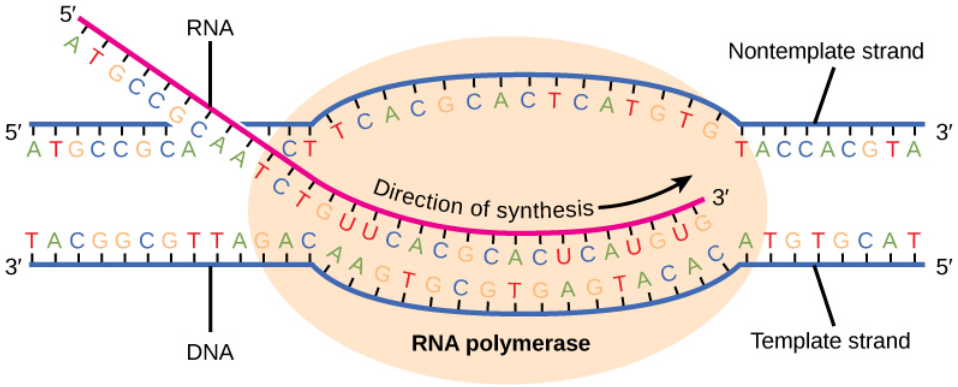


Figure 15.3.2: During elongation, the prokaryotic RNA polymerase tracks along the DNA template, synthesizes mRNA in the 5' to 3' direction, and unwinds and rewinds the DNA as it is read.

Prokaryotic Termination Signals

Once a gene is transcribed, the prokaryotic polymerase needs to be instructed to dissociate from the DNA template and liberate the newly made mRNA. Depending on the gene being transcribed, there are two kinds of termination signals. One is protein-based and the other is RNA-based. Rho-dependent termination is controlled by the rho protein, which tracks along behind the polymerase on the growing mRNA chain. Near the end of the gene, the polymerase encounters a run of G nucleotides on the DNA template and it stalls. As a result, the rho protein collides with the polymerase. The interaction with rho releases the mRNA from the transcription bubble.

Rho-independent termination is controlled by specific sequences in the DNA template strand. As the polymerase nears the end of the gene being transcribed, it encounters a region rich in C–G nucleotides. The mRNA folds back on itself, and the complementary C–G nucleotides bind together. The result is a stable hairpin that causes the polymerase to stall as soon as it begins to transcribe a region rich in A–T nucleotides. The complementary U–A region of the mRNA transcript forms only a weak interaction with the template DNA. This, coupled with the stalled polymerase, induces enough instability for the core enzyme to break away and liberate the new mRNA transcript.

Upon termination, the process of transcription is complete. By the time termination occurs, the prokaryotic transcript would already have been used to begin synthesis of numerous copies of the encoded protein because these processes can occur concurrently. The unification of transcription, translation, and even mRNA degradation is possible because all of these processes occur in the same 5' to 3' direction, and because there is no membranous compartmentalization in the prokaryotic cell (Figure 15.3.3). In contrast, the presence of a nucleus in eukaryotic cells precludes simultaneous transcription and translation.

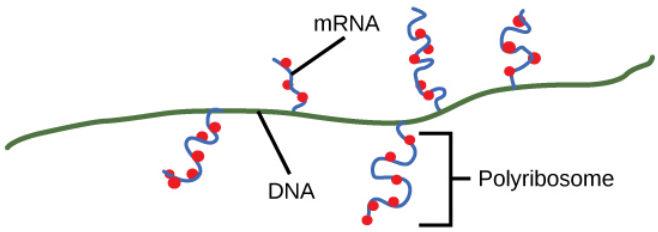
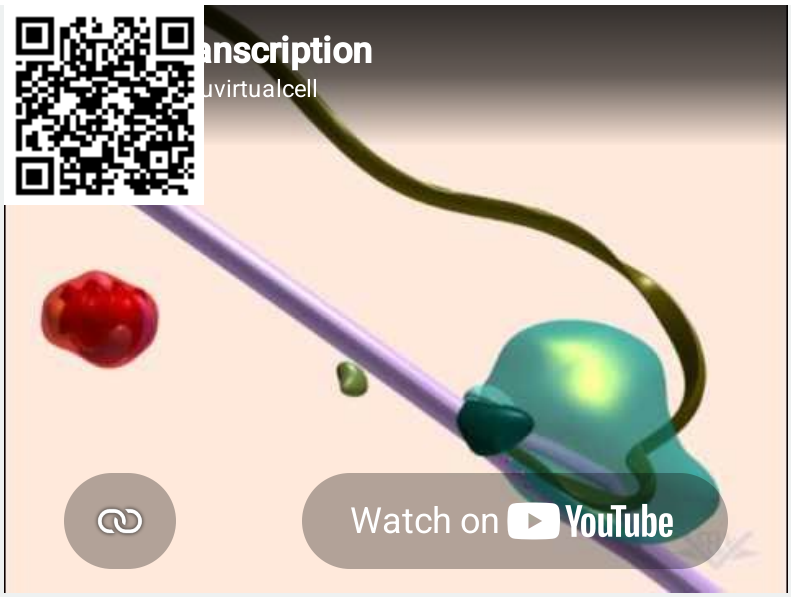


Figure 15.3.3: Multiple polymerases can transcribe a single bacterial gene while numerous ribosomes concurrently translate the mRNA transcripts into polypeptides. In this way, a specific protein can rapidly reach a high concentration in the bacterial cell.

Link to Learning



Visit this BioStudio animation to see the process of prokaryotic transcription.

Summary

In prokaryotes, mRNA synthesis is initiated at a promoter sequence on the DNA template comprising two consensus sequences that recruit RNA polymerase. The prokaryotic polymerase consists of a core enzyme of four protein subunits and a σ protein that assists only with initiation. Elongation synthesizes mRNA in the 5' to 3' direction at a rate of 40 nucleotides per second. Termination liberates the mRNA and occurs either by rho protein interaction or by the formation of an mRNA hairpin.

Glossary

consensus
DNA sequence that is used by many species to perform the same or similar functions

core enzyme
prokaryotic RNA polymerase consisting of α, α, β, and β' but missing σ; this complex performs elongation

downstream
nucleotides following the initiation site in the direction of mRNA transcription; in general, sequences that are toward the 3' end relative to a site on the mRNA

hairpin
structure of RNA when it folds back on itself and forms intramolecular hydrogen bonds between complementary nucleotides

holoenzyme
prokaryotic RNA polymerase consisting of α, α, β, β', and σ; this complex is responsible for transcription initiation

initiation site
nucleotide from which mRNA synthesis proceeds in the 5' to 3' direction; denoted with a “+1”

nontemplate strand
strand of DNA that is not used to transcribe mRNA; this strand is identical to the mRNA except that T nucleotides in the DNA are replaced by U nucleotides in the mRNA

plasmid

extrachromosomal, covalently closed, circular DNA molecule that may only contain one or a few genes; common in prokaryotes

promoter
DNA sequence to which RNA polymerase and associated factors bind and initiate transcription

Rho-dependent termination
in prokaryotes, termination of transcription by an interaction between RNA polymerase and the rho protein at a run of G nucleotides on the DNA template

Rho-independent
termination sequence-dependent termination of prokaryotic mRNA synthesis; caused by hairpin formation in the mRNA that stalls the polymerase

TATA box
conserved promoter sequence in eukaryotes and prokaryotes that helps to establish the initiation site for transcription

template strand
strand of DNA that specifies the complementary mRNA molecule

transcription bubble
region of locally unwound DNA that allows for transcription of mRNA

upstream
nucleotides preceding the initiation site; in general, sequences toward the 5' end relative to a site on the mRNA

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15.4: Eukaryotic Transcription

Skills to Develop

- List the steps in eukaryotic transcription
- Discuss the role of RNA polymerases in transcription
- Compare and contrast the three RNA polymerases
- Explain the significance of transcription factors

Prokaryotes and eukaryotes perform fundamentally the same process of transcription, with a few key differences. The most important difference between prokaryotes and eukaryotes is the latter's membrane-bound nucleus and organelles. With the genes bound in a nucleus, the eukaryotic cell must be able to transport its mRNA to the cytoplasm and must protect its mRNA from degrading before it is translated. Eukaryotes also employ three different polymerases that each transcribe a different subset of genes. Eukaryotic mRNAs are usually monogenic, meaning that they specify a single protein.

Initiation of Transcription in Eukaryotes

Unlike the prokaryotic polymerase that can bind to a DNA template on its own, eukaryotes require several other proteins, called transcription factors, to first bind to the promoter region and then help recruit the appropriate polymerase.

The Three Eukaryotic RNA Polymerases

The features of eukaryotic mRNA synthesis are markedly more complex those of prokaryotes. Instead of a single polymerase comprising five subunits, the eukaryotes have three polymerases that are each made up of 10 subunits or more. Each eukaryotic polymerase also requires a distinct set of transcription factors to bring it to the DNA template.

RNA polymerase I is located in the nucleolus, a specialized nuclear substructure in which ribosomal RNA (rRNA) is transcribed, processed, and assembled into ribosomes (Table **15.4.1**). The rRNA molecules are considered structural RNAs because they have a cellular role but are not translated into protein. The rRNAs are components of the ribosome and are essential to the process of translation. RNA polymerase I synthesizes all of the rRNAs except for the 5S rRNA molecule. The "S" designation applies to "Svedberg" units, a nonadditive value that characterizes the speed at which a particle sediments during centrifugation.

Table **15.4.1**: Locations, Products, and Sensitivities of the Three Eukaryotic RNA Polymerases

RNA Polymerase	Cellular Compartment	Product of Transcription	α-Amanitin Sensitivity
I	Nucleolus	All rRNAs except 5S rRNA	Insensitive
II	Nucleus	All protein-coding nuclear pre-mRNAs	Extremely sensitive
III	Nucleus	5S rRNA, tRNAs, and small nuclear RNAs	Moderately sensitive

RNA polymerase II is located in the nucleus and synthesizes all protein-coding nuclear pre-mRNAs. Eukaryotic pre-mRNAs undergo extensive processing after transcription but before translation. For clarity, this module's discussion of transcription and translation in eukaryotes will use the term "mRNAs" to describe only the mature, processed molecules that are ready to be translated. RNA polymerase II is responsible for transcribing the overwhelming majority of eukaryotic genes.

RNA polymerase III is also located in the nucleus. This polymerase transcribes a variety of structural RNAs that includes the 5S pre-rRNA, transfer pre-RNAs (pre-tRNAs), and small nuclear pre-RNAs. The tRNAs have a critical role in translation; they serve as the adaptor molecules between the mRNA template and the growing polypeptide chain. Small nuclear RNAs have a variety of functions, including "splicing" pre-mRNAs and regulating transcription factors.

A scientist characterizing a new gene can determine which polymerase transcribes it by testing whether the gene is expressed in the presence of a particular mushroom poison, α-amanitin (table above). Interestingly, α-amanitin produced by *Amanita phalloides*, the

Death Cap mushroom, affects the three polymerases very differently. RNA polymerase I is completely insensitive to α-amanitin, meaning that the polymerase can transcribe DNA in vitro in the presence of this poison. In contrast, RNA polymerase II is extremely sensitive to α-amanitin, and RNA polymerase III is moderately sensitive. Knowing the transcribing polymerase can clue a researcher into the general function of the gene being studied. Because RNA polymerase II transcribes the vast majority of genes, we will focus on this polymerase in our subsequent discussions about eukaryotic transcription factors and promoters.

Structure of an RNA Polymerase II Promoter

Eukaryotic promoters are much larger and more complex than prokaryotic promoters, but both have a TATA box. For example, in the mouse thymidine kinase gene, the TATA box is located at approximately -30 relative to the initiation (+1) site (Figure **15.4.1**). For this gene, the exact TATA box sequence is TATAAAA, as read in the 5' to 3' direction on the nontemplate strand. This sequence is not identical to the *E. coli* TATA box, but it conserves the A–T rich element. The thermostability of A–T bonds is low and this helps the DNA template to locally unwind in preparation for transcription.

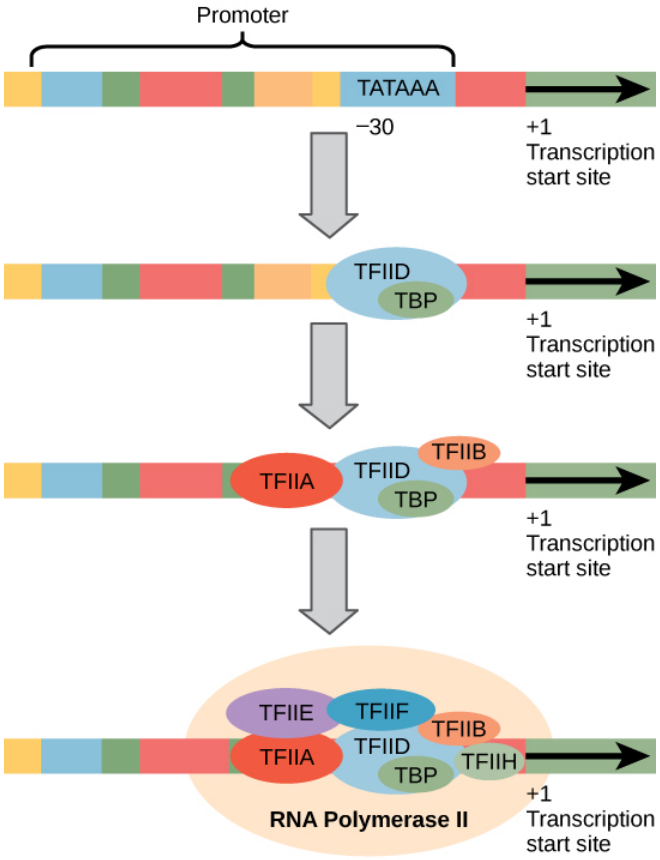


Figure **15.4.1**: A generalized promoter of a gene transcribed by RNA polymerase II is shown. Transcription factors recognize the promoter. RNA polymerase II then binds and forms the transcription initiation complex.

Art Connection

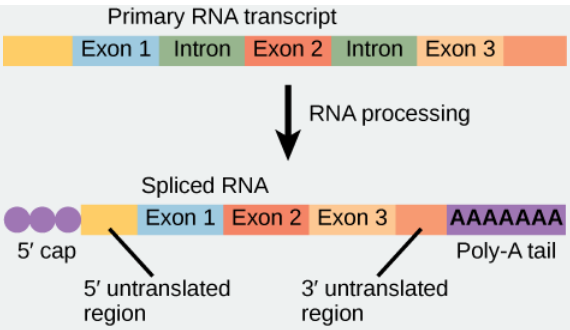


Figure **15.4.2**: Eukaryotic mRNA contains introns that must be spliced out. A 5' cap and 3' poly-A tail are also added.

A scientist splices a eukaryotic promoter in front of a bacterial gene and inserts the gene in a bacterial chromosome. Would you expect the bacteria to transcribe the gene?

The mouse genome includes one gene and two pseudogenes for cytoplasmic thymidine kinase. Pseudogenes are genes that have lost their protein-coding ability or are no longer expressed by the cell. These pseudogenes are copied from mRNA and incorporated into the chromosome. For example, the mouse thymidine kinase promoter also has a conserved CAAT box (GGCCAATCT) at approximately -80. This sequence is essential and is involved in binding transcription factors. Further upstream of the TATA box, eukaryotic promoters may also contain one or more GC-rich boxes (GGCG) or octamer boxes (ATTTGCAT). These elements bind cellular factors that increase the efficiency of transcription initiation and are often identified in more “active” genes that are constantly being expressed by the cell.

Transcription Factors for RNA Polymerase II

The complexity of eukaryotic transcription does not end with the polymerases and promoters. An army of basal transcription factors, enhancers, and silencers also help to regulate the frequency with which pre-mRNA is synthesized from a gene. Enhancers and silencers affect the efficiency of transcription but are not necessary for transcription to proceed. Basal transcription factors are crucial in the formation of a preinitiation complex on the DNA template that subsequently recruits RNA polymerase II for transcription initiation.

The names of the basal transcription factors begin with “TFII” (this is the transcription factor for RNA polymerase II) and are specified with the letters A–J. The transcription factors systematically fall into place on the DNA template, with each one further stabilizing the preinitiation complex and contributing to the recruitment of RNA polymerase II.

The processes of bringing RNA polymerases I and III to the DNA template involve slightly less complex collections of transcription factors, but the general theme is the same. Eukaryotic transcription is a tightly regulated process that requires a variety of proteins to interact with each other and with the DNA strand. Although the process of transcription in eukaryotes involves a greater metabolic investment than in prokaryotes, it ensures that the cell transcribes precisely the pre-mRNAs that it needs for protein synthesis.

Evolution Connection: The Evolution of Promoters

The evolution of genes may be a familiar concept. Mutations can occur in genes during DNA replication, and the result may or may not be beneficial to the cell. By altering an enzyme, structural protein, or some other factor, the process of mutation can transform functions or physical features. However, eukaryotic promoters and other gene regulatory sequences may evolve as well. For instance, consider a gene that, over many generations, becomes more valuable to the cell. Maybe the gene encodes a structural protein that the cell needs to synthesize in abundance for a certain function. If this is the case, it would be beneficial to the cell for that gene’s promoter to recruit transcription factors more efficiently and increase gene expression.

Scientists examining the evolution of promoter sequences have reported varying results. In part, this is because it is difficult to infer exactly where a eukaryotic promoter begins and ends. Some promoters occur within genes; others are located very far upstream, or even downstream, of the genes they are regulating. However, when researchers limited their examination to human core promoter sequences that were defined experimentally as sequences that bind the preinitiation complex, they found that promoters evolve even faster than protein-coding genes.

> It is still unclear how promoter evolution might correspond to the evolution of humans or other higher organisms. However, the evolution of a promoter to effectively make more or less of a given gene product is an intriguing alternative to the evolution of the genes themselves.[1]

Promoter Structures for RNA Polymerases I and III

In eukaryotes, the conserved promoter elements differ for genes transcribed by RNA polymerases I, II, and III. RNA polymerase I transcribes genes that have two GC-rich promoter sequences in the -45 to +20 region. These sequences alone are sufficient for transcription initiation to occur, but promoters with additional sequences in the region from -180 to -105 upstream of the initiation site will further enhance initiation. Genes that are transcribed by RNA polymerase III have upstream promoters or promoters that occur within the genes themselves.

Eukaryotic Elongation and Termination

Following the formation of the preinitiation complex, the polymerase is released from the other transcription factors, and elongation is allowed to proceed as it does in prokaryotes with the polymerase synthesizing pre-mRNA in the 5' to 3' direction. As discussed previously, RNA polymerase II transcribes the major share of eukaryotic genes, so this section will focus on how this polymerase accomplishes elongation and termination.

Although the enzymatic process of elongation is essentially the same in eukaryotes and prokaryotes, the DNA template is more complex. When eukaryotic cells are not dividing, their genes exist as a diffuse mass of DNA and proteins called chromatin. The DNA is tightly packaged around charged histone proteins at repeated intervals. These DNA–histone complexes, collectively called nucleosomes, are regularly spaced and include 146 nucleotides of DNA wound around eight histones like thread around a spool.

For polynucleotide synthesis to occur, the transcription machinery needs to move histones out of the way every time it encounters a nucleosome. This is accomplished by a special protein complex called FACT, which stands for “facilitates chromatin transcription.” This complex pulls histones away from the DNA template as the polymerase moves along it. Once the pre-mRNA is synthesized, the FACT complex replaces the histones to recreate the nucleosomes.

The termination of transcription is different for the different polymerases. Unlike in prokaryotes, elongation by RNA polymerase II in eukaryotes takes place 1,000–2,000 nucleotides beyond the end of the gene being transcribed. This pre-mRNA tail is subsequently removed by cleavage during mRNA processing. On the other hand, RNA polymerases I and III require termination signals. Genes transcribed by RNA polymerase I contain a specific 18-nucleotide sequence that is recognized by a termination protein. The process of termination in RNA polymerase III involves an mRNA hairpin similar to rho-independent termination of transcription in prokaryotes.

Summary

Transcription in eukaryotes involves one of three types of polymerases, depending on the gene being transcribed. RNA polymerase II transcribes all of the protein-coding genes, whereas RNA polymerase I transcribes rRNA genes, and RNA polymerase III transcribes rRNA, tRNA, and small nuclear RNA genes. The initiation of transcription in eukaryotes involves the binding of several transcription factors to complex promoter sequences that are usually located upstream of the gene being copied. The mRNA is synthesized in the 5' to 3' direction, and the FACT complex moves and reassembles nucleosomes as the polymerase passes by. Whereas RNA polymerases I and III terminate transcription by protein- or RNA hairpin-dependent methods, RNA polymerase II transcribes for 1,000 or more nucleotides beyond the gene template and cleaves the excess during pre-mRNA processing.

Art Connections

Figure **15.4.2**: A scientist splices a eukaryotic promoter in front of a bacterial gene and inserts the gene in a bacterial chromosome. Would you expect the bacteria to transcribe the gene?

Answer

No. Prokaryotes use different promoters than eukaryotes.

Footnotes

1. 1 H Liang et al., “Fast evolution of core promoters in primate genomes,” *Molecular Biology and Evolution* 25 (2008): 1239–44.

Glossary

CAAT box
(GGCCAATCT) essential eukaryotic promoter sequence involved in binding transcription factors

FACT
complex that “facilitates chromatin transcription” by disassembling nucleosomes ahead of a transcribing RNA polymerase II and reassembling them after the polymerase passes by

GC-rich box
(GGCG) nonessential eukaryotic promoter sequence that binds cellular factors to increase the efficiency of transcription; may be present several times in a promoter

Octamer box
(ATTTGCAT) nonessential eukaryotic promoter sequence that binds cellular factors to increase the efficiency of transcription; may be present several times in a promoter

preinitiation complex
cluster of transcription factors and other proteins that recruit RNA polymerase II for transcription of a DNA template

small nuclear RNA
molecules synthesized by RNA polymerase III that have a variety of functions, including splicing pre-mRNAs and regulating transcription factors

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15.5: Eukaryotic pre-mRNA Splicing

Skills to Develop

- Describe the different steps in RNA processing
- Understand the significance of exons, introns, and splicing
- Explain how tRNAs and rRNAs are processed

After transcription, eukaryotic pre-mRNAs must undergo several processing steps before they can be translated. Eukaryotic (and prokaryotic) tRNAs and rRNAs also undergo processing before they can function as components in the protein synthesis machinery.

mRNA Processing

The eukaryotic pre-mRNA undergoes extensive processing before it is ready to be translated. The additional steps involved in eukaryotic mRNA maturation create a molecule with a much longer half-life than a prokaryotic mRNA. Eukaryotic mRNAs last for several hours, whereas the typical *E. coli* mRNA lasts no more than five seconds.

Pre-mRNAs are first coated in RNA-stabilizing proteins; these protect the pre-mRNA from degradation while it is processed and exported out of the nucleus. The three most important steps of pre-mRNA processing are the addition of stabilizing and signaling factors at the 5' and 3' ends of the molecule, and the removal of intervening sequences that do not specify the appropriate amino acids. In rare cases, the mRNA transcript can be “edited” after it is transcribed.

Evolution Connection: RNA Editing in Trypanosomes

The trypanosomes are a group of protozoa that include the pathogen *Trypanosoma brucei*, which causes sleeping sickness in humans (Figure **15.5.1**). Trypanosomes, and virtually all other eukaryotes, have organelles called mitochondria that supply the cell with chemical energy. Mitochondria are organelles that express their own DNA and are believed to be the remnants of a symbiotic relationship between a eukaryote and an engulfed prokaryote. The mitochondrial DNA of trypanosomes exhibit an interesting exception to The Central Dogma: their pre-mRNAs do not have the correct information to specify a functional protein. Usually, this is because the mRNA is missing several U nucleotides. The cell performs an additional RNA processing step called RNA editing to remedy this.



Figure **15.5.1**: *Trypanosoma brucei* is the causative agent of sleeping sickness in humans. The mRNAs of this pathogen must be modified by the addition of nucleotides before protein synthesis can occur. (credit: modification of work by Torsten Ochsenreiter)

Other genes in the mitochondrial genome encode 40- to 80-nucleotide guide RNAs. One or more of these molecules interacts by complementary base pairing with some of the nucleotides in the pre-mRNA transcript. However, the guide RNA has more A nucleotides than the pre-mRNA has U nucleotides to bind with. In these regions, the guide RNA loops out. The 3' ends of guide RNAs have a long poly-U tail, and these U bases are inserted in regions of the pre-mRNA transcript at which the guide RNAs are looped. This process is entirely mediated by RNA molecules. That is, guide RNAs—rather than proteins—serve as the catalysts in RNA editing.

RNA editing is not just a phenomenon of trypanosomes. In the mitochondria of some plants, almost all pre-mRNAs are edited. RNA editing has also been identified in mammals such as rats, rabbits, and even humans. What could be the evolutionary reason for this additional step in pre-mRNA processing? One possibility is that the mitochondria, being remnants of ancient prokaryotes, have an equally ancient RNA-based method for regulating gene expression. In support of this hypothesis, edits made to pre-mRNAs differ depending on cellular conditions. Although speculative, the process of RNA editing may be a holdover from a primordial time when RNA molecules, instead of proteins, were responsible for catalyzing reactions.

5' Capping

While the pre-mRNA is still being synthesized, a 7-methylguanosine cap is added to the 5' end of the growing transcript by a phosphate linkage. This moiety (functional group) protects the nascent mRNA from degradation. In addition, factors involved in protein synthesis recognize the cap to help initiate translation by ribosomes.

3' Poly-A Tail

Once elongation is complete, the pre-mRNA is cleaved by an endonuclease between an AAUAAA consensus sequence and a GU-rich sequence, leaving the AAUAAA sequence on the pre-mRNA. An enzyme called poly-A polymerase then adds a string of approximately 200 A residues, called the poly-A tail. This modification further protects the pre-mRNA from degradation and signals the export of the cellular factors that the transcript needs to the cytoplasm.

Pre-mRNA Splicing

Eukaryotic genes are composed of exons, which correspond to protein-coding sequences (*ex*-on signifies that they are *ex*pressed), and *int*ervening sequences called introns (*int*-ron denotes their *int*ervening role), which may be involved in gene regulation but are removed from the pre-mRNA during processing. Intron sequences in mRNA do not encode functional proteins.

The discovery of introns came as a surprise to researchers in the 1970s who expected that pre-mRNAs would specify protein sequences without further processing, as they had observed in prokaryotes. The genes of higher eukaryotes very often contain one or more introns. These regions may correspond to regulatory sequences; however, the biological significance of having many introns or having very long introns in a gene is unclear. It is possible that introns slow down gene expression because it takes longer to transcribe pre-mRNAs with lots of introns. Alternatively, introns may be nonfunctional sequence remnants left over from the fusion of ancient genes throughout evolution. This is supported by the fact that separate exons often encode separate protein subunits or domains. For the most part, the sequences of introns can be mutated without ultimately affecting the protein product.

All of a pre-mRNA's introns must be completely and precisely removed before protein synthesis. If the process errs by even a single nucleotide, the reading frame of the rejoined exons would shift, and the resulting protein would be dysfunctional. The process of removing introns and reconnecting exons is called splicing (Figure **15.5.2**). Introns are removed and degraded while the pre-mRNA is still in the nucleus. Splicing occurs by a sequence-specific mechanism that ensures introns will be removed and exons rejoined with the accuracy and precision of a single nucleotide. The splicing of pre-mRNAs is conducted by complexes of proteins and RNA molecules called spliceosomes.

Art Connection

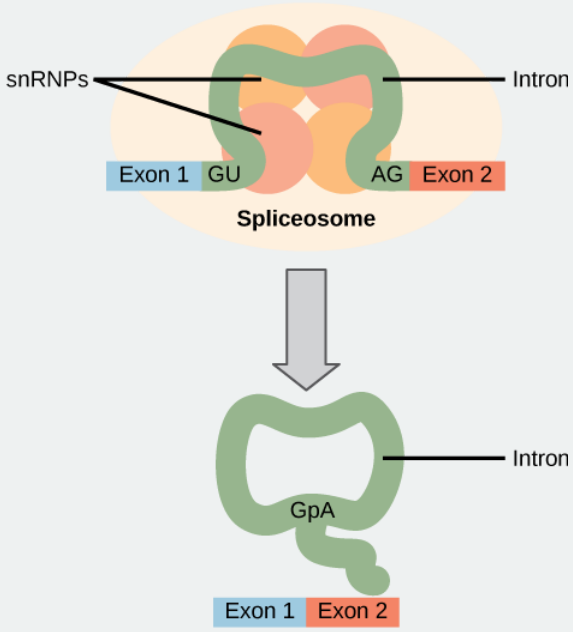
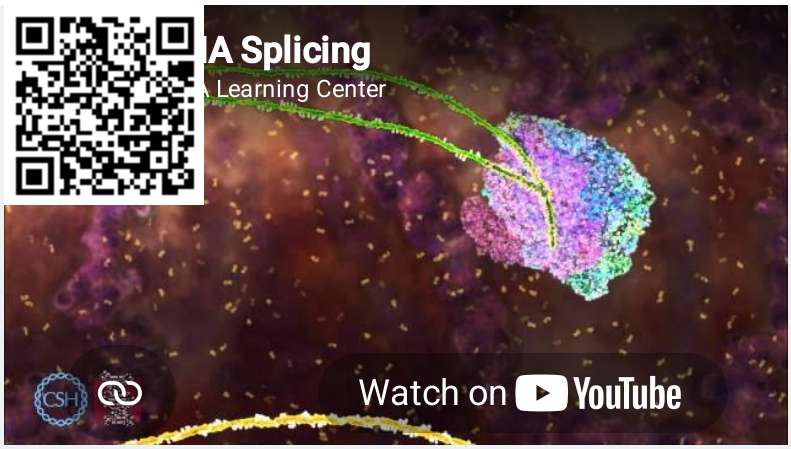


Figure **15.5.2**: Pre-mRNA splicing involves the precise removal of introns from the primary RNA transcript. The splicing process is catalyzed by protein complexes called spliceosomes that are composed of proteins and RNA molecules called snRNAs. Spliceosomes recognize sequences at the 5' and 3' end of the intron.

Errors in splicing are implicated in cancers and other human diseases. What kinds of mutations might lead to splicing errors? Think of different possible outcomes if splicing errors occur.

Note that more than 70 individual introns can be present, and each has to undergo the process of splicing—in addition to 5' capping and the addition of a poly-A tail—just to generate a single, translatable mRNA molecule.

Link to Learning



See how introns are removed during RNA splicing at this website.

Processing of tRNAs and rRNAs

The tRNAs and rRNAs are structural molecules that have roles in protein synthesis; however, these RNAs are not themselves translated. Pre-rRNAs are transcribed, processed, and assembled into ribosomes in the nucleolus. Pre-tRNAs are transcribed and processed in the nucleus and then released into the cytoplasm where they are linked to free amino acids for protein synthesis.

Most of the tRNAs and rRNAs in eukaryotes and prokaryotes are first transcribed as a long precursor molecule that spans multiple rRNAs or tRNAs. Enzymes then cleave the precursors into subunits corresponding to each structural RNA. Some of the bases of pre-rRNAs are methylated; that is, a $–CH_3$ moiety (methyl functional group) is added for stability. Pre-tRNA molecules also undergo methylation. As with pre-mRNAs, subunit excision occurs in eukaryotic pre-RNAs destined to become tRNAs or rRNAs.

Mature rRNAs make up approximately 50 percent of each ribosome. Some of a ribosome's RNA molecules are purely structural, whereas others have catalytic or binding activities. Mature tRNAs take on a three-dimensional structure through intramolecular hydrogen bonding to position the amino acid binding site at one end and the anticodon at the other end (Figure **15.5.3**). The anticodon is a three-nucleotide sequence in a tRNA that interacts with an mRNA codon through complementary base pairing.

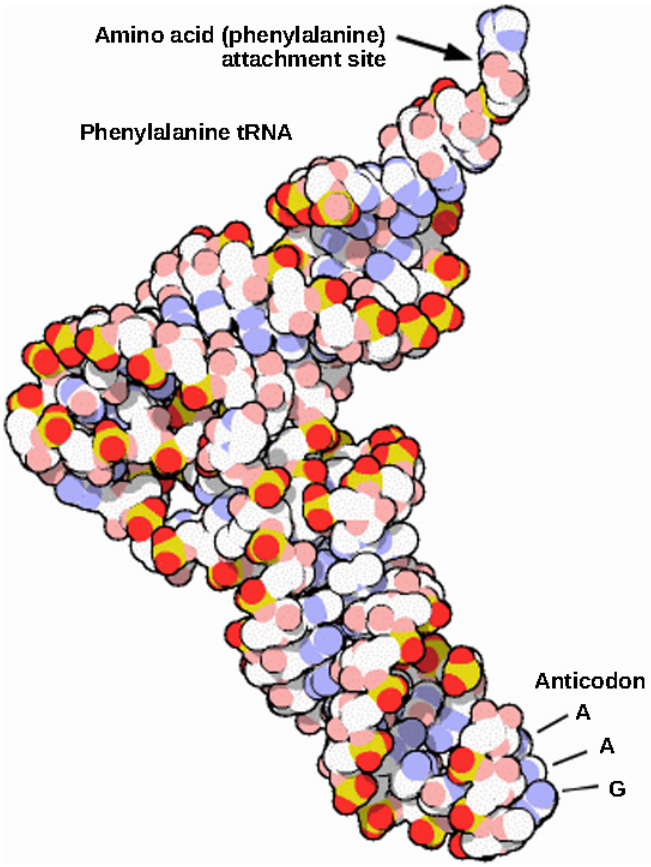


Figure **15.5.3**: This is a space-filling model of a tRNA molecule that adds the amino acid phenylalanine to a growing polypeptide chain. The anticodon AAG binds the Codon UUC on the mRNA. The amino acid phenylalanine is attached to the other end of the tRNA.

Summary

Eukaryotic pre-mRNAs are modified with a 5' methylguanosine cap and a poly-A tail. These structures protect the mature mRNA from degradation and help export it from the nucleus. Pre-mRNAs also undergo splicing, in which introns are removed and exons are reconnected with single-nucleotide accuracy. Only finished mRNAs that have undergone 5' capping, 3' polyadenylation, and intron splicing are exported from the nucleus to the cytoplasm. Pre-rRNAs and pre-tRNAs may be processed by intramolecular cleavage, splicing, methylation, and chemical conversion of nucleotides. Rarely, RNA editing is also performed to insert missing bases after an mRNA has been synthesized.

Art Connections

Figure **15.5.2**: Errors in splicing are implicated in cancers and other human diseases. What kinds of mutations might lead to splicing errors? Think of different possible outcomes if splicing errors occur.

Answer

Mutations in the spliceosome recognition sequence at each end of the intron, or in the proteins and RNAs that make up the spliceosome, may impair splicing. Mutations may also add new spliceosome recognition sites. Splicing errors could lead to introns being retained in spliced RNA, exons being excised, or changes in the location of the splice site.

Glossary

7-methylguanosine cap

modification added to the 5' end of pre-mRNAs to protect mRNA from degradation and assist translation

anticodon

three-nucleotide sequence in a tRNA molecule that corresponds to an mRNA codon

exon

sequence present in protein-coding mRNA after completion of pre-mRNA splicing

intron

non–protein-coding intervening sequences that are spliced from mRNA during processing

poly-A tail

modification added to the 3' end of pre-mRNAs to protect mRNA from degradation and assist mRNA export from the nucleus

RNA editing

direct alteration of one or more nucleotides in an mRNA that has already been synthesized

splicing

process of removing introns and reconnecting exons in a pre-mRNA

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15.6: The Structure of tRNA and Ribosomes

Skills to Develop

- Describe the different steps in protein synthesis
- Discuss the role of ribosomes in protein synthesis

The synthesis of proteins consumes more of a cell's energy than any other metabolic process. In turn, proteins account for more mass than any other component of living organisms (with the exception of water), and proteins perform virtually every function of a cell. The process of translation, or protein synthesis, involves the decoding of an mRNA message into a polypeptide product. Amino acids are covalently strung together by interlinking peptide bonds in lengths ranging from approximately 50 amino acid residues to more than 1,000. Each individual amino acid has an amino group (NH_2) and a carboxyl (COOH) group. Polypeptides are formed when the amino group of one amino acid forms an amide (i.e., peptide) bond with the carboxyl group of another amino acid (Figure **15.6.1**). This reaction is catalyzed by ribosomes and generates one water molecule.

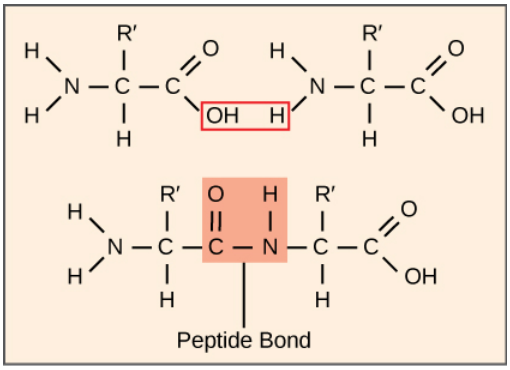


Figure **15.6.1**: A peptide bond links the carboxyl end of one amino acid with the amino end of another, expelling one water molecule. For simplicity in this image, only the functional groups involved in the peptide bond are shown. The R and R' designations refer to the rest of each amino acid structure.

The Protein Synthesis Machinery

In addition to the mRNA template, many molecules and macromolecules contribute to the process of translation. The composition of each component may vary across species; for instance, ribosomes may consist of different numbers of rRNAs and polypeptides depending on the organism. However, the general structures and functions of the protein synthesis machinery are comparable from bacteria to human cells. Translation requires the input of an mRNA template, ribosomes, tRNAs, and various enzymatic factors.

Link to Learning

Click through the steps of this PBS interactive to see protein synthesis in action.

Ribosomes

Even before an mRNA is translated, a cell must invest energy to build each of its ribosomes. In *E. coli*, there are between 10,000 and 70,000 ribosomes present in each cell at any given time. A ribosome is a complex macromolecule composed of structural and catalytic rRNAs, and many distinct polypeptides. In eukaryotes, the nucleolus is completely specialized for the synthesis and assembly of rRNAs.

Ribosomes exist in the cytoplasm in prokaryotes and in the cytoplasm and rough endoplasmic reticulum in eukaryotes. Mitochondria and chloroplasts also have their own ribosomes in the matrix and stroma, which look more similar to prokaryotic ribosomes (and have similar drug sensitivities) than the ribosomes just outside their outer membranes in the cytoplasm. Ribosomes dissociate into large and small subunits when they are not synthesizing proteins and reassociate during the initiation of translation. In *E. coli*, the small subunit is described as 30S, and the large subunit is 50S, for a total of 70S (recall that Svedberg units are not additive). Mammalian ribosomes have a small 40S subunit and a large 60S subunit, for a total of 80S. The small subunit is responsible for binding the mRNA template, whereas the large subunit sequentially binds tRNAs. Each mRNA molecule is simultaneously translated by many ribosomes, all synthesizing protein in the same direction: reading the mRNA from 5' to 3' and synthesizing the polypeptide from the N terminus to the C terminus. The complete mRNA/poly-ribosome structure is called a polysome.

tRNAs

The tRNAs are structural RNA molecules that were transcribed from genes by RNA polymerase III. Depending on the species, 40 to 60 types of tRNAs exist in the cytoplasm. Serving as adaptors, specific tRNAs bind to sequences on the mRNA template and add the corresponding amino acid to the polypeptide chain. Therefore, tRNAs are the molecules that actually “translate” the language of RNA into the language of proteins.

Of the 64 possible mRNA codons—or triplet combinations of A, U, G, and C—three specify the termination of protein synthesis and 61 specify the addition of amino acids to the polypeptide chain. Of these 61, one codon (AUG) also encodes the initiation of translation. Each tRNA anticodon can base pair with one of the mRNA codons and add an amino acid or terminate translation, according to the genetic code. For instance, if the sequence CUA occurred on an mRNA template in the proper reading frame, it would bind a tRNA expressing the complementary sequence, GAU, which would be linked to the amino acid leucine.

As the adaptor molecules of translation, it is surprising that tRNAs can fit so much specificity into such a small package. Consider that tRNAs need to interact with three factors: 1) they must be recognized by the correct aminoacyl synthetase (see below); 2) they must be recognized by ribosomes; and 3) they must bind to the correct sequence in mRNA.

Aminoacyl tRNA Synthetases

The process of pre-tRNA synthesis by RNA polymerase III only creates the RNA portion of the adaptor molecule. The corresponding amino acid must be added later, once the tRNA is processed and exported to the cytoplasm. Through the process of tRNA “charging,” each tRNA molecule is linked to its correct amino acid by a group of enzymes called aminoacyl tRNA synthetases. At least one type of aminoacyl tRNA synthetase exists for each of the 20 amino acids; the exact number of aminoacyl tRNA synthetases varies by species. These enzymes first bind and hydrolyze ATP to catalyze a high-energy bond between an amino acid and adenosine monophosphate (AMP); a pyrophosphate molecule is expelled in this reaction. The activated amino acid is then transferred to the tRNA, and AMP is released.

The Mechanism of Protein Synthesis

As with mRNA synthesis, protein synthesis can be divided into three phases: initiation, elongation, and termination. The process of translation is similar in prokaryotes and eukaryotes. Here we’ll explore how translation occurs in *E. coli*, a representative prokaryote, and specify any differences between prokaryotic and eukaryotic translation.

Initiation of Translation

Protein synthesis begins with the formation of an initiation complex. In *E. coli*, this complex involves the small 30S ribosome, the mRNA template, three initiation factors (IFs; IF-1, IF-2, and IF-3), and a special initiator tRNA, called $\mathbf{tRNA_f^{Met}}$. The initiator tRNA interacts with the start codon AUG (or rarely, GUG), links to a formylated methionine called fMet, and can also bind IF-2. Formylated methionine is inserted by $\mathbf{fMet - tRNA_f^{Met}}$ at the beginning of every polypeptide chain synthesized by *E. coli*, but it is usually clipped off after translation is complete. When an in-frame AUG is encountered during translation elongation, a non-formylated methionine is inserted by a regular Met-$tRNA^{Met}$.

In *E. coli* mRNA, a sequence upstream of the first AUG codon, called the Shine-Dalgarno sequence (AGGAGG), interacts with the rRNA molecules that compose the ribosome. This interaction anchors the 30S ribosomal subunit at the correct location on the

mRNA template. Guanosine triphosphate (GTP), which is a purine nucleotide triphosphate, acts as an energy source during translation—both at the start of elongation and during the ribosome's translocation.

In eukaryotes, a similar initiation complex forms, comprising mRNA, the 40S small ribosomal subunit, IFs, and nucleoside triphosphates (GTP and ATP). The charged initiator tRNA, called Met-$tRNA_i$, does not bind fMet in eukaryotes, but is distinct from other Met-tRNAs in that it can bind IFs.

Instead of depositing at the Shine-Dalgarno sequence, the eukaryotic initiation complex recognizes the 7-methylguanosine cap at the 5' end of the mRNA. A cap-binding protein (CBP) and several other IFs assist the movement of the ribosome to the 5' cap. Once at the cap, the initiation complex tracks along the mRNA in the 5' to 3' direction, searching for the AUG start codon. Many eukaryotic mRNAs are translated from the first AUG, but this is not always the case. According to Kozak's rules, the nucleotides around the AUG indicate whether it is the correct start codon. Kozak's rules state that the following consensus sequence must appear around the AUG of vertebrate genes: 5'-gccRccAUGG-3'. The R (for purine) indicates a site that can be either A or G, but cannot be C or U. Essentially, the closer the sequence is to this consensus, the higher the efficiency of translation.

Once the appropriate AUG is identified, the other proteins and CBP dissociate, and the 60S subunit binds to the complex of Met-$tRNA_i$, mRNA, and the 40S subunit. This step completes the initiation of translation in eukaryotes.

Translation, Elongation, and Termination

In prokaryotes and eukaryotes, the basics of elongation are the same, so we will review elongation from the perspective of *E. coli*. The 50S ribosomal subunit of *E. coli* consists of three compartments: the A (aminoacyl) site binds incoming charged aminoacyl tRNAs. The P (peptidyl) site binds charged tRNAs carrying amino acids that have formed peptide bonds with the growing polypeptide chain but have not yet dissociated from their corresponding tRNA. The E (exit) site releases dissociated tRNAs so that they can be recharged with free amino acids. There is one exception to this assembly line of tRNAs: in *E. coli*, $\mathrm{fMet-tRNA_f^{Met}}$ is capable of entering the P site directly without first entering the A site. Similarly, the eukaryotic Met-$tRNA_i$, with help from other proteins of the initiation complex, binds directly to the P site. In both cases, this creates an initiation complex with a free A site ready to accept the tRNA corresponding to the first codon after the AUG.

During translation elongation, the mRNA template provides specificity. As the ribosome moves along the mRNA, each mRNA codon comes into register, and specific binding with the corresponding charged tRNA anticodon is ensured. If mRNA were not present in the elongation complex, the ribosome would bind tRNAs nonspecifically.

Elongation proceeds with charged tRNAs entering the A site and then shifting to the P site followed by the E site with each single-codon "step" of the ribosome. Ribosomal steps are induced by conformational changes that advance the ribosome by three bases in the 3' direction. The energy for each step of the ribosome is donated by an elongation factor that hydrolyzes GTP. Peptide bonds form between the amino group of the amino acid attached to the A-site tRNA and the carboxyl group of the amino acid attached to the P-site tRNA. The formation of each peptide bond is catalyzed by peptidyl transferase, an RNA-based enzyme that is integrated into the 50S ribosomal subunit. The energy for each peptide bond formation is derived from GTP hydrolysis, which is catalyzed by a separate elongation factor. The amino acid bound to the P-site tRNA is also linked to the growing polypeptide chain. As the ribosome steps across the mRNA, the former P-site tRNA enters the E site, detaches from the amino acid, and is expelled (Figure **15.6.2**). Amazingly, the *E. coli* translation apparatus takes only 0.05 seconds to add each amino acid, meaning that a 200-amino acid protein can be translated in just 10 seconds.

Art Connection

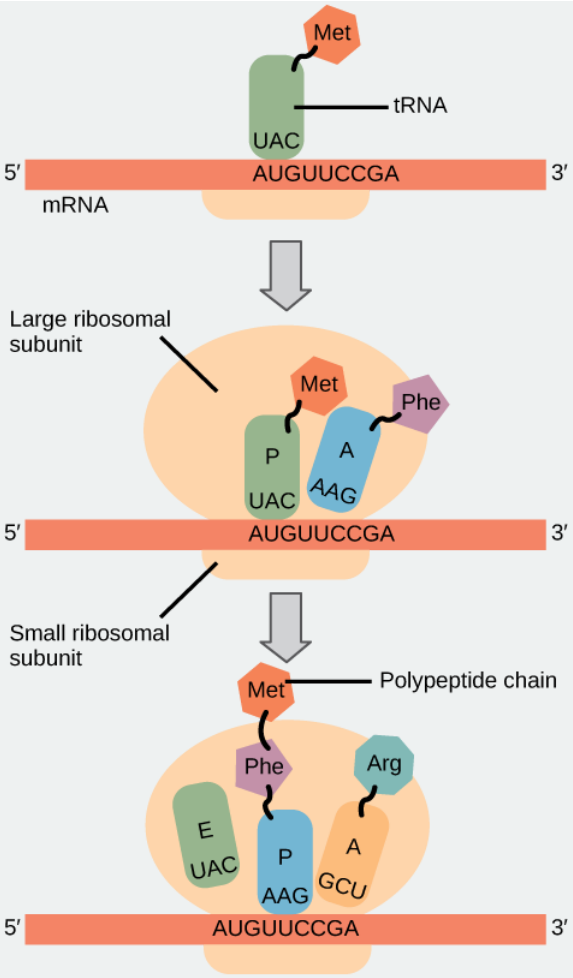


Figure **15.6.2**: Translation begins when an initiator tRNA anticodon recognizes a codon on mRNA. The large ribosomal subunit joins the small subunit, and a second tRNA is recruited. As the mRNA moves relative to the ribosome, the polypeptide chain is formed. Entry of a release factor into the A site terminates translation and the components dissociate.

Many antibiotics inhibit bacterial protein synthesis. For example, tetracycline blocks the A site on the bacterial ribosome, and chloramphenicol blocks peptidyl transfer. What specific effect would you expect each of these antibiotics to have on protein synthesis?

Tetracycline would directly affect:

a. tRNA binding to the ribosome
b. ribosome assembly
c. growth of the protein chain

Chloramphenicol would directly affect

a. tRNA binding to the ribosome
b. ribosome assembly
c. growth of the protein chain

Termination of translation occurs when a nonsense codon (UAA, UAG, or UGA) is encountered. Upon aligning with the A site, these nonsense codons are recognized by release factors in prokaryotes and eukaryotes that instruct peptidyl transferase to add a water molecule to the carboxyl end of the P-site amino acid. This reaction forces the P-site amino acid to detach from its tRNA, and the newly made protein is released. The small and large ribosomal subunits dissociate from the mRNA and from each other; they are recruited almost immediately into another translation initiation complex. After many ribosomes have completed translation, the mRNA is degraded so the nucleotides can be reused in another transcription reaction.

Protein Folding, Modification, and Targeting

During and after translation, individual amino acids may be chemically modified, signal sequences may be appended, and the new protein "folds" into a distinct three-dimensional structure as a result of intramolecular interactions. A signal sequence is a short tail of amino acids that directs a protein to a specific cellular compartment. These sequences at the amino end or the carboxyl end of the protein can be thought of as the protein's "train ticket" to its ultimate destination. Other cellular factors recognize each signal sequence and help transport the protein from the cytoplasm to its correct compartment. For instance, a specific sequence at the amino terminus will direct a protein to the mitochondria or chloroplasts (in plants). Once the protein reaches its cellular destination, the signal sequence is usually clipped off.

Many proteins fold spontaneously, but some proteins require helper molecules, called chaperones, to prevent them from aggregating during the complicated process of folding. Even if a protein is properly specified by its corresponding mRNA, it could take on a completely dysfunctional shape if abnormal temperature or pH conditions prevent it from folding correctly.

Summary

The players in translation include the mRNA template, ribosomes, tRNAs, and various enzymatic factors. The small ribosomal subunit forms on the mRNA template either at the Shine-Dalgarno sequence (prokaryotes) or the 5' cap (eukaryotes). Translation begins at the initiating AUG on the mRNA, specifying methionine. The formation of peptide bonds occurs between sequential amino acids specified by the mRNA template according to the genetic code. Charged tRNAs enter the ribosomal A site, and their amino acid bonds with the amino acid at the P site. The entire mRNA is translated in three-nucleotide "steps" of the ribosome. When a nonsense codon is encountered, a release factor binds and dissociates the components and frees the new protein. Folding of the protein occurs during and after translation.

Art Connections

Figure **15.6.2**: Many antibiotics inhibit bacterial protein synthesis. For example, tetracycline blocks the A site on the bacterial ribosome, and chloramphenicol blocks peptidyl transfer. What specific effect would you expect each of these antibiotics to have on protein synthesis?

Tetracycline would directly affect:

a. tRNA binding to the ribosome
b. ribosome assembly
c. growth of the protein chain

Chloramphenicol would directly affect

a. tRNA binding to the ribosome
b. ribosome assembly
c. growth of the protein chain

Answer

Tetracycline: a; Chloramphenicol: c.

Glossary

aminoacyl tRNA synthetase
enzyme that "charges" tRNA molecules by catalyzing a bond between the tRNA and a corresponding amino acid

initiator tRNA
in prokaryotes, called $\mathbf{tRNA_f^{Met}}$; in eukaryotes, called $tRNA_i$; a tRNA that interacts with a start codon, binds directly to the ribosome P site, and links to a special methionine to begin a polypeptide chain

Kozak's rules

determines the correct initiation AUG in a eukaryotic mRNA; the following consensus sequence must appear around the AUG: 5’-GCC(**purine**)CCAUG**G**-3’; the bolded bases are most important

peptidyl transferase

RNA-based enzyme that is integrated into the 50S ribosomal subunit and catalyzes the formation of peptide bonds

polysome

mRNA molecule simultaneously being translated by many ribosomes all going in the same direction

Shine-Dalgarno sequence

(AGGAGG); initiates prokaryotic translation by interacting with rRNA molecules comprising the 30S ribosome

signal sequence

short tail of amino acids that directs a protein to a specific cellular compartment

start codon

AUG (or rarely, GUG) on an mRNA from which translation begins; always specifies methionine

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SECTION OVERVIEW

15.7: The Process of Translation

The synthesis of proteins is one of a cell's most energy-consuming metabolic processes. In turn, proteins account for more mass than any other component of living organisms (with the exception of water), and proteins perform a wide variety of the functions of a cell. The process of translation, or protein synthesis, involves decoding an mRNA message into a polypeptide product. Amino acids are covalently strung together in lengths ranging from approximately 50 amino acids to more than 1,000.

The Protein Synthesis Machinery

In addition to the mRNA template, many other molecules contribute to the process of translation. The composition of each component may vary across species; for instance, ribosomes may consist of different numbers of ribosomal RNAs (rRNA) and polypeptides depending on the organism. However, the general structures and functions of the protein synthesis machinery are comparable from bacteria to human cells. Translation requires the input of an mRNA template, ribosomes, tRNAs, and various enzymatic factors (Figure 15.7.1).

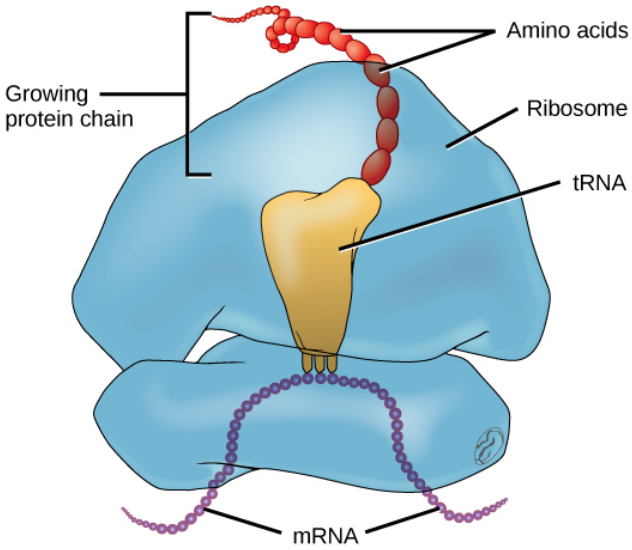


Figure 15.7.1: The protein synthesis machinery includes the large and small subunits of the ribosome, mRNA, and tRNA. (credit: modification of work by NIGMS, NIH)

In *E. coli*, there are 200,000 ribosomes present in every cell at any given time. A ribosome is a complex macromolecule composed of structural and catalytic rRNAs, and many distinct polypeptides. In eukaryotes, the nucleolus is completely specialized for the synthesis and assembly of rRNAs.

Ribosomes are located in the cytoplasm in prokaryotes and in the cytoplasm and endoplasmic reticulum of eukaryotes. Ribosomes are made up of a large and a small subunit that come together for translation. The small subunit is responsible for binding the mRNA template, whereas the large subunit sequentially binds tRNAs, a type of RNA molecule that brings amino acids to the growing chain of the polypeptide. Each mRNA molecule is simultaneously translated by many ribosomes, all synthesizing protein in the same direction.

Depending on the species, 40 to 60 types of tRNA exist in the cytoplasm. Serving as adaptors, specific tRNAs bind to sequences on the mRNA template and add the corresponding amino acid to the polypeptide chain. Therefore, tRNAs are the molecules that actually "translate" the language of RNA into the language of proteins. For each tRNA to function, it must have its specific amino acid bonded to it. In the process of tRNA "charging," each tRNA molecule is bonded to its correct amino acid.

The Genetic Code

To summarize what we know to this point, the cellular process of transcription generates messenger RNA (mRNA), a mobile molecular copy of one or more genes with an alphabet of A, C, G, and uracil (U). Translation of the mRNA template converts nucleotide-based genetic information into a protein product. Protein sequences consist of 20 commonly occurring amino acids; therefore, it can be said that the protein alphabet consists of 20 letters. Each amino acid is defined by a three-nucleotide sequence called the triplet codon. The relationship between a nucleotide codon and its corresponding amino acid is called the genetic code.

Given the different numbers of "letters" in the mRNA and protein "alphabets," combinations of nucleotides corresponded to single amino acids. Using a three-nucleotide code means that there are a total of 64 (4 × 4 × 4) possible combinations; therefore, a given amino acid is encoded by more than one nucleotide triplet (Figure **15.7.2**).

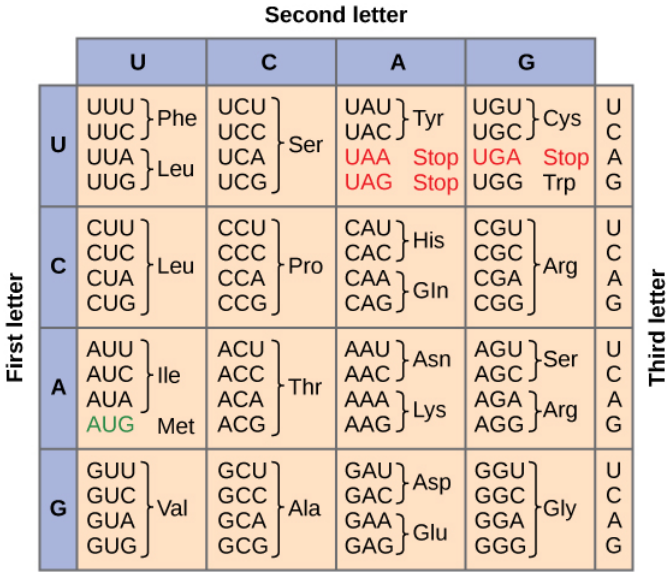


Figure 15.7.2: This figure shows the genetic code for translating each nucleotide triplet, or codon, in mRNA into an amino acid or a termination signal in a nascent protein. (credit: modification of work by NIH)

Three of the 64 codons terminate protein synthesis and release the polypeptide from the translation machinery. These triplets are called stop codons. Another codon, AUG, also has a special function. In addition to specifying the amino acid methionine, it also serves as the start codon to initiate translation. The reading frame for translation is set by the AUG start codon near the 5' end of the mRNA. The genetic code is universal. With a few exceptions, virtually all species use the same genetic code for protein synthesis, which is powerful evidence that all life on Earth shares a common origin.

The Mechanism of Protein Synthesis

Just as with mRNA synthesis, protein synthesis can be divided into three phases: initiation, elongation, and termination. The process of translation is similar in prokaryotes and eukaryotes. Here we will explore how translation occurs in *E. coli*, a representative prokaryote, and specify any differences between prokaryotic and eukaryotic translation.

Protein synthesis begins with the formation of an initiation complex. In *E. coli*, this complex involves the small ribosome subunit, the mRNA template, three initiation factors, and a special initiator tRNA. The initiator tRNA interacts with the AUG start codon, and links to a special form of the amino acid methionine that is typically removed from the polypeptide after translation is complete.

In prokaryotes and eukaryotes, the basics of polypeptide elongation are the same, so we will review elongation from the perspective of *E. coli*. The large ribosomal subunit of *E. coli* consists of three compartments: the A site binds incoming charged tRNAs (tRNAs with their attached specific amino acids). The P site binds charged tRNAs carrying amino acids that have formed bonds with the growing polypeptide chain but have not yet dissociated from their corresponding tRNA. The E site releases dissociated tRNAs so they can be recharged with free amino acids. The ribosome shifts one codon at a time, catalyzing each process that occurs in the three sites. With each step, a charged tRNA enters the complex, the polypeptide becomes one amino acid longer, and an uncharged tRNA departs. The energy for each bond between amino acids is derived from GTP, a molecule similar to

ATP (Figure 15.7.3). Amazingly, the *E. coli* translation apparatus takes only 0.05 seconds to add each amino acid, meaning that a 200-amino acid polypeptide could be translated in just 10 seconds.

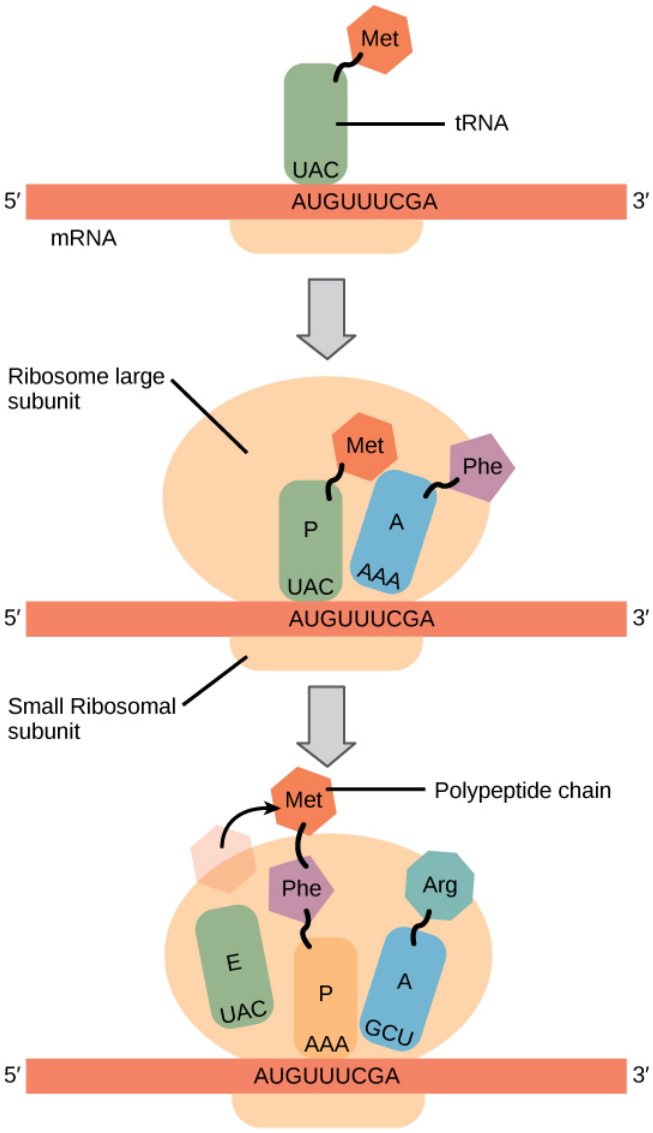


Figure 15.7.3: Translation begins when a tRNA anticodon recognizes a codon on the mRNA. The large ribosomal subunit joins the small subunit, and a second tRNA is recruited. As the mRNA moves relative to the ribosome, the polypeptide chain is formed. Entry of a release factor into the A site terminates translation and the components dissociate.

Termination of translation occurs when a stop codon (UAA, UAG, or UGA) is encountered. When the ribosome encounters the stop codon, the growing polypeptide is released and the ribosome subunits dissociate and leave the mRNA. After many ribosomes have completed translation, the mRNA is degraded so the nucleotides can be reused in another transcription reaction.

CONCEPT IN ACTION

Transcribe a gene and translate it to protein using complementary pairing and the genetic code at this site.

Summary

The central dogma describes the flow of genetic information in the cell from genes to mRNA to proteins. Genes are used to make mRNA by the process of transcription; mRNA is used to synthesize proteins by the process of translation. The genetic code is the correspondence between the three-nucleotide mRNA codon and an amino acid. The genetic code is "translated" by the tRNA molecules, which associate a specific codon with a specific amino acid. The genetic code is degenerate because 64 triplet codons in

mRNA specify only 20 amino acids and three stop codons. This means that more than one codon corresponds to an amino acid. Almost every species on the planet uses the same genetic code.

The players in translation include the mRNA template, ribosomes, tRNAs, and various enzymatic factors. The small ribosomal subunit binds to the mRNA template. Translation begins at the initiating AUG on the mRNA. The formation of bonds occurs between sequential amino acids specified by the mRNA template according to the genetic code. The ribosome accepts charged tRNAs, and as it steps along the mRNA, it catalyzes bonding between the new amino acid and the end of the growing polypeptide. The entire mRNA is translated in three-nucleotide "steps" of the ribosome. When a stop codon is encountered, a release factor binds and dissociates the components and frees the new protein.

Glossary

codon
: three consecutive nucleotides in mRNA that specify the addition of a specific amino acid or the release of a polypeptide chain during translation

genetic code
: the amino acids that correspond to three-nucleotide codons of mRNA

rRNA
: ribosomal RNA; molecules of RNA that combine to form part of the ribosome

stop codon
: one of the three mRNA codons that specifies termination of translation

start codon
: the AUG (or, rarely GUG) on an mRNA from which translation begins; always specifies methionine

tRNA
: transfer RNA; an RNA molecule that contains a specific three-nucleotide anticodon sequence to pair with the mRNA codon and also binds to a specific amino acid

Contributors and Attributions

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15.7.1: Regulating protein localization

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15.7.1: Regulating protein localization

The synthesis of proteins occurs in the cytoplasm, where mature ribosomes are located. Generally, if no information is added, a newly synthesized polypeptide will remain in the cytoplasm. Yet even in the structurally simplest of cells, those of the bacteria and archaea, there is more than one place that a protein may need to be to function correctly: it can remain in the cytoplasm, it can be inserted into the plasma membrane or it may be secreted from the cell. Both membrane and secreted polypeptides must be inserted into, or pass through, the plasma membrane.

Polypeptides destined for the membrane or for secretion are generally marked by a specific tag, known as a signal sequence. The signal sequence consists of a stretch of hydrophobic amino acids, often located at the N-terminus of the polypeptide. As the signal sequence emerges from the ribosomal tunnel it interacts with a signal recognition particle (SRP) - a complex of polypeptides and a structural RNA. The binding of SRP to the signal sequence causes translation to pause. SRP acts as a chaperone for a subset of membrane proteins. The nascent mRNA/ribosome/nascent polypeptide/SRP complex will find (by diffusion), and attach to, a ribosome/SRP receptor complex on the cytoplasmic surface of the plasma membrane (in bacteria and archaea) or a cytoplasmic facing membrane (in eukaryotes). This ribosome/SRP receptor is associated with a polypeptide pore. When the ribosome/SRP complex docks with the receptor, translation resumes and the nascent polypeptide passes through the protein pore and so enters into or passes through the membrane. As the polypeptide emerges on the external, non-cytoplasmic face of the membrane, the signal sequence is generally removed by an enzyme, signal sequence peptidase. If the polypeptide is a membrane protein, it will fold and remain within the membrane. If it is a secreted polypeptide, it will be released into the periplasmic space, that is the region topologically outside of the cytoplasm (either within a vesicle or other side of the plasma membrane. Other mechanisms can lead to the release of the protein from the cell.

Because eukaryotic cells are structurally and topologically more complex than bacterial and archaeal cells there are more places for a newly synthesized protein to end up. While we will not discuss the details of those processes, one rule of thumb is worth keeping in mind. Generally, in the absence of added information, a newly synthesized polypeptide will end up in the cytoplasm. As in bacteria and archaea, a eukaryotic polypeptides destined for secretion or insertion into the cell's plasma membrane or internal membrane systems (that is the endoplasmic reticulum and Golgi apparatus) are directed to their final location by a signal sequence/SRP system. Proteins that must function in the nucleus generally get there because they have a nuclear localization sequence, other proteins are actively excluded from the nucleus using a nuclear exclusion sequence (see above). Likewise, other localization signals and receptors are used to direct proteins to other intracellular compartments, including mitochondria and chloroplasts. While details of these targeting systems are beyond the scope of this course, you can assume that each specific targeting event requires signals, receptors, and various mechanisms that drive what are often thermodynamically unfavorable reactions.

Contributors and Attributions

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15.8: Summarizing Gene Expression

Skills to Develop

- Discuss why every cell does not express all of its genes
- Describe how prokaryotic gene regulation occurs at the transcriptional level
- Discuss how eukaryotic gene regulation occurs at the epigenetic, transcriptional, post-transcriptional, translational, and post-translational levels

For a cell to function properly, necessary proteins must be synthesized at the proper time. All cells control or regulate the synthesis of proteins from information encoded in their DNA. The process of turning on a gene to produce RNA and protein is called gene expression. Whether in a simple unicellular organism or a complex multi-cellular organism, each cell controls when and how its genes are expressed. For this to occur, there must be a mechanism to control when a gene is expressed to make RNA and protein, how much of the protein is made, and when it is time to stop making that protein because it is no longer needed.

The regulation of gene expression conserves energy and space. It would require a significant amount of energy for an organism to express every gene at all times, so it is more energy efficient to turn on the genes only when they are required. In addition, only expressing a subset of genes in each cell saves space because DNA must be unwound from its tightly coiled structure to transcribe and translate the DNA. Cells would have to be enormous if every protein were expressed in every cell all the time.

The control of gene expression is extremely complex. Malfunctions in this process are detrimental to the cell and can lead to the development of many diseases, including cancer.

Prokaryotic versus Eukaryotic Gene Expression

To understand how gene expression is regulated, we must first understand how a gene codes for a functional protein in a cell. The process occurs in both prokaryotic and eukaryotic cells, just in slightly different manners.

Prokaryotic organisms are single-celled organisms that lack a cell nucleus, and their DNA therefore floats freely in the cell cytoplasm. To synthesize a protein, the processes of transcription and translation occur almost simultaneously. When the resulting protein is no longer needed, transcription stops. As a result, the primary method to control what type of protein and how much of each protein is expressed in a prokaryotic cell is the regulation of DNA transcription. All of the subsequent steps occur automatically. When more protein is required, more transcription occurs. Therefore, in prokaryotic cells, the control of gene expression is mostly at the transcriptional level.

Eukaryotic cells, in contrast, have intracellular organelles that add to their complexity. In eukaryotic cells, the DNA is contained inside the cell's nucleus and there it is transcribed into RNA. The newly synthesized RNA is then transported out of the nucleus into the cytoplasm, where ribosomes translate the RNA into protein. The processes of transcription and translation are physically separated by the nuclear membrane; transcription occurs only within the nucleus, and translation occurs only outside the nucleus in the cytoplasm. The regulation of gene expression can occur at all stages of the process (Figure 15.8.1). Regulation may occur when the DNA is uncoiled and loosened from nucleosomes to bind transcription factors (epigenetic level), when the RNA is transcribed (transcriptional level), when the RNA is processed and exported to the cytoplasm after it is transcribed (post-transcriptional level), when the RNA is translated into protein (translational level), or after the protein has been made (post-translational level).

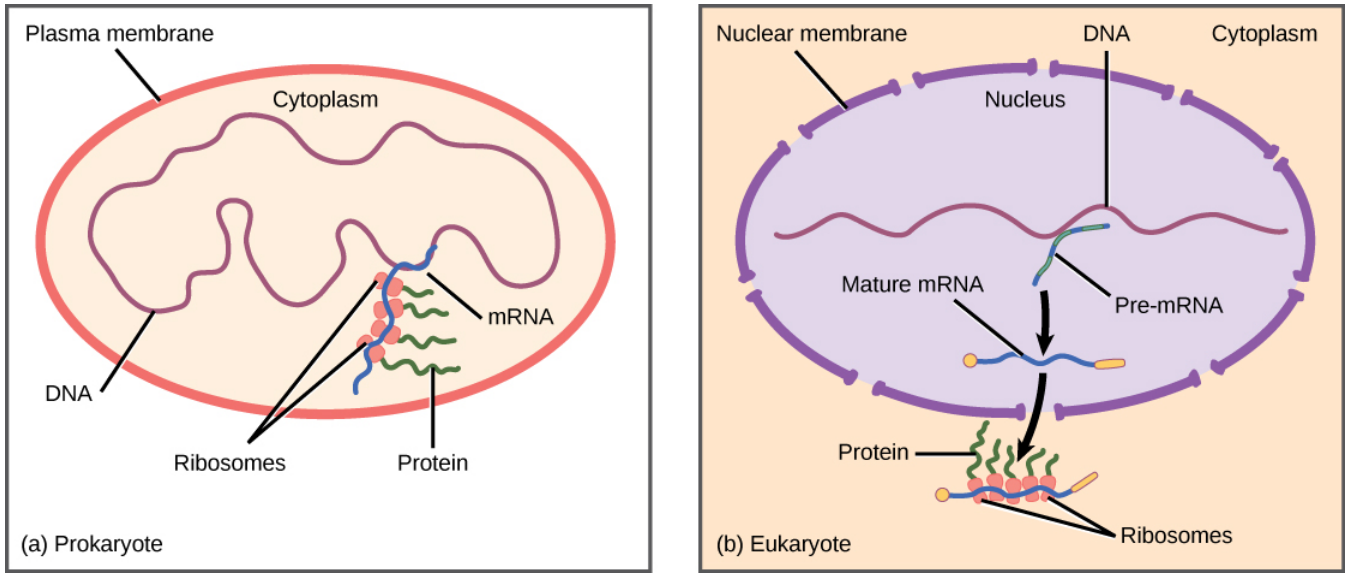


Figure 15.8.1: Prokaryotic transcription and translation occur simultaneously in the cytoplasm, and regulation occurs at the transcriptional level. Eukaryotic gene expression is regulated during transcription and RNA processing, which take place in the nucleus, and during protein translation, which takes place in the cytoplasm. Further regulation may occur through post-translational modifications of proteins.

The differences in the regulation of gene expression between prokaryotes and eukaryotes are summarized below. The regulation of gene expression is discussed in detail in subsequent modules.

Table 15.8.1: Differences in the Regulation of Gene Expression of Prokaryotic and Eukaryotic Organisms

Prokaryotic organisms	Eukaryotic organisms
Lack nucleus	Contain nucleus
DNA is found in the cytoplasm	DNA is confined to the nuclear compartment
RNA transcription and protein formation occur almost simultaneously	RNA transcription occurs prior to protein formation, and it takes place in the nucleus. Translation of RNA to protein occurs in the cytoplasm.
Gene expression is regulated primarily at the transcriptional level	Gene expression is regulated at many levels (epigenetic, transcriptional, nuclear shuttling, post-transcriptional, translational, and post-translational)

Evolution Connection: Evolution of Gene Regulation

Prokaryotic cells can only regulate gene expression by controlling the amount of transcription. As eukaryotic cells evolved, the complexity of the control of gene expression increased. For example, with the evolution of eukaryotic cells came compartmentalization of important cellular components and cellular processes. A nuclear region that contains the DNA was formed. Transcription and translation were physically separated into two different cellular compartments. It therefore became possible to control gene expression by regulating transcription in the nucleus, and also by controlling the RNA levels and protein translation present outside the nucleus.

Some cellular processes arose from the need of the organism to defend itself. Cellular processes such as gene silencing developed to protect the cell from viral or parasitic infections. If the cell could quickly shut off gene expression for a short period of time, it would be able to survive an infection when other organisms could not. Therefore, the organism evolved a new process that helped it survive, and it was able to pass this new development to offspring.

Summary

While all somatic cells within an organism contain the same DNA, not all cells within that organism express the same proteins. Prokaryotic organisms express the entire DNA they encode in every cell, but not necessarily all at the same time. Proteins are expressed only when they are needed. Eukaryotic organisms express a subset of the DNA that is encoded in any given cell. In each cell type, the type and amount of protein is regulated by controlling gene expression. To express a protein, the DNA is first transcribed into RNA, which is then translated into proteins. In prokaryotic cells, these processes occur almost simultaneously. In eukaryotic cells, transcription occurs in the nucleus and is separate from the translation that occurs in the cytoplasm. Gene expression in prokaryotes is regulated only at the transcriptional level, whereas in eukaryotic cells, gene expression is regulated at the epigenetic, transcriptional, post-transcriptional, translational, and post-translational levels.

Glossary

epigenetic
: heritable changes that do not involve changes in the DNA sequence

gene expression
: processes that control the turning on or turning off of a gene

post-transcriptional
: control of gene expression after the RNA molecule has been created but before it is translated into protein

post-translational
: control of gene expression after a protein has been created

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15.9: Mutation- Altered Genes

In the living cell, DNA undergoes frequent chemical change, especially when it is being replicated (in S phase of the eukaryotic cell cycle). Most of these changes are quickly repaired. Those that are not result in a mutation. Thus, **mutation is a failure of DNA repair**.

Single-base substitutions

A single base, say an A, becomes replaced by another. Single base substitutions are also called **point mutations**. (If one purine [A or G] or pyrimidine [C or T] is replaced by the other, the substitution is called a **transition**. If a purine is replaced by a pyrimidine or vice-versa, the substitution is called a **transversion**.)

Missense mutations

With a missense mutation, the new nucleotide alters the codon so as to produce an altered amino acid in the protein product.

Deasese: Sickle Cell anemia

The replacement of A by T at the 17th nucleotide of the gene for the beta chain of hemoglobin changes the codon GAG (for glutamic acid) to GTG (which encodes valine). Thus the 6th amino acid in the chain becomes valine instead of glutamic acid.
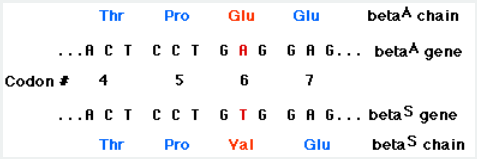


Figure 10.1.1 Sickle Cell Mutation

Nonsense mutations

With a nonsense mutation, the new nucleotide changes a codon that specified an amino acid to one of the **STOP** codons (**TAA**, **TAG**, or **TGA**). Therefore, **translation** of the messenger RNA **transcribed** from this mutant gene will stop prematurely. The earlier in the gene that this occurs, the more truncated the protein product and the more likely that it will be unable to function.

Cystic Fibrosis

Here is a sampling of mutations that have been found in patients with **cystic fibrosis**. Each of these mutations occurs in a huge gene that encodes a protein (of 1480 amino acids) called the **c**ystic **f**ibrosis **t**ransmembrane conductance **r**egulator (**CFTR**). The protein is responsible for transporting chloride and bicarbonate ions through the plasma membrane. The gene encompasses over 188,000 base pairs on chromosome 7 embedded in which are 27 exons encoding the protein. The numbers in the mutation column represent the number of the nucleotides affected. Defects in the protein cause the various symptoms of the disease. Unlike sickle-cell disease, then, no single mutation is responsible for all cases of cystic fibrosis. People with cystic fibrosis inherit two mutant genes, but the mutations need not be the same.

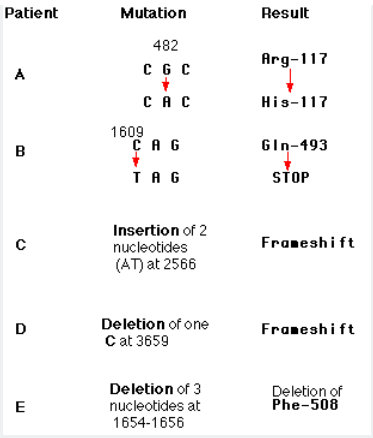


Figure 10.1.2 Cystic Fibrosis Mutation

In one patient with cystic fibrosis (**Patient B**), the substitution of a T for a C at nucleotide 1609 converted a glutamine codon (**CAG**) to a **STOP** codon (**TAG**). The protein produced by this patient had only the first 493 amino acids of the normal chain of 1480 and could not function.

Silent mutations

Most amino acids are encoded by several different codons. For example, if the third base in the **TCT** codon for **serine** is changed to any one of the other three bases, serine will still be encoded. Such mutations are said to be silent because they cause no change in their product and cannot be detected without sequencing the gene (or its mRNA).

Splice-site mutations

The removal of intron sequences, as pre-mRNA is being processed to form mRNA, must be done with great precision. Nucleotide signals at the splice sites guide the enzymatic machinery. If a mutation alters one of these signals, then the intron is not removed and remains as part of the final RNA molecule. The translation of its sequence alters the sequence of the protein product.

Insertions and Deletions (Indels)

Extra base pairs may be added (**insertions**) or removed (**deletions**) from the DNA of a gene. The number can range from one to thousands. Collectively, these mutations are called **indels**.

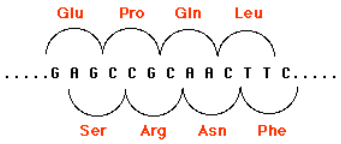


Figure 10.1.3: Frameshifting

Indels involving one or two base pairs (or multiples of two) can have devastating consequences to the gene because translation of the gene is "frameshifted". This figure shows how by **shifting the reading frame** one nucleotide to the right, the same sequence of nucleotides encodes a different sequence of amino acids. The mRNA is translated in new groups of three nucleotides and the protein specified by these new codons will be worthless. Scroll up to see two other examples (**Patients C and D**).

Frameshifts often create new **STOP** codons and thus generate nonsense mutations. Perhaps that is just as well as the protein would probably be too garbled anyway to be useful to the cell.

Indels of three nucleotides or multiples of three may be less serious because they preserve the reading frame (see the above figure).

However, a number of inherited human disorders are caused by the insertion of many copies of the same triplet of nucleotides. **Huntington's disease** and the **fragile X syndrome** are examples of such **trinucleotide repeat** diseases.

Disease: Fragile X Syndrome

Several disorders in humans are caused by the inheritance of genes that have undergone insertions of a string of 3 or 4 nucleotides repeated over and over. A locus on the human X chromosome contains such a stretch of nucleotides in which the triplet **CGG** is repeated (CGGCGGCGGCGG, etc.). The number of CGGs may be as few as 5 or as many as 50 without causing a harmful phenotype (these repeated nucleotides are in a noncoding region of the gene). Even 100 repeats usually cause no harm. However, these longer repeats have a tendency to grow longer still from one generation to the next (to as many as 4000 repeats).

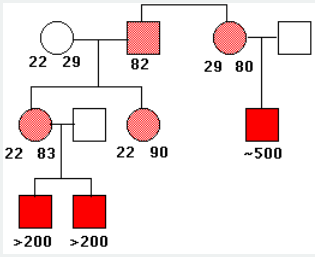


Figure 10.1.4 Fragile X Syndrome

This causes a constriction in the X chromosome, which makes it quite fragile. Males who inherit such a chromosome (only from their mothers, of course) show a number of harmful phenotypic effects including mental retardation. Females who inherit a fragile X (also from their mothers; males with the syndrome seldom become fathers) are only mildly affected.

The above image shows the pattern of inheritance of the fragile X syndrome in one family. The number of times that the trinucleotide **CGG** is repeated is given under the symbols. The gene is on the X chromosome, so women (circles) have two copies of it; men (squares) have only one. People with a gene containing 80–90 repeats are normal (light red), but this gene is unstable, and the number of repeats can increase into the hundreds in their offspring. Males who inherit such an enlarged gene suffer from the syndrome (solid red squares). (Data from C. T. Caskey, et al.).

Polyglutamine Diseases

In these disorders, the repeated trinucleotide is **CAG**, which adds a string of glutamines (Gln) to the encoded protein. These have been implicated in a number of central nervous system disorders including

- **Huntington's disease** (where the protein called **huntingtin** carries the extra glutamines). The abnormal protein increases the level of the p53 protein in brain cells causing their death by apoptosis.
- some cases of Parkinson's disease where the extra glutamines are in the protein ataxin-2.

Muscular Dystrophy

Some forms of muscular dystrophy that appear in adults are caused by tri- or tetranucleotide, e.g. (CTG)n and (CCTG)n, repeats where n may run into the thousands. The huge RNA transcripts that result interfere with the alternative splicing of other transcripts in the nucleus.

Amyotrophic Lateral Sclerosis (ALS)

ALS is a neurodegenerative disorder leading to dementia and muscle weakness. (ALS is often called "Lou Gehrig's disease" after the baseball player who died from it.)

The most common mutation in ALS is an expansion of the number of repeats of the hexanucleotide GGGGCC in a gene on chromosome 9 from the normal two, or at least fewer than three dozen, to hundreds or even several thousand. Translation of both the sense and the antisense strands containing these repeats (and in all 3 reading frames; there is no ATG start codon) produces polymers with long strings of gly-ala, gly-pro, gly-arg (from the sense strand) as well as pro-ala, another pro-gly, and pro-arg from the antisense strand. These proteins, especially those containing arginine (arg) form aggregates that damage brain cells.

Duplications

Duplications are a doubling of a section of the genome. During meiosis, crossing over between sister chromatids that are out of alignment can produce one chromatid with a duplicated gene and the other (not shown) with the two genes with deletions. In the

case shown here, unequal crossing over created a second copy of a gene needed for the synthesis of the steroid hormone **aldosterone**.

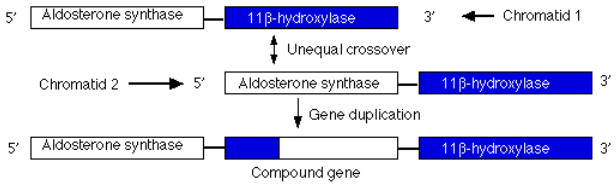


Figure 10.1.5 Gene Duplication

However, this new gene carries inappropriate promoters at its 5' end (acquired from the 11-beta hydroxylase gene) that cause it to be expressed more strongly than the normal gene. The mutant gene is dominant: all members of one family (through four generations) who inherited at least one chromosome carrying this duplication suffered from high blood pressure and were prone to early death from stroke.

Gene duplication has also been implicated in several human neurological disorders.

Gene duplication has occurred repeatedly during the evolution of eukaryotes. Genome analysis reveals many genes with similar sequences in a single organism. Presumably these paralogous genes have arisen by repeated duplication of an ancestral gene.

Such gene duplication can be beneficial.

- Over time, the duplicates can acquire different functions.
  - The proteins they encode can take on different functions; for example, if the original gene product carried out two different functions (see "pleiotropy"), each duplicated gene can now specialize at one function and do a better job at it than the parental gene.
  - But even if they do not, changes in the regulatory sequences of the genes (promoters and enhancers) may cause the same protein to be expressed at different times, at different levels, and/or in different tissues.

  Either situation can provide the basis for adaptive evolution.
- But even while two paralogous genes are still similar in sequence and function, their existence provides **redundancy** ("belt and suspenders"). This may be a major reason why knocking out genes in yeast, "knockout mice", etc. so often has such a mild effect on the phenotype. The function of the knocked out gene can be taken over by a paralog.
- After gene duplication, random loss — or inactivation — of one of these genes at a later time in
  - one group of descendants
  - different from the loss in another group

  could provide a barrier (a "post-zygotic isolating mechanism") to the two groups interbreeding. Such a barrier could cause speciation: the evolution of two different species from a single ancestral species.

Translocations

Translocations are the transfer of a piece of one chromosome to a **nonhomologous chromosome**. Translocations are often reciprocal; that is, the two nonhomologues swap segments.

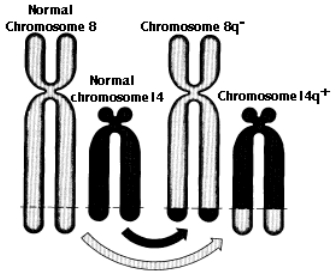


Figure 10.1.6 Translocations

Translocations can alter the phenotype is several ways:

- the break may occur **within** a gene destroying its function

- translocated genes may come under the influence of different promoters and enhancers so that their expression is altered. The t(8;14) translocation in Burkitt's lymphoma (figure) is an example.
- the breakpoint may occur **within a gene** creating a hybrid gene. This may be transcribed and translated into a protein with an N-terminal of one normal cell protein coupled to the C-terminal of another. The Philadelphia chromosome found so often in the leukemic cells of patients with **chronic myelogenous leukemia** (**CML**) is the result of a translocation which produces a compound gene (**bcr-abl**).

Frequency of Mutations

Mutations are rare events. This is surprising. Humans inherit 3 x 10^9 base pairs of DNA from each parent. Just considering single-base substitutions, this means that each cell has 6 billion (6 x 10^9) different base pairs that can be the target of a substitution. Single-base substitutions are most apt to occur when DNA is being copied; for eukaryotes that means during S phase of the cell cycle.

No process is 100% accurate. Even the most highly skilled typist will introduce errors when copying a manuscript. So it is with DNA replication. Like a conscientious typist, the cell does proofread the accuracy of its copy. But, even so, errors slip through. It has been estimated that in humans and other mammals, uncorrected errors (= mutations) occur at the rate of about 1 in every 50 million (5 x 10^7) nucleotides added to the chain. (Not bad — I wish that I could type so accurately.) But with 6 x 10^9 base pairs in a human cell, that means that each new cell contains some 120 new mutations.

Should we be worried? The evidence is not clear. Only 1.2% of our DNA encodes the exons of our proteome, and for a long time it was thought that much of the rest was "junk" DNA. Mutations in it would most likely be harmless. And even in coding regions, the existence of synonymous codons could result in the altered (mutated) gene still encoding the same amino acid in the protein. But it now appears that as much as 80% of our DNA seems to participate in regulating which genes are expressed, and how strongly, in each of the multitude of differentiated cell types in our body as each responds to the signals (nutrients, hormones, etc.) it receives. So mutations in these regions might well have harmful, if subtle, effects.

As more vertebrate genomes are sequenced, it turns out that some of these stretches of DNA that do not encode proteins none-the-less have been remarkably conserved during vertebrate evolution. Some of these regions have accumulated even fewer mutations than protein-encoding genes have. This suggests that these sequences are extremely important to the welfare of the organism. However, other regions of the genome seem able to sustain point mutations with no detectible harm.

Recent advances have enabled the coding portions of the genome of **single cells** to be sequenced. Preliminary results indicate that each **normal cell** in an adult has accumulated ~20 somatic mutations, and that its collection of mutations differs from cell to cell. **Cancer cells** accumulate many more mutations (often in the hundreds).

How can we measure the frequency at which phenotype-altering mutations occur? In humans, it is not easy.

- First we must be sure that the mutation is **newly-arisen**. (Some populations have high frequencies of a particular mutation, not because the gene is especially susceptible, but because it has been passed down through the generations from a early "founder".
- Recessive mutations (most of them are) will not be seen except on the rare occasions that both parents contribute a mutation at the same locus to their child.
- This leaves us with estimating mutation frequencies for genes that are inherited as
  - **autosomal dominants**
  - **X-linked recessives**; that is, recessives on the X chromosome which will be expressed in males because they inherit only one X chromosome.

Examples

Frequency is expressed as the frequency of mutations occurring at that locus in the gametes

- **Autosomal dominants**
  - **Retinoblastoma**
    in the ***RB*** gene: about 8 per million (8 x 10^{-6})
  - **Osteogenesis imperfecta**
    in one or the other of the two genes that encode **Type I collagen**: about 1 per 100,000 (10^{-5})

- Inherited tendency to polyps (and later cancer) in the colon.
  in a tumor suppressor gene (*APC*): ~10^{-5}
- **X-linked recessives**
  - Hemophilia A
    ~3 x 10^{-5} (the **Factor VIII** gene)
  - Duchenne Muscular Dystrophy (DMD)
    >8 x 10^{-5} (the **dystrophin** gene)
    Why should the mutation frequency in the dystrophin gene be so much larger than most of the others? It's probably a matter of size. The dystrophin gene stretches over 2.4 x 10^{6} base pairs of DNA. This is almost 0.1% of the entire human genome! Such a huge gene offers many possibilities for damage.

Measuring Mutation Rate

The **frequency** with which a given mutation is seen in a population (e.g., the mutation that causes cystic fibrosis) provides only a rough approximation of mutation **rate** — the rate at which fresh mutations occur — because of historical factors at work such as *natural selection* (positive or negative), *drift*, and *founder effect*. In addition, most methods for counting mutations require that the mutation have a visible effect on the phenotype. Thus

- many (but not all) mutations in noncoding DNA
- mutations that produce
  - synonymous codons (encode the same amino acid)
  - or, sometimes, new codons that encode a chemically-similar amino acid
- mutations which disrupt a gene whose functions are redundant; that is, can be compensated for by other genes

will not be seen. But now these problems have been largely solved. The story is told in a report by D. R. Denver, *et al.* in the 5 August 2004 issue of **Nature**.

C. elegans

The Procedure

- Their organism = *C. elegans*
- Its advantages
  - compact genome
  - hermaphroditic — it fertilizes its own eggs and any new germline mutation will soon be either lost or appear on both homologous chromosomes.
  - rapid generation time (4 days)
- They created 198 different experimental lines of worms.
- They grew them under optimum conditions to minimize any effects of natural selection.
- Only one offspring was kept at each new generation.
- Each line was maintained for several hundred generations.
- At the end of this time, random stretches of DNA
  - derived from multiple locations on each of the six *C. elegans* chromosomes and
  - totalling an average of ~21 thousand base pairs for each line

  were sequenced from each of the 198 lines and the sequences compared with the same loci in natural populations of *C. elegans*.

Results

Examining the DNA sequences from their experimental animals (a total of over 4 million base pairs!), and comparing them with the controls, turned up a total of 30 mutations.

- 17 of these were insertions or deletions ("indels')
  - 7 in exons — all but 2 of which produced frameshifts and a premature STOP codon.

  - 10 in introns or between genes
- 13 of these were single base substitutions ("point" mutations)
  - 3 in exons : one "silent" producing a synonymous codon; two that changed the encoded amino acid.
  - 10 in introns or between genes

Calculating Mutation Rate

From these results I have pooled their data to calculate an approximate rate at which spontaneous mutations occur throughout the genome.

Mutation Rate = # of mutations observed [30] ÷ (# of experimental lines [198]) x (average # of generations [339]) x (average # of base pairs sequenced [~21,000])

yielding a rate of 2.1 x 10^{-8} mutations per base pair per generation.

The total *C. elegans* genome contains some 10^8 base pairs so this tells us that **two** new germline mutations occur somewhere in each of *C. elegans*'s two haploid genomes in each generation.

A similar analysis for Drosophila (whose genome is about the same size as that of *C. elegans*) showed a similar mutation rate: ~10^{-8} mutations per base pair per generation. As for the green plant *Arabidopsis thaliana*, its spontaneous mutation rate is slightly lower: ~7 x 10^{-9} mutations per base pair per generation.

In the 30 April 2010 issue of **Science**, Roach, J. C., *et al*., reported that the rate for **humans** is in the same range: ~1.1 x 10^{-8} mutations per base pair in the haploid genome. With a diploid genome of 6 x 10^9 base pairs, that works out to some 70 new mutations in each child. They derived these numbers from comparing the complete genome sequence of two children and their parents.

In the 20 July 2012 issue of **Cell**, Wang, J., *et al*. reported the results of sequencing 8 individual sperm cells from a 40-year-old man. They found a mutation rate ranging from 2.0 x 10^{-8} to 3.8 x 10^{-8}.

Should we be worried about such spontaneous mutation rates? Probably not too much. With our high proportion of noncoding DNA, many mutations will occur in regions that will have no effect on our phenotype. Evidence: out of a total of 251 mutations found in the 8 sperm cells, only 3 were missense mutations altering a gene product. However, even in noncoding DNA, point mutations may affect the expression of genes, so perhaps as many as 10% of the point mutations a child inherits may have harmful, if subtle, effects.

Males Contribute More Mutations Than Females

If most mutations occur during S phase of cell division, then males should be more at risk. This is because only two dozen (24) or so mitotic divisions occur from the fertilized egg that starts a little girl's embryonic development and the setting aside of her future eggs (which is done long before she is even born). Furthermore, the sperm of a 30-year old man, in contrast, are the descendants of at least 400 mitotic divisions since the fertilized egg that formed him.

So, fathers are more likely than mothers to transmit newly-formed mutations to their children. The sperm of a 25-year-old man might carry some 45 new mutations. This number rises at a rate of about 1 per year, so the sperm of a 40-year-old man may transmit some 60 new mutations to his children (about 20 of these in coding regions). No matter what the age of the mother, she transmits only about 15 new mutations to her offspring. (But **chromosomal aberrations**, like aneuploidy, are more apt to arise in eggs than in sperm, and the incidence of these increases with maternal age.) These data explain why the children of aged fathers suffer more genetic disorders than those of young fathers.

Somatic vs. Germline Mutations

The significance of mutations is profoundly influenced by the distinction between germline and soma. Mutations that occur in a **somatic cell**, in the bone marrow or liver for example, may

- damage the cell
- make the cell cancerous
- kill the cell

Whatever the effect, the ultimate fate of that **somatic mutation** is to disappear when the cell in which it occurred, or its owner, dies.

Germline mutations, in contrast, will be found in every cell descended from the zygote to which that mutant gamete contributed. If an adult is successfully produced, every one of its cells will contain the mutation. Included among these will be the next generation of gametes, so if the owner is able to become a parent, that mutation will pass down to yet another generation.

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CHAPTER OVERVIEW

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16.1: Control of Gene Expression

For a cell to function properly, necessary proteins must be synthesized at the proper time. All organisms and cells control or regulate the transcription and translation of their DNA into protein. The process of turning on a gene to produce RNA and protein is called gene expression. Whether in a simple unicellular organism or in a complex multicellular organism, each cell controls when and how its genes are expressed. For this to occur, there must be a mechanism to control when a gene is expressed to make RNA and protein, how much of the protein is made, and when it is time to stop making that protein because it is no longer needed.

Cells in multicellular organisms are specialized; cells in different tissues look very different and perform different functions. For example, a muscle cell is very different from a liver cell, which is very different from a skin cell. These differences are a consequence of the expression of different sets of genes in each of these cells. All cells have certain basic functions they must perform for themselves, such as converting the energy in sugar molecules into energy in ATP. Each cell also has many genes that are not expressed, and expresses many that are not expressed by other cells, such that it can carry out its specialized functions. In addition, cells will turn on or off certain genes at different times in response to changes in the environment or at different times during the development of the organism. Unicellular organisms, both eukaryotic and prokaryotic, also turn on and off genes in response to the demands of their environment so that they can respond to special conditions.

The control of gene expression is extremely complex. Malfunctions in this process are detrimental to the cell and can lead to the development of many diseases, including cancer.

Prokaryotic versus Eukaryotic Gene Expression

To understand how gene expression is regulated, we must first understand how a gene becomes a functional protein in a cell. The process occurs in both prokaryotic and eukaryotic cells, just in slightly different fashions.

Because prokaryotic organisms lack a cell nucleus, the processes of transcription and translation occur almost simultaneously. When the protein is no longer needed, transcription stops. As a result, the primary method to control what type and how much protein is expressed in a prokaryotic cell is through the regulation of DNA transcription into RNA. All the subsequent steps happen automatically. When more protein is required, more transcription occurs. Therefore, in prokaryotic cells, the control of gene expression is almost entirely at the transcriptional level.

The first example of such control was discovered using *E. coli* in the 1950s and 1960s by French researchers and is called the *lac* operon. The *lac* operon is a stretch of DNA with three adjacent genes that code for proteins that participate in the absorption and metabolism of lactose, a food source for *E. coli*. When lactose is not present in the bacterium's environment, the *lac* genes are transcribed in small amounts. When lactose is present, the genes are transcribed and the bacterium is able to use the lactose as a food source. The operon also contains a promoter sequence to which the RNA polymerase binds to begin transcription; between the promoter and the three genes is a region called the operator. When there is no lactose present, a protein known as a repressor binds to the operator and prevents RNA polymerase from binding to the promoter, except in rare cases. Thus very little of the protein products of the three genes is made. When lactose is present, an end product of lactose metabolism binds to the repressor protein and prevents it from binding to the operator. This allows RNA polymerase to bind to the promoter and freely transcribe the three genes, allowing the organism to metabolize the lactose.

Eukaryotic cells, in contrast, have intracellular organelles and are much more complex. Recall that in eukaryotic cells, the DNA is contained inside the cell's nucleus and it is transcribed into mRNA there. The newly synthesized mRNA is then transported out of the nucleus into the cytoplasm, where ribosomes translate the mRNA into protein. The processes of transcription and translation are physically separated by the nuclear membrane; transcription occurs only within the nucleus, and translation only occurs outside the nucleus in the cytoplasm. The regulation of gene expression can occur at all stages of the process (Figure **16.1.1**). Regulation may occur when the DNA is uncoiled and loosened from nucleosomes to bind transcription factors (epigenetic level), when the RNA is transcribed (transcriptional level), when RNA is processed and exported to the cytoplasm after it is transcribed (post-transcriptional level), when the RNA is translated into protein (translational level), or after the protein has been made (post-translational level).

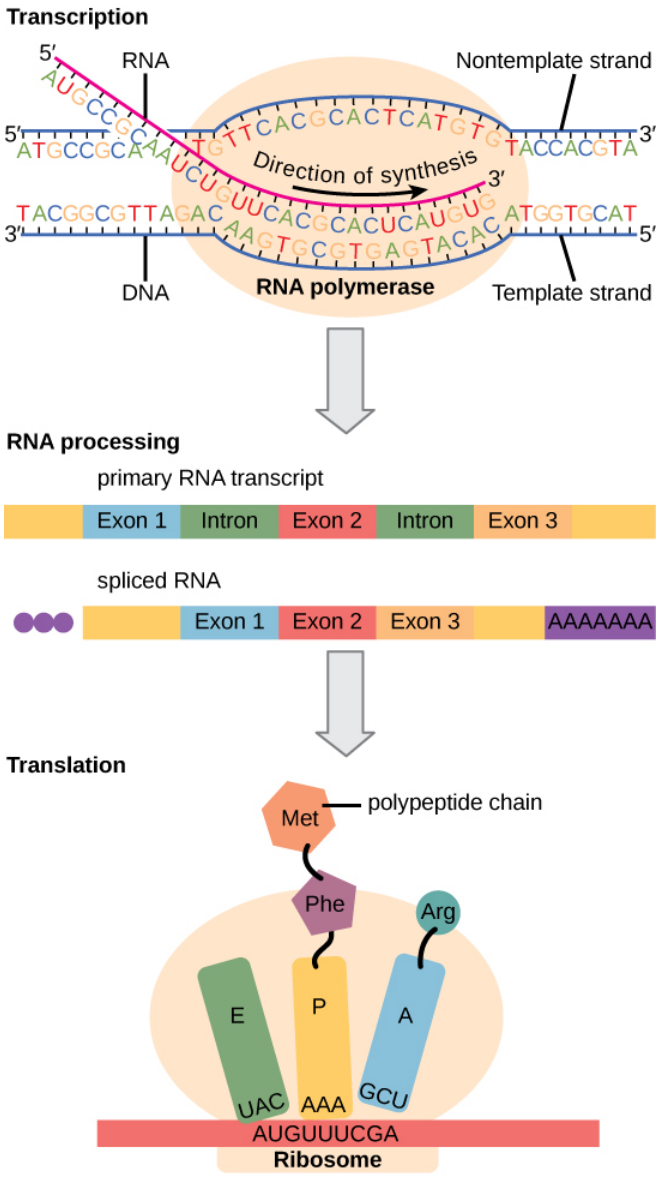


Figure 16.1.1: Eukaryotic gene expression is regulated during transcription and RNA processing, which take place in the nucleus, as well as during protein translation, which takes place in the cytoplasm. Further regulation may occur through post-translational modifications of proteins.

The differences in the regulation of gene expression between prokaryotes and eukaryotes are summarized in Table **16.1.1**.

Table 16.1.1: Differences in the Regulation of Gene Expression of Prokaryotic and Eukaryotic Organisms

Prokaryotic organisms	Eukaryotic organisms
Lack nucleus	Contain nucleus
RNA transcription and protein translation occur almost simultaneously	• RNA transcription occurs prior to protein translation, and it takes place in the nucleus. RNA translation to protein occurs in the cytoplasm. • RNA post-processing includes addition of a 5' cap, poly-A tail, and excision of introns and splicing of exons.
Gene expression is regulated primarily at the transcriptional level	Gene expression is regulated at many levels (epigenetic, transcriptional, post-transcriptional, translational, and post-translational)

EVOLUTION IN ACTION: Alternative RNA Splicing

In the 1970s, genes were first observed that exhibited alternative RNA splicing. Alternative RNA splicing is a mechanism that allows different protein products to be produced from one gene when different combinations of introns (and sometimes exons) are removed from the transcript (Figure **16.1.2**). This alternative splicing can be haphazard, but more often it is controlled and acts as a mechanism of gene regulation, with the frequency of different splicing alternatives controlled by the cell as a way to control the production of different protein products in different cells, or at different stages of development. Alternative splicing is now understood to be a common mechanism of gene regulation in eukaryotes; according to one estimate, 70% of genes in humans are expressed as multiple proteins through alternative splicing.

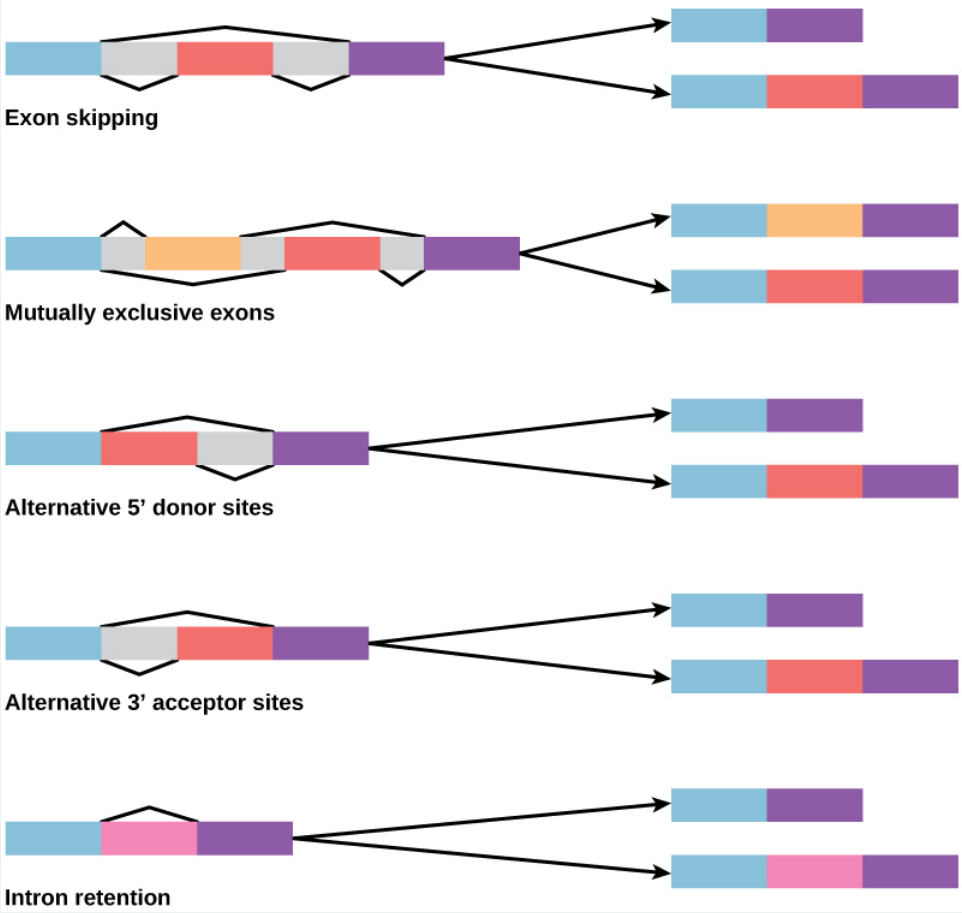


Figure 16.1.2: There are five basic modes of alternative splicing. Segments of pre-mRNA with exons shown in blue, red, orange, and pink can be spliced to produce a variety of new mature mRNA segments.

How could alternative splicing evolve? Introns have a beginning and ending recognition sequence, and it is easy to imagine the failure of the splicing mechanism to identify the end of an intron and find the end of the next intron, thus removing two introns and the intervening exon. In fact, there are mechanisms in place to prevent such exon skipping, but mutations are likely to lead to their failure. Such "mistakes" would more than likely produce a nonfunctional protein. Indeed, the cause of many genetic diseases is alternative splicing rather than mutations in a sequence. However, alternative splicing would create a protein variant without the loss of the original protein, opening up possibilities for adaptation of the new variant to new functions. Gene duplication has played an important role in the evolution of new functions in a similar way—by providing genes that may evolve without eliminating the original functional protein.

Summary

While all somatic cells within an organism contain the same DNA, not all cells within that organism express the same proteins. Prokaryotic organisms express the entire DNA they encode in every cell, but not necessarily all at the same time. Proteins are expressed only when they are needed. Eukaryotic organisms express a subset of the DNA that is encoded in any given cell. In each

cell type, the type and amount of protein is regulated by controlling gene expression. To express a protein, the DNA is first transcribed into RNA, which is then translated into proteins. In prokaryotic cells, these processes occur almost simultaneously. In eukaryotic cells, transcription occurs in the nucleus and is separate from the translation that occurs in the cytoplasm. Gene expression in prokaryotes is regulated only at the transcriptional level, whereas in eukaryotic cells, gene expression is regulated at the epigenetic, transcriptional, post-transcriptional, translational, and post-translational levels.

Glossary

alternative RNA splicing
: a post-transcriptional gene regulation mechanism in eukaryotes in which multiple protein products are produced by a single gene through alternative splicing combinations of the RNA transcript

epigenetic
: describing non-genetic regulatory factors, such as changes in modifications to histone proteins and DNA that control accessibility to genes in chromosomes

gene expression
: processes that control whether a gene is expressed

post-transcriptional
: control of gene expression after the RNA molecule has been created but before it is translated into protein

post-translational
: control of gene expression after a protein has been created

Contributors and Attributions

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SECTION OVERVIEW

16.2: Regulatory Proteins

16.2.1: D5. DNA Binding Proteins

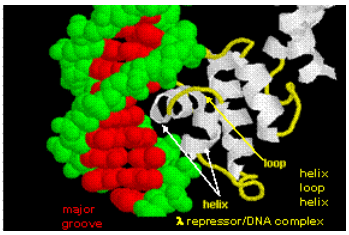
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16.2.1: D5. DNA Binding Proteins

Given the relative structural simplicity and repetitiveness of DNA, it would follow that proteins that bind specifically to it might have common DNA binding domain motifs but with specific amino acids side chains allowing for specific binding interactions.

- helix-turn-helix: found in prokaryotic DNA binding proteins.

Figure: helix-turn-helix



The figures shows two such proteins, the cro repressor from bacteriophage 434 and the lambda repressor from the bacteriophage lambda. (Bacteriophages are viruses that infect bacteia.) Notice how specificity is achieved, in part, by the formation of specific H-bonds between the protein and the major grove of the operator DNA.

Figure: Lambda Repressor/DNA Complex

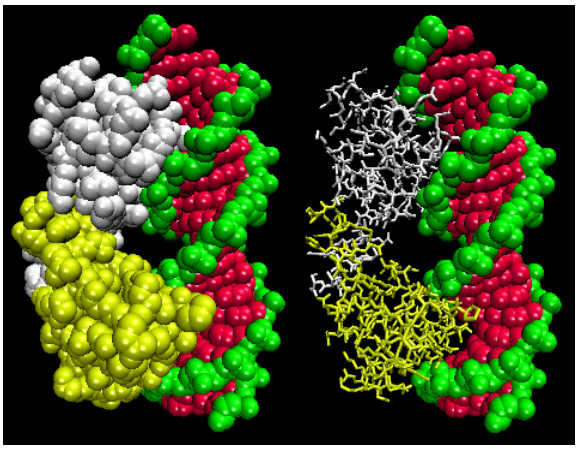
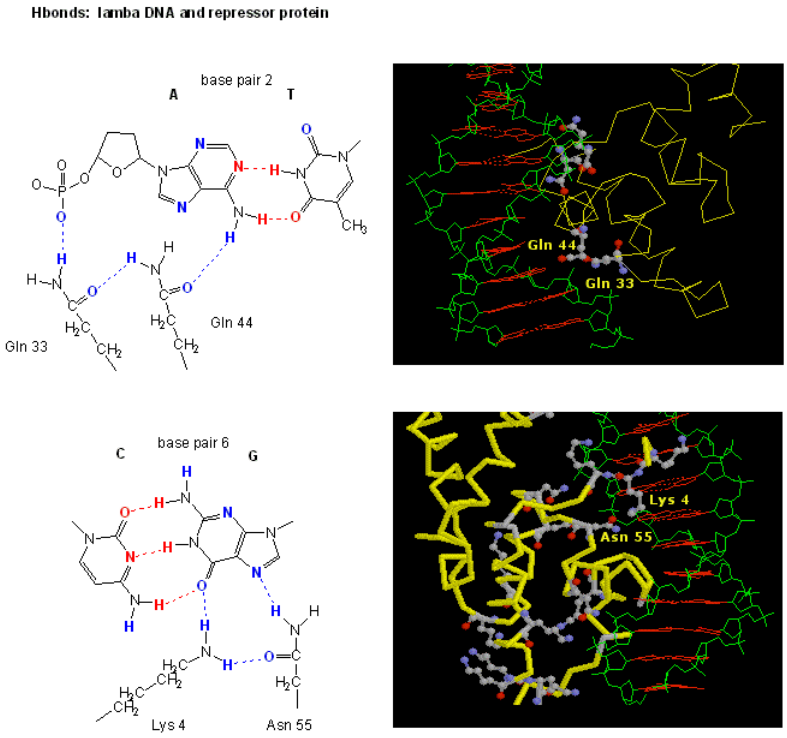


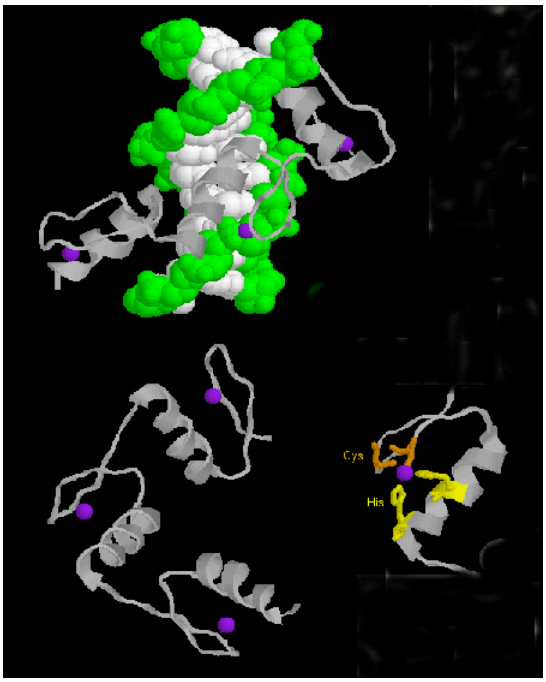
Figure: H Bond interactions betweenλ repressor and DNA



Jmol: Updated Lambda Repressor/DNA complex Jmol14 (Java) | JSMol (HTML5)

- zinc finger: (eukaryotes) These proteins have a common sequence motif of X3-Cys-X2-4-Cys-X12-His-X3-4-His-X4- in which X is any amino acid. Zn2+ is tetrahedrally coordinated with the Cys and His side chains, which are on one of two antiparallel beta strands, and an alpha helix, respectively. The zinc finger, stabilized by the zinc, binds to the major groove of DNA.]

Figure: zinc finger



Jmol: Updated Zif268:DNA Complex Jmol14 (Java) | JSMol (HTML5)

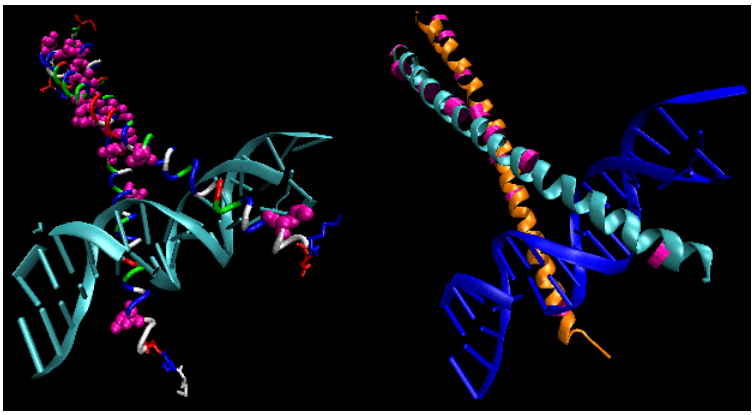
Zn finger proteins, of which 900 are encoded in the human genome (including the eukaryotic insulators binding protein CTCF described above) can be mobilized to actual repair specific mutations in cells, which if carried out in a high enough percentage of mutant cells could cure specific genetic diseases such as some forms of severe combined immunodeficiency disease. In this new technique (Urnov et al, 2005), multiple linked Zn finger binding domains, (one of the natural-occurring ones or mutant forms produced in the lab), each one specific for a certain nucleotide sequence, is linked to a nonspeciifc endonuclease, derived from the enzyme FokI. The nuclease is active in dimeric form so the active complex requires two endonuclease domains, each bound to four different Zn finger domains, to assemble at the target site. Specificity of binding is achieved by selection by the Zn finger domains. A nick is then made by the DNA by the nuclease, and host cell repair mechanisms ensue. This process involves strand separation, homologous recombination of the nicked region with complementary DNA within the cell, and repair of the nick. If excess wild type (non-mutated) DNA is added to the cells and uses as the template, the normal DNA repair mutation would fix the mutation. Urnov et al have shown the up to 20% of cultured cells containing a mutation can be repair in the lab. If these cells gain a selective growth advantage, the mutated cells would eventually be replaced with wild type cells.

- steroid hormone receptors: (eukaryotes) In contrast to most hormones, which bind to cell surface receptors, steroid hormones (derivatives of cholesterol) pass through the cell membrane and bind to cytoplasmic receptors through a hormone binding domain. This changes the shape of the receptor which then binds to a specific site on the DNA (hormone response element) though a DNA binding domain. In a structure analogous to the zinc finger, Zn 2+ is tetrahedrally coordinated to 4 Cys, in a globular-like structure which binds as a dimer to two identical, but reversed sequences of DNA (palindrome) within the major grove. (Examples of palindromes: Able was I ere I saw Elba; Dennis and Edna dine, said I, as Enid and Edna sinned.

Consider the glucocorticoid receptor (GR) as a specific example. It binds DNA as a dimer. The two DNA binding domains of the dimer associate with two adjacent major grooves of the DNA in the GR binding sequence (GBS), a short sequence of DNA within the promoter. Meijsing, et al. have found that not only does the GBS act as a binding site for GR, allowing transcription of genes, but it also affects the conformation of the receptor, causing gene transcription to be regulated in another way. The group constructed luciferase "reporters genes" which have GBS linked to the gene for the protein luciferase, that would express the protein luciferase (which fluoresces) if they were being transcribed, with the GBS. They found that relative transcriptional activity did not correlate to relative binding affinity of GR to the GBS. GBSs which were much more active than others bound comparably with those of lower activity, while GBSs with similar transcriptional activity bound with different affinities. This shows that the GBS is conferring unique function to the GR associated with it (i.e. transcription is not simply affected by whether or not the GR is bound to the GBS). A "lever arm" of the receptor was found to undergo conformational changes when bound to DNA, with changes specific to the sequence to which it was bound. A mutant protein, GR-γ, was made to be identical to the wild-type protein, GR-α, except in the lever arm was found to have different transcriptional activity even though they were binding to the same site on the DNA, showing that the lever arm and its conformation affects transcription.

- leucine zippers (or scissors): (eukaryotes) These proteins contain stretches of 35 amino acids in which Leu is found repeatedly at 7 amino acid intervals. These regions of the protein form amphiphilic helices, with Leu on one face, one Leu after two turns of a helix. Two of these proteins can form a dimer, stabilized by the binding of these nonpolar, leucine-rich amphiphilic helices to one another, forming a coiled-coil, much as in the muscle protein myosin. The leucine zipper represents the protein binding domain of the protein. The DNA binding domain is found in the first 30 N-terminal amino acids, which are basic and form an alpha helix when the protein binds to DNA. The leucine zipper then functions to bring two DNA binding proteins together, allowing the N-terminal bases helices to interact with the major grove of DNA in a base-specific fashion. Valine and isoleucine, along with leucine, are often found in stretches of amino acids that can interact to form other types of coiled coils.

Figure: leucine zippers (made with VMD)



Jmol: Updated Leucine Zipper Jmol14 (Java) | JSMol (HTML5)

Just as Zinc fingers nucleases have been used to induce repair of mutations, another study of the rat genome used specially designed ZFNs to cause breaks in ds-DNA that contain mutations from inaccurate DNA repair mechanism (by NHEJ) and hence contained specific mutations (Geurts, et al. 2009). This process, knockout of the gene, prevents the production of the protein normally transcribed by the target gene. Five- and six-finger ZFNs were used to achieve a high level of specificity in the targeted binding to the gene for three different proteins: green fluorescent protein (GFP), Immunoglobulin M (IgM) and Rab38. The knockout was successful in 12% of the rats tested; these animals had no wild-type protein and no expression. The ZFNs were sufficiently specific that no mutations were observed at any of 20 predicted non-target sites. This study supports the viability of control of transcription and expression for the treatment of disease and the importance of specific binding.

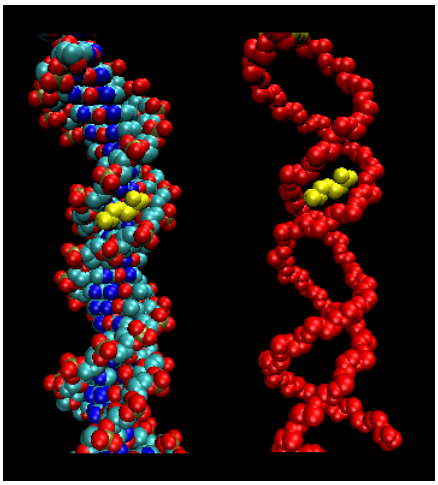
We have seen that two main factors contribute to the specific recognition of DNA by proteins; the formation of hydrogen bonds to specific nucleotide donors and acceptors in the major groove, and sequence-dependent deformations of the DNA helix to altered shapes with increased affinity of protein ligands. For example the Tata Binding Protein (TBP) can interact with a widened minor grove in the TATA box. New findings support that in addition proteins are able to use information in minor grooves that have become "narrowed" depending on the nucleotide sequence.

Tracks of DNA enriched in A can lead to twisting conformations that cause inter-base-pair hydrogen bonding in the major grooves, results in the narrowing of minor grooves. High amounts of AT base pairs are concentrated in narrow minor grooves (width <5.0) and CG base pairs are found more frequently in wide minor grooves.

How does minor groove narrowing affect DNA recognition? Narrow minor groves enhance the negative electrostatic potential of the DNA, making it a more specific and recognizable site. The backbone phosphates of the DNA are closer to the middle of the groove when it is narrow, thus correlating narrow minor grooves with a more negative electrostatic potential.

The minor grove-interacting parts of proteins contain arginine whose side chain can be accommodated into the more narrow and negative minor groove. Arginines can bind and in some cases insert themselves as short sequence motifs which enhance the specificity of the DNA shape recognition. Arg is preferred over Lys since the effective radii of the charge in Arg is greater than of the charge carrier in Lys. This would lead to a decreased desolvation energy for Arg which would promote its binding to the narrowed major grove. This discovery shows that "the role of DNA shape must be taken into consideration when annotating the entire genome and predicting transcription-factor-binding sites".

Figure: Arg in T3c Transposase binding in Narrowed Minor Grove of T3c Transposon



- Sliding Model for protein/DNA Interactions

Contributors and Attributions

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16.3: Prokaryotic Regulation

Skills to Develop

- Describe the steps involved in prokaryotic gene regulation
- Explain the roles of activators, inducers, and repressors in gene regulation

The DNA of prokaryotes is organized into a circular chromosome supercoiled in the nucleoid region of the cell cytoplasm. Proteins that are needed for a specific function, or that are involved in the same biochemical pathway, are encoded together in blocks called operons. For example, all of the genes needed to use lactose as an energy source are coded next to each other in the lactose (or *lac*) operon.

In prokaryotic cells, there are three types of regulatory molecules that can affect the expression of operons: repressors, activators, and inducers. Repressors are proteins that suppress transcription of a gene in response to an external stimulus, whereas activators are proteins that increase the transcription of a gene in response to an external stimulus. Finally, inducers are small molecules that either activate or repress transcription depending on the needs of the cell and the availability of substrate.

The *trp* Operon: A Repressor Operon

Bacteria such as *E. coli* need amino acids to survive. Tryptophan is one such amino acid that *E. coli* can ingest from the environment. *E. coli* can also synthesize tryptophan using enzymes that are encoded by five genes. These five genes are next to each other in what is called the tryptophan (*trp*) operon (Figure **16.3.1**). If tryptophan is present in the environment, then *E. coli* does not need to synthesize it and the switch controlling the activation of the genes in the *trp* operon is switched off. However, when tryptophan availability is low, the switch controlling the operon is turned on, transcription is initiated, the genes are expressed, and tryptophan is synthesized.

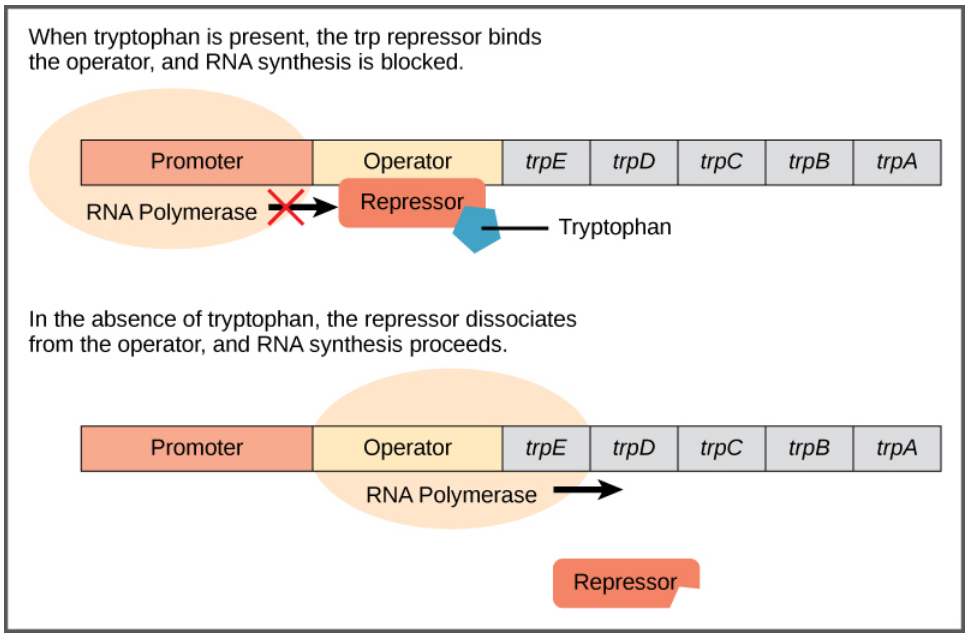


Figure **16.3.1**: The five genes that are needed to synthesize tryptophan in *E. coli* are located next to each other in the *trp* operon. When tryptophan is plentiful, two tryptophan molecules bind the repressor protein at the operator sequence. This physically blocks the RNA polymerase from transcribing the tryptophan genes. When tryptophan is absent, the repressor protein does not bind to the operator and the genes are transcribed.

A DNA sequence that codes for proteins is referred to as the coding region. The five coding regions for the tryptophan biosynthesis enzymes are arranged sequentially on the chromosome in the operon. Just before the coding region is the transcriptional start site. This is the region of DNA to which RNA polymerase binds to initiate transcription. The promoter sequence is upstream of the transcriptional start site; each operon has a sequence within or near the promoter to which proteins (activators or repressors) can bind and regulate transcription.

A DNA sequence called the operator sequence is encoded between the promoter region and the first *trp* coding gene. This operator contains the DNA code to which the repressor protein can bind. When tryptophan is present in the cell, two tryptophan molecules bind to the *trp* repressor, which changes shape to bind to the *trp* operator. Binding of the tryptophan–repressor complex at the operator physically prevents the RNA polymerase from binding, and transcribing the downstream genes.

When tryptophan is not present in the cell, the repressor by itself does not bind to the operator; therefore, the operon is active and tryptophan is synthesized. Because the repressor protein actively binds to the operator to keep the genes turned off, the *trp* operon is negatively regulated and the proteins that bind to the operator to silence *trp* expression are negative regulators.

Link to Learning



Watch this video to learn more about the *trp* operon.

Catabolite Activator Protein (CAP): An Activator Regulator

Just as the *trp* operon is negatively regulated by tryptophan molecules, there are proteins that bind to the operator sequences that act as a positive regulator to turn genes on and activate them. For example, when glucose is scarce, *E. coli* bacteria can turn to other sugar sources for fuel. To do this, new genes to process these alternate genes must be transcribed. When glucose levels drop, cyclic AMP (cAMP) begins to accumulate in the cell. The cAMP molecule is a signaling molecule that is involved in glucose and energy metabolism in *E. coli*. When glucose levels decline in the cell, accumulating cAMP binds to the positive regulator catabolite activator protein (CAP), a protein that binds to the promoters of operons that control the processing of alternative sugars. When cAMP binds to CAP, the complex binds to the promoter region of the genes that are needed to use the alternate sugar sources (Figure **16.3.2**). In these operons, a CAP binding site is located upstream of the RNA polymerase binding site in the promoter. This increases the binding ability of RNA polymerase to the promoter region and the transcription of the genes.

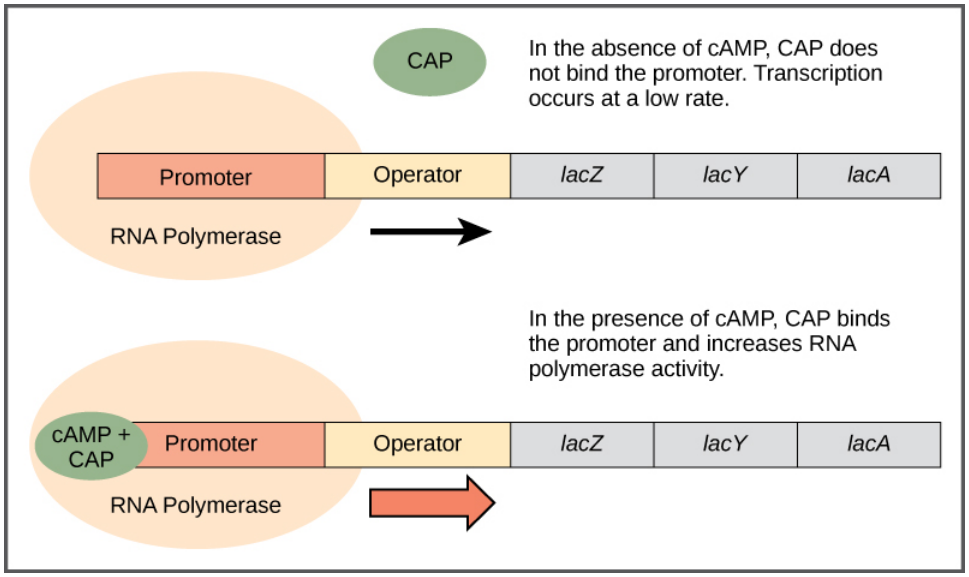


Figure **16.3.2**: When glucose levels fall, *E. coli* may use other sugars for fuel but must transcribe new genes to do so. As glucose supplies become limited, cAMP levels increase. This cAMP binds to the CAP protein, a positive regulator that binds to an operator region upstream of the genes required to use other sugar sources.

The *lac* Operon: An Inducer Operon

The third type of gene regulation in prokaryotic cells occurs through inducible operons, which have proteins that bind to activate or repress transcription depending on the local environment and the needs of the cell. The *lac* operon is a typical inducible operon. As mentioned previously, *E. coli* is able to use other sugars as energy sources when glucose concentrations are low. To do so, the cAMP–CAP protein complex serves as a positive regulator to induce transcription. One such sugar source is lactose. The *lac* operon encodes the genes necessary to acquire and process the lactose from the local environment. CAP binds to the operator sequence upstream of the promoter that initiates transcription of the *lac* operon. However, for the *lac* operon to be activated, two conditions must be met. First, the level of glucose must be very low or non-existent. Second, lactose must be present. Only when glucose is absent and lactose is present will the *lac* operon be transcribed (Figure **16.3.3**). This makes sense for the cell, because it would be energetically wasteful to create the proteins to process lactose if glucose was plentiful or lactose was not available.

Art Connection

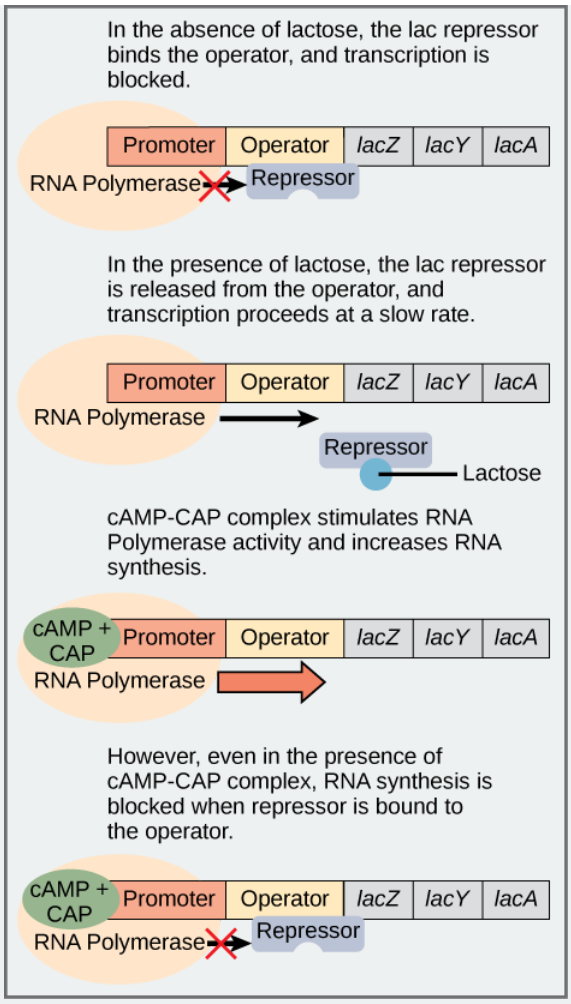


Figure **16.3.3**: Transcription of the *lac* operon is carefully regulated so that its expression only occurs when glucose is limited and lactose is present to serve as an alternative fuel source.

In *E. coli*, the *trp* operon is on by default, while the *lac* operon is off. Why do you think this is the case?

If glucose is absent, then CAP can bind to the operator sequence to activate transcription. If lactose is absent, then the repressor binds to the operator to prevent transcription. If either of these requirements is met, then transcription remains off. Only when both conditions are satisfied is the *lac* operon transcribed (Table **16.3.1**).

Table **16.3.1**: Signals that Induce or Repress Transcription of the lac Operon

Glucose	CAP binds	Lactose	Repressor binds	Transcription
+	-	-	+	No
+	-	+	-	Some
-	+	-	+	No
-	+	+	-	Yes

Link to Learning



Watch an animated tutorial about the workings of *lac* operon here.

Summary

The regulation of gene expression in prokaryotic cells occurs at the transcriptional level. There are three ways to control the transcription of an operon: repressive control, activator control, and inducible control. Repressive control, typified by the *trp* operon, uses proteins bound to the operator sequence to physically prevent the binding of RNA polymerase and the activation of transcription. Therefore, if tryptophan is not needed, the repressor is bound to the operator and transcription remains off. Activator control, typified by the action of CAP, increases the binding ability of RNA polymerase to the promoter when CAP is bound. In this case, low levels of glucose result in the binding of cAMP to CAP. CAP then binds the promoter, which allows RNA polymerase to bind to the promoter better. In the last example—the *lac* operon—two conditions must be met to initiate transcription. Glucose must not be present, and lactose must be available for the *lac* operon to be transcribed. If glucose is absent, CAP binds to the operator. If lactose is present, the repressor protein does not bind to its operator. Only when both conditions are met will RNA polymerase bind to the promoter to induce transcription.

Art Connections

Figure **16.3.3**: In *E. coli*, the *trp* operon is on by default, while the *lac* operon is off. Why do you think that this is the case?

Answer

Tryptophan is an amino acid essential for making proteins, so the cell always needs to have some on hand. However, if plenty of tryptophan is present, it is wasteful to make more, and the expression of the *trp* receptor is repressed. Lactose, a sugar found in milk, is not always available. It makes no sense to make the enzymes necessary to digest an energy source that is not available, so the *lac* operon is only turned on when lactose is present.

Glossary

activator
protein that binds to prokaryotic operators to increase transcription

catabolite activator protein (CAP)
protein that complexes with cAMP to bind to the promoter sequences of operons that control sugar processing when glucose is not available

inducible operon
operon that can be activated or repressed depending on cellular needs and the surrounding environment

lac operon
operon in prokaryotic cells that encodes genes required for processing and intake of lactose

negative regulator
protein that prevents transcription

operator
region of DNA outside of the promoter region that binds activators or repressors that control gene expression in prokaryotic cells

operon
collection of genes involved in a pathway that are transcribed together as a single mRNA in prokaryotic cells

positive regulator
protein that increases transcription

repressor
protein that binds to the operator of prokaryotic genes to prevent transcription

transcriptional start site
site at which transcription begins

trp operon
series of genes necessary to synthesize tryptophan in prokaryotic cells

tryptophan
amino acid that can be synthesized by prokaryotic cells when necessary

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SECTION OVERVIEW

16.4: Eukaryotic Regulation

16.4.1: The Promoter and the Transcription Machinery

16.4.2: Transcriptional Enhancers and Repressors

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16.4.1: The Promoter and the Transcription Machinery

Learning Objectives

- Describe the role of promoters in RNA transcription

Genes are organized to make the control of gene expression easier. The promoter region is immediately upstream of the coding sequence. This region can be short (only a few nucleotides in length) or quite long (hundreds of nucleotides long). The longer the promoter, the more available space for proteins to bind. This also adds more control to the transcription process. The length of the promoter is gene-specific and can differ dramatically between genes. Consequently, the level of control of gene expression can also differ quite dramatically between genes. The purpose of the promoter is to bind transcription factors that control the initiation of transcription.

Within the promoter region, just upstream of the transcriptional start site, resides the TATA box. This box is simply a repeat of thymine and adenine dinucleotides (literally, TATA repeats). RNA polymerase binds to the transcription initiation complex, allowing transcription to occur. To initiate transcription, a transcription factor (TFIID) is the first to bind to the TATA box. Binding of TFIID recruits other transcription factors, including TFIIB, TFIIE, TFIIF, and TFIIH to the TATA box. Once this transcription initiation complex is assembled, RNA polymerase can bind to its upstream sequence. When bound along with the transcription factors, RNA polymerase is phosphorylated. This releases part of the protein from the DNA to activate the transcription initiation complex and places RNA polymerase in the correct orientation to begin transcription; DNA-bending protein brings the enhancer, which can be quite a distance from the gene, in contact with transcription factors and mediator proteins.

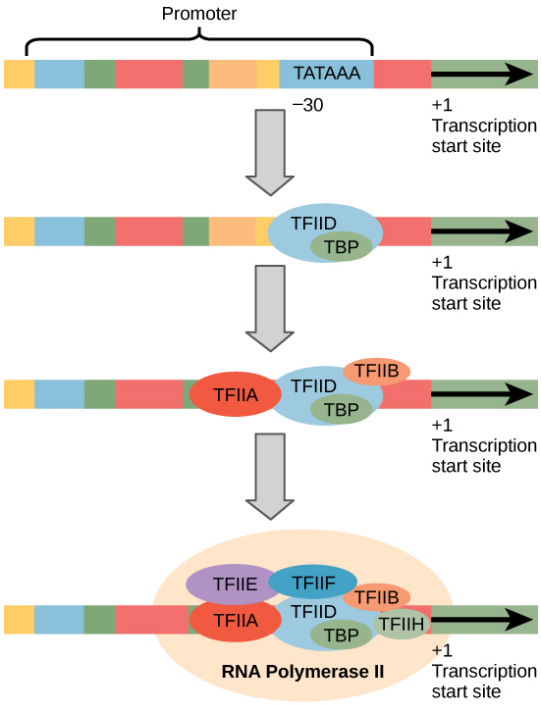


Figure 16.4.1.1: Promoters: A generalized promoter of a gene transcribed by RNA polymerase II is shown. Transcription factors recognize the promoter. RNA polymerase II then binds and forms the transcription initiation complex.

In addition to the general transcription factors, other transcription factors can bind to the promoter to regulate gene transcription. These transcription factors bind to the promoters of a specific set of genes. They are not general transcription factors that bind to every promoter complex, but are recruited to a specific sequence on the promoter of a specific gene. There are hundreds of transcription factors in a cell that each bind specifically to a particular DNA sequence motif. When transcription factors bind to the promoter just upstream of the encoded gene, they are referred to as cis-acting elements because they are on the same chromosome, just next to the gene. The region that a particular transcription factor binds to is called the transcription factor binding site.

Transcription factors respond to environmental stimuli that cause the proteins to find their binding sites and initiate transcription of the gene that is needed.

Key Points

- The purpose of the promoter is to bind transcription factors that control the initiation of transcription.
- The promoter region can be short or quite long; the longer the promoter is, the more available space for proteins to bind.
- To initiate transcription, a transcription factor (TFIID) binds to the TATA box, which causes other transcription factors to subsequently bind to the TATA box.
- Once the transcription initiation complex is assembled, RNA polymerase can bind to its upstream sequence and is then phosphorylated.
- Phosphorylation of RNA polymerase releases part of the protein from the DNA to activate the transcription initiation complex and places RNA polymerase in the correct orientation to begin transcription.
- Transcription factors respond to environmental stimuli that cause the proteins to find their binding sites and initiate transcription of the gene that is needed.

Key Terms

- **TATA box**: a DNA sequence (cis-regulatory element) found in the promoter region of genes in archaea and eukaryotes
- **transcription factor**: a protein that binds to specific DNA sequences, thereby controlling the flow (or transcription) of genetic information from DNA to mRNA
- **promoter**: the section of DNA that controls the initiation of RNA transcription

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16.4.2: Transcriptional Enhancers and Repressors

Learning Objectives

- Explain how enhancers and repressors regulate gene expression

Enhancers and Transcription

In some eukaryotic genes, there are regions that help increase or enhance transcription. These regions, called enhancers, are not necessarily close to the genes they enhance. They can be located upstream of a gene, within the coding region of the gene, downstream of a gene, or may be thousands of nucleotides away.

Enhancer regions are binding sequences, or sites, for transcription factors. When a DNA-bending protein binds to an enhancer, the shape of the DNA changes. This shape change allows the interaction between the activators bound to the enhancers and the transcription factors bound to the promoter region and the RNA polymerase to occur. Whereas DNA is generally depicted as a straight line in two dimensions, it is actually a three-dimensional object. Therefore, a nucleotide sequence thousands of nucleotides away can fold over and interact with a specific promoter.

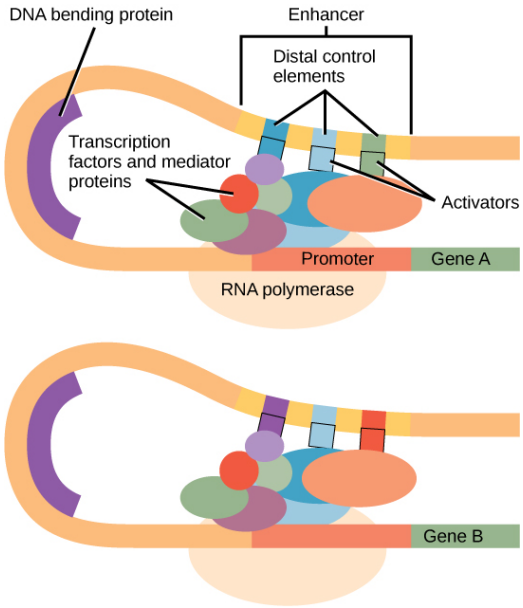


Figure **16.4.2.1**: Enhancers: An enhancer is a DNA sequence that promotes transcription. Each enhancer is made up of short DNA sequences called distal control elements. Activators bound to the distal control elements interact with mediator proteins and transcription factors.

Turning Genes Off: Transcriptional Repressors

Like prokaryotic cells, eukaryotic cells also have mechanisms to prevent transcription. Transcriptional repressors can bind to promoter or enhancer regions and block transcription. Like the transcriptional activators, repressors respond to external stimuli to prevent the binding of activating transcription factors.

A corepressor is a protein that decreases gene expression by binding to a transcription factor that contains a DNA-binding domain. The corepressor is unable to bind DNA by itself. The corepressor can repress transcriptional initiation by recruiting histone deacetylase, which catalyzes the removal of acetyl groups from lysine residues. This increases the positive charge on histones, which strengthens the interaction between the histones and DNA, making the DNA less accessible to the process of transcription.

Key Points

- Enhancers can be located upstream of a gene, within the coding region of the gene, downstream of a gene, or thousands of nucleotides away.

- When a DNA -bending protein binds to the enhancer, the shape of the DNA changes, which allows interactions between the activators and transcription factors to occur.
- Repressors respond to external stimuli to prevent the binding of activating transcription factors.
- Corepressors can repress transcriptional initiation by recruiting histone deacetylase.
- Histone deactylation increases the positive charge on histones, which strengthens the interaction between the histones and DNA, making the DNA less accessible to transcription.

Key Terms

- **enhancer**: a short region of DNA that can increase transcription of genes
- **repressor**: any protein that binds to DNA and thus regulates the expression of genes by decreasing the rate of transcription
- **activator**: any chemical or agent which regulates one or more genes by increasing the rate of transcription

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SECTION OVERVIEW

16.5: Chromatin Structure Affects Gene Expression

16.5.1: Epigenetic Control- Regulating Access to Genes within the Chromosome

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16.5.1: Epigenetic Control- Regulating Access to Genes within the Chromosome

Learning Objectives

- Discuss how eukaryotic gene regulation occurs at the epigenetic level and the various epigenetic changes that can be made to DNA

Epigenetic Control: Regulating Access to Genes within the Chromosome

The human genome encodes over 20,000 genes; each of the 23 pairs of human chromosomes encodes thousands of genes. The DNA in the nucleus is precisely wound, folded, and compacted into chromosomes so that it will fit into the nucleus. It is also organized so that specific segments can be accessed as needed by a specific cell type.

The first level of organization, or packing, is the winding of DNA strands around histone proteins. Histones package and order DNA into structural units called nucleosome complexes, which can control the access of proteins to the DNA regions. Under the electron microscope, this winding of DNA around histone proteins to form nucleosomes looks like small beads on a string. These beads (histone proteins) can move along the string (DNA) and change the structure of the molecule.

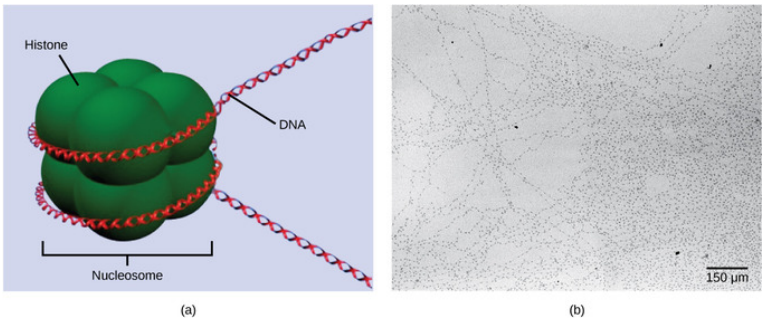


Figure **16.5.1.1**: DNA Packaging: DNA is folded around histone proteins to create (a) nucleosome complexes. These nucleosomes control the access of proteins to the underlying DNA. When viewed through an electron microscope (b), the nucleosomes look like beads on a string.

If DNA encoding a specific gene is to be transcribed into RNA, the nucleosomes surrounding that region of DNA can slide down the DNA to open that specific chromosomal region and allow for the transcriptional machinery (RNA polymerase) to initiate transcription. Nucleosomes can move to open the chromosome structure to expose a segment of DNA, but do so in a very controlled manner.

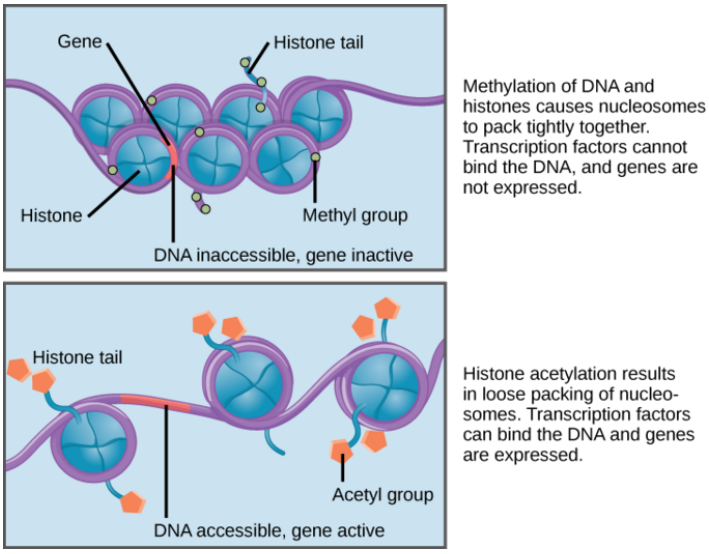


Figure 16.5.1.1: Nucleosomes can change position to allow transcription of genes: Nucleosomes can slide along DNA. When nucleosomes are spaced closely together (top), transcription factors cannot bind and gene expression is turned off. When the nucleosomes are spaced far apart (bottom), the DNA is exposed. Transcription factors can bind, allowing gene expression to occur. Modifications to the histones and DNA affect nucleosome spacing.

How the histone proteins move is dependent on signals found on both the histone proteins and on the DNA. These signals are tags, or modifications, added to histone proteins and DNA that tell the histones if a chromosomal region should be open or closed. These tags are not permanent, but may be added or removed as needed. They are chemical modifications (phosphate, methyl, or acetyl groups) that are attached to specific amino acids in the protein or to the nucleotides of the DNA. The tags do not alter the DNA base sequence, but they do alter how tightly wound the DNA is around the histone proteins. DNA is a negatively-charged molecule; therefore, changes in the charge of the histone will change how tightly wound the DNA molecule will be. When unmodified, the histone proteins have a large positive charge; by adding chemical modifications, such as acetyl groups, the charge becomes less positive.

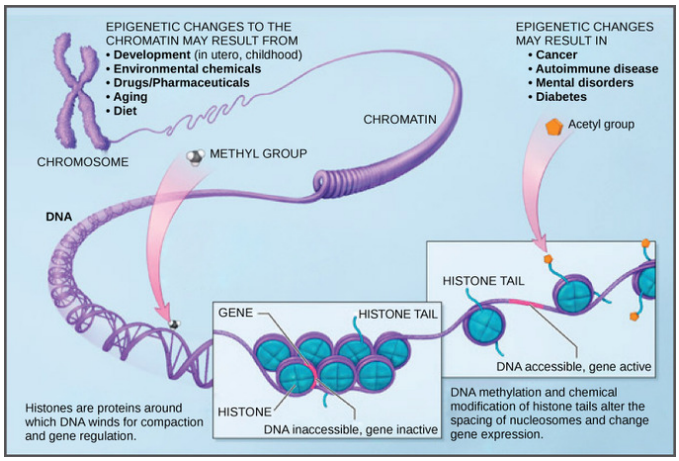


Figure 16.5.1.1: Modifications to histones and DNA can alter gene expression: Histone proteins and DNA nucleotides can be modified chemically. Modifications affect nucleosome spacing and gene expression.

The DNA molecule itself can also be modified. This occurs within very specific regions called CpG islands. These are stretches with a high frequency of cytosine and guanine dinucleotide DNA pairs (CG) found in the promoter regions of genes. When this configuration exists, the cytosine member of the pair can be methylated (a methyl group is added). This modification changes how the DNA interacts with proteins, including the histone proteins that control access to the region. Highly-methylated (hypermethylated) DNA regions with deacetylated histones are tightly coiled and transcriptionally inactive. These changes to DNA are inherited from parent to offspring, such that while the DNA sequence is not altered, the pattern of gene expression is passed to the next generation.

This type of gene regulation is called epigenetic regulation. Epigenetics means “above genetics.” The changes that occur to the histone proteins and DNA do not alter the nucleotide sequence and are not permanent. Instead, these changes are temporary (although they often persist through multiple rounds of cell division) and alter the chromosomal structure (open or closed) as needed. A gene can be turned on or off depending upon the location and modifications to the histone proteins and DNA. If a gene is to be transcribed, the histone proteins and DNA are modified surrounding the chromosomal region encoding that gene. This opens the chromosomal region to allow access for RNA polymerase and other proteins, called transcription factors, to bind to the promoter region, located just upstream of the gene, and initiate transcription. If a gene is to remain turned off, or silenced, the histone proteins and DNA have different modifications that signal a closed chromosomal configuration. In this closed configuration, the RNA polymerase and transcription factors do not have access to the DNA and transcription cannot occur.

Key Points

- DNA is packaged by wrapping around histone proteins into structures called nucleosomes, which resemble beads on a string.
- When DNA is to be transcribed, the nucleosomes can slide away from that region of DNA, opening it up to the transcription machinery of the cell.
- Chemical modifications to either the histone proteins or the DNA itself signals whether or not a particular region of the genome should be “open” or “closed” to the transcription machinery.
- Modifications such as acetylation or methylation of the histones can alter how tightly DNA is wrapped around them, while methylation of DNA changes how the DNA interacts with proteins, including the histone proteins that control access to the region.
- This type of genetic regulation is called epigenetic regulation (“above genetics”) as it does not change the nucleotide sequence of the DNA.

Key Terms

- **nucleosome**: any of the subunits that repeat in chromatin; a coil of DNA surrounding a histone core
- **epigenetics**: the study of heritable changes caused by the activation and deactivation of genes without any change in DNA sequence
- **histone**: any of various simple water-soluble proteins that are rich in the basic amino acids lysine and arginine and are complexed with DNA in the nucleosomes of eukaryotic chromatin

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SECTION OVERVIEW

16.6: Eukaryotic Posttranscriptional Regulation

16.6.1: miRNA

16.6.2: The Translation of RNA into Proteins

16.6.3: RNA Splicing

16.6.4: The Initiation Complex and Translation Rate

16.6.5: Regulating Protein Activity and Longevity

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16.6.1: miRNA

Learning Objectives

- Gene expression can be regulated at various stages after an RNA transcript has been produced.
- Some transcripts can undergo **alternative splicing**. This regulated process makes different mRNAs and proteins from the same initial RNA transcript.
- Some mRNAs are targeted by small regulatory RNAs, including **miRNAs**, which can cause mRNA degradation or block translation.
- A protein's activity may be regulated after translation by mechanisms such as proteolysis ("snipping out" of pieces) and addition of chemical groups.

The genes that a eukaryotic cell turns "on" largely determine its identity and properties. For instance, a photoreceptor cell in your eye can detect light because it expresses genes for light-sensitive proteins, as well as as genes for neurotransmitters that allow signals to be relayed to the brain.

In eukaryotic cells like photoreceptors, gene expression is often controlled primarily at the level of transcription. However, that doesn't mean transcription is the last chance for regulation. Later stages of gene expression can also be regulated, including the following:

- RNA processing, such as splicing, capping, and addition of a poly-A tail
- Messenger RNA (mRNA) translation and lifetime in the cytosol
- Protein modifications, such as addition of chemical groups or removal of amino acids

In the sections below, we'll discuss some common types of gene regulation that occur after an RNA transcript has been made.

Regulation of RNA processing

When a eukaryotic gene is transcribed in the nucleus, the primary transcript (freshly made RNA molecule) isn't yet considered a messenger RNA. Instead, it's an "immature" molecule called a pre-mRNA.

The pre-mRNA has to go through some modifications to become a mature mRNA molecule that can leave the nucleus and be translated. These include splicing, capping, and addition of a poly-A tail, all of which can potentially be regulated – sped up, slowed down, or altered to result in a different product.

Alternative splicing

Most pre-mRNA molecules have sections that are removed from the molecule, called **introns**, and sections that are linked or together to make the final mRNA, called **exons**. This process is called **splicing**.

In the process of **alternative splicing**, different portions of an mRNA can be selected for use as exons. This allows either of two (or more) mRNA molecules to be made from one pre-mRNA.

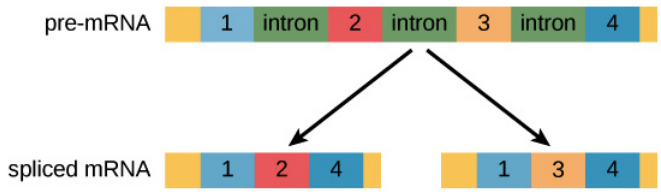


Figure 1. Image modified from "Eukaryotic Post-transcriptional Gene Regulation," by OpenStax College, Biology (CC BY 3.0).

Alternative splicing is not a random process. Instead, it's typically controlled by regulatory proteins. The proteins bind to specific sites on the pre-mRNA and "tell" the splicing factors which exons should be used. Different cell types may express different regulatory proteins, so different exon combinations can be used in each cell type, leading to the production of different proteins.

Small regulatory RNA

Once an mRNA has left the nucleus, it may or may not be translated many times to make proteins. Two key determinants of how much protein is made from an mRNA are its “lifespan” (how long it floats around in the cytosol) and how readily the translation machinery, such as the ribosome, can attach to it.

A recently discovered class of regulators, called small regulatory RNAs, can control mRNA lifespan and translation. Let’s see how this works.

microRNAs

microRNAs (miRNAs) were among the first small regulatory RNAs to be discovered. A miRNA is first transcribed as a long RNA molecule, which forms base pairs with itself and folds over to make a hairpin. Next, the hairpin is chopped up by enzymes, releasing a small double-stranded fragment of about 20 nucleotides. One of the strands in this fragment is the mature miRNA, which binds to a specific protein to make an RNA-protein complex.

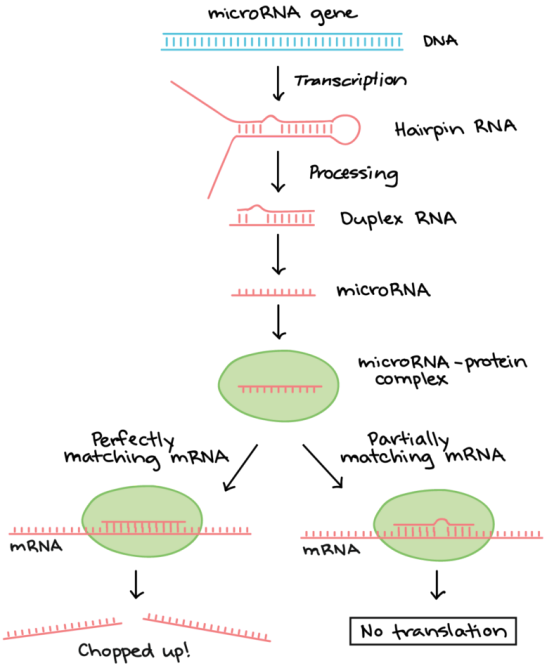


Figure 2. Image modifed from “miRNA biogenesis,” by Narayanese (CC BY-SA 3.0). The modified image is licensed under a CC BY-SA 3.0 license.

The miRNA directs the protein complex to “matching” mRNA molecules (ones that form base pairs with the miRNA). When the RNA-protein complex binds:

- If the miRNA and its target match perfectly, an enzyme in the RNA-protein complex will typically chop the mRNA in half, leading to its breakdown.
- If the miRNA and its target have some mismatches, the RNA-protein complex may instead bind to the mRNA and keep it from being translated.

These are not the only ways that miRNAs inhibit expression of their targets, and scientists are still investigating their many modes of action.[1]

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1. Carthew, R. W. and Sontheimer, E. J. (2009). Origins and mechanisms of miRNAs and siRNAs. *Cell*, *136*(4), 642–655. [1]http://dx.doi.org/10.1016/j.cell.2009.01.035. ↵

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16.6.2: The Translation of RNA into Proteins

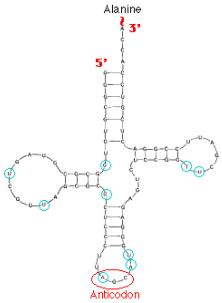


Figure 6.4.1 A**lanine transfer RNA**

This image shows the structure of **alanine transfer RNA** (**tRNA^{ala}**) from yeast. It consists of a single strand of 77 ribonucleotides. The chain is folded on itself, and many of the bases pair with each other forming four helical regions. Loops are formed in the unpaired regions of the chain. (The bases circled in blue have been chemically-modified following synthesis of the molecule.)

At least one kind of tRNA is present for each of the 20 amino acids used in protein synthesis. (Some amino acids employ the services of two or three different tRNAs, so most cells contain as many as 32 different kinds of tRNA.) The amino acid is attached to the appropriate tRNA by an activating enzyme (one of 20 **aminoacyl-tRNA synthetases**) specific for that amino acid as well as for the tRNA assigned to it.

Each kind of tRNA has a sequence of 3 unpaired nucleotides — the **anticodon** — which can bind, following the rules of base pairing, to the complementary triplet of nucleotides — the **codon** — in a **messenger RNA** (**mRNA**) molecule. Just as DNA replication and transcription involve base pairing of nucleotides running in opposite direction, so the reading of codons in mRNA (5' -> 3') requires that the anticodons bind in the opposite direction.

Anticodon: 3' CGA 5'
Codon: 5' GCU 3'

The RNA Codons

Second nucleotide

	U	C	A	G	
U	UUU **Phenylalanine** (Phe)	UCU **Serine** (Ser)	UAU **Tyrosine** (Tyr)	UGU **Cysteine** (Cys)	U
	UUC Phe	UCC Ser	UAC Tyr	UGC Cys	C
	UUA **Leucine** (Leu)	UCA Ser	UAA **STOP**	UGA **STOP**	A
	UUG Leu	UCG Ser	UAG **STOP**	UGG **Tryptophan** (Trp)	G
C	CUU **Leucine** (Leu)	CCU **Proline** (Pro)	CAU **Histidine** (His)	CGU **Arginine** (Arg)	U
	CUC Leu	CCC Pro	CAC His	CGC Arg	C
	CUA Leu	CCA Pro	CAA **Glutamine** (Gln)	CGA Arg	A
	CUG Leu	CCG Pro	CAG Gln	CGG Arg	G
A	AUU **Isoleucine** (Ile)	ACU **Threonine** (Thr)	AAU **Asparagine** (Asn)	AGU **Serine** (Ser)	U
	AUC Ile	ACC Thr	AAC Asn	AGC Ser	C
	AUA Ile	ACA Thr	AAA **Lysine** (Lys)	AGA **Arginine** (Arg)	A
	AUG **Methionine** (Met) or **START**	ACG Thr	AAG Lys	AGG Arg	G
G	GUU **Valine** Val	GCU **Alanine** (Ala)	GAU **Aspartic acid** (Asp)	GGU **Glycine** (Gly)	U
	GUC (Val)	GCC Ala	GAC Asp	GGC Gly	C
	GUA Val	GCA Ala	GAA **Glutamic acid** (Glu)	GGA Gly	A
	GUG Val	GCG Ala	GAG Glu	GGG Gly	G

Note:

- Most of the amino acids are encoded by synonymous codons that differ in the third position of the codon.
- In some cases, a single tRNA can recognize two or more of these synonymous codons.
- Example: phenylalanine tRNA with the anticodon 3' AAG 5' recognizes not only UUC but also UUU.
- The violation of the usual rules of base pairing at the third nucleotide of a codon is called "wobble"
- The codon **AUG** serves two related functions
  - It begins every message; that is, it signals the **start of translation** placing the amino acid **methionine** at the amino terminal of the polypeptide to be synthesized.
  - When it occurs within a message, it guides the incorporation of methionine.
- Three codons, **UAA**, **UAG**, and **UGA**, act as signals to terminate translation. They are called **STOP** codons.

The Steps of Translation

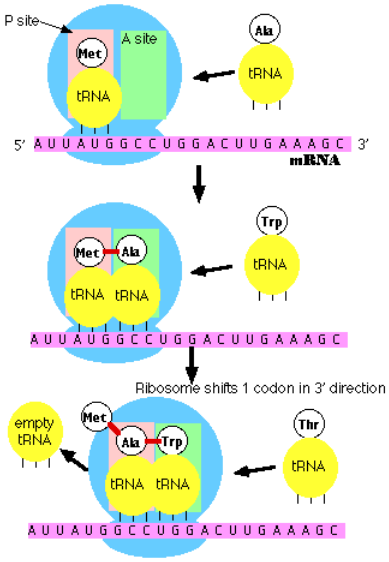


Figure 6.4.2 Translation

Initiation

- The **small subunit** of the ribosome binds to a site "upstream" (on the 5' side) of the start of the message.
- It proceeds downstream (5' -> 3') until it encounters the start codon **AUG**. (The region between the mRNA cap and the AUG is known as the 5'-untranslated region [**5'-UTR**].)
- Here it is joined by the **large subunit** and a special **initiator tRNA**.
- The initiator tRNA binds to the **P site** (shown in pink) on the ribosome.
- In eukaryotes, initiator tRNA carries **methionine** (Met). (Bacteria use a modified methionine designated **fMet**.)

Elongation

- An **aminoacyl-tRNA** (a tRNA covalently bound to its amino acid) able to base pair with the next codon on the mRNA arrives at the **A site** (green) associated with:
  - an **elongation factor** (called EF-Tu in bacteria; EF-1 in eukaryotes)
  - GTP (the source of the needed energy)
- The preceding amino acid (Met at the start of translation) is covalently linked to the incoming amino acid with a peptide bond (shown in red).
- The initiator tRNA is released from the P site.
- The ribosome moves one codon downstream.
- This shifts the more recently-arrived tRNA, with its attached peptide, to the P site and opens the A site for the arrival of a new aminoacyl-tRNA.
- This last step is promoted by another protein **elongation factor** (called EF-G in bacteria; EF-2 in eukaryotes) and the energy of another molecule of **GTP**.

Note: the initiator tRNA is the only member of the tRNA family that can bind directly to the P site. The P site is so-named because, with the exception of initiator tRNA, it binds only to a **p**eptidyl-tRNA molecule; that is, a tRNA with the growing peptide attached.

The A site is so-named because it binds only to the incoming **a**minoacyl-tRNA; that is the tRNA bringing the next amino acid. So, for example, the tRNA that brings Met into the interior of the polypeptide can bind only to the A site.

Termination

- The end of translation occurs when the ribosome reaches one or more **STOP** codons (**UAA**, **UAG**, **UGA**). (The nucleotides from this point to the poly(A) tail make up the 3'-untranslated region [**3'-UTR**] of the mRNA.)
- There are no tRNA molecules with anticodons for STOP codons.
- However, protein **release factors** recognize these codons when they arrive at the A site.

- Binding of these proteins —along with a molecule of **GTP** — releases the polypeptide from the ribosome.
- The ribosome splits into its subunits, which can later be reassembled for another round of protein synthesis.

Polysomes

A single mRNA molecule usually has many ribosomes traveling along it, in various stages of synthesizing the protein. This complex is called a **polysome.**

Codon Bias

All but two of the amino acids (Met and Trp) can be encoded by from 2 to 6 different codons. However, the genome of most organisms reveals that certain codons are preferred over others. In humans, for example, alanine is encoded by GCC four times as often as by GCG. This probably reflects a greater translation efficiency by the translation apparatus for certain codons over their synonyms.

- At the start of translation, two or more of a set of synonymous codons (e.g., the 6 codons that incorporate leucine in the growing protein) are used **alternately**. The need to locate first one and then another tRNA for that amino acid slows down the rate of translation.
  - This may aid in keeping ribosomes from bumping into each other on the polysome.
  - It may also provide more time for the nascent protein to begin to fold correctly as it emerges from the ribosome.
- Once translation is well underway (after 30–50 amino acids have been added), one particular codon tends to be chosen each time its amino acid is called for. Presumably this now increases the efficiency (speed) of translation.
- Most organisms have more than the 61 genes needed to encode a tRNA for each of the 61 codons (we have 270 tRNA genes). The presence of multiple genes for tRNAs with an **identical anticodon** increases the concentration of tRNAs able to bind a particular codon. Messenger RNAs — especially those of active genes — tend to favor codons that correspond to abundant tRNAs carrying the anticodon.

Codon bias even extends to pairs of codons: wherever a human protein contains the amino acids Ala-Glu, the gene encoding those amino acids is seven times as likely to use the codons GCAGAG rather than the synonymous GCCGAA. Codon bias is exploited by the biotechnology industry to improve the yield of the desired product. The ability to manipulate codon bias may also usher in a era of safer vaccines.

Quality Control

Defective mRNA molecules can be produced by mutations in the gene as well as errors introduced during transcription (albeit at a remarkably low rate). In addition to producing mRNAs with incorrect codons for amino acids, these errors can produce mRNA molecules that have

- Premature Termination Codons (PTCs); that is, the introduction of a STOP codon before the normal end of the message. Translation of these mRNAs produces a truncated protein that is probably ineffective and may be harmful. The problem can sometimes be solved by Nonsense-Mediated mRNA Decay (NMD).
- **no** STOP codon. These produce "nonstop" transcripts. The problem can be solved by Nonstop mRNA Decay.

Nonsense-Mediated mRNA Decay (NMD)

Premature termination codons (PTCs) may be generated by "nonsense" mutations, frameshifts, and RNA processing (intron removal) errors. They are also an inevitable consequence of creating antigen receptors on B cells and T cells.

Mechanisms

- During RNA processing within the nucleus, protein complexes are added at each spot where adjacent exons are spliced together. (These are important signals for exporting the mRNA to the cytoplasm.)
- In the cytoplasm, as the ribosome moves down the mRNA, these complexes are removed (and sent back to the nucleus for reuse).
- If the ribosome encounters a premature termination codon, the final exon-exon tag(s) are not removed, and this marks the defective mRNA for destruction (in P bodies).

Mutations that introduce premature termination codons are responsible for some cases of such inherited human diseases as cystic fibrosis and Duchenne muscular dystrophy (DMD).

A drug, designated **PTC124** or ataluren, causes the ribosome to skip over PTCs while still enabling normal termination of translation. PTC124 has shown promise in animal models of cystic fibrosis and DMD and phase II clinical trials are now being conducted on humans.

Nonstop mRNA Decay

Nonstop transcripts occur when there is no STOP codon in the message. As a result the ribosome is unable to recruit the **release factors** needed to leave the mRNA. Nonstop transcripts are formed during RNA processing, e.g., by having the poly(A) tail put on before the STOP codon is reached.

Mechanisms

Eukaryotes and bacteria handle the problem of no STOP codon differently.

- In **eukaryotes**, when the ribosome stalls at the end of the poly(A) tail, **proteins** are recruited to release the ribosome for reuse and to degrade the faulty message.
- In **bacteria**, a special RNA molecule — called **tmRNA** saves the day. It is called tmRNA because it has the properties of both a **t**ransfer RNA and a **m**essenger RNA. The transfer part adds alanine to the A site on the ribosome. The ribosome then moves on to the messenger part which encodes 10 amino acids that target the molecule for destruction (and releases the ribosome for reuse).

Regulation of Translation

The expression of most genes is controlled at the level of their transcription. Transcription factors (proteins) bind to promoters and enhancers turning on (or off) the genes they control. However, gene expression can also be controlled at the level of translation.

By General RNA-Degradation Machinery

P bodies

The cytosol of eukaryotes contains protein complexes that compete with ribosomes for access to mRNAs. As these increase their activity, they sequester mRNAs in larger aggregates called **P bodies** (for "processing bodies", but this processing should not be confused with the processing of pre-mRNA to mature mRNA that occurs in the nucleus).

These protein complexes break down the mRNA by

- removing its "cap"
- removing its poly(A) tail
- degrading the remaining message (nibbling away in the 5' -> 3' direction)

What controls the dynamic balance between ribosomes and P bodies for access to mRNAs remains to be learned. But this mechanism provides for

- destruction of "bad" mRNAs (e.g., those with premature STOP codons
- turnover of mRNAs thus increasing the flexibility of gene expression in the cell

Exosomes

These are hollow macromolecular complexes with two openings. They take in unfolded RNA molecules and degrade them in the 3' -> 5' direction. (In neither structure nor function do these exosomes resemble the exosomes involved in antigen presentation that unfortunately share the same name.)

By MicroRNAs (miRNAs)

Here small RNA molecules bind to a complementary portion in the 3'-UTR of the **mRNA** and prevent it from being translated by ribosomes and/or trigger its destruction. Both these activities take place in P bodies.

By Riboswitches

It turns out that the regulation of the level of certain metabolites is controlled by riboswitches. A riboswitch is a part of a molecule of messenger RNA (mRNA) with a specific binding site for the metabolite (or a close relative).

Examples:

- If thiamine pyrophosphate (the active form of thiamine [vitamin B_1]) is available in the culture medium of *E. coli*,
  - It binds to a messenger RNA whose protein product is an enzyme needed to synthesize thiamine from the ingredients in minimal medium.
  - Binding induces an allosteric shift in the structure of the mRNA so that it can no longer bind to a ribosome and thus cannot be translated into the enzyme.
  - E. coli no longer wastes resources on synthesizing a vitamin that is available preformed.

  A thiamine pyrophosphate riboswitch has also been found in plants, archaea, and Neurospora. The one in Neurospora regulates genes involved in vitamin B_1 metabolism by alternative splicing of their transcripts. (Other riboswitches act on transcription rather than translation
- If vitamin B_{12} is present in the cell, it binds to the mRNA which encodes a protein needed to import the vitamin from the culture medium. This, too, induces an allosteric shift in the mRNA that prevents it from binding a ribosome. *E. coli* no longer wastes resources on synthesizing a transporter for a vitamin that it already has enough of.
- Some Gram-positive bacteria (*E. coli* is Gram-negative) control the level of a sugar needed to synthesize their cell wall with a riboswitch. In this case, as the concentration of the sugar builds up, it binds to the messenger RNA (mRNA) whose product is the enzyme that makes the sugar. This causes the mRNA to self-destruct so production of the enzyme — and thus the sugar — ceases.

It has been suggested that these regulatory mechanisms, which do not involve any protein, are a relict from an "RNA world".

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16.6.3: RNA Splicing

Learning Objectives

- Explain the role of RNA splicing in regulating gene expression

RNA splicing, the first stage of post-transcriptional control

Gene expression is the process that transfers genetic information from a gene made of DNA to a functional gene product made of RNA or protein. Genetic Information flows from DNA to RNA by the process of transcription and then from RNA to protein by the process of translation. In order to ensure that the proper products are produced, gene expression is regulated at many different stages during and in between transcription and translation. In eukaryotes, the gene contains extra sequences that do not code for protein. In these organisms, transcription of DNA produces pre-mRNA. These pre-mRNA transcripts often contain regions, called introns, that are intervening sequences which must be removed prior to translation by the process of splicing. The regions of RNA that code for protein are called exons. Splicing can be regulated so that different mRNAs can contain or lack exons, in a process called alternative splicing. Alternative splicing allows more than one protein to be produced from a gene and is an important regulatory step in determining which functional proteins are produced from gene expression. Thus, splicing is the first stage of post-transcriptional control.

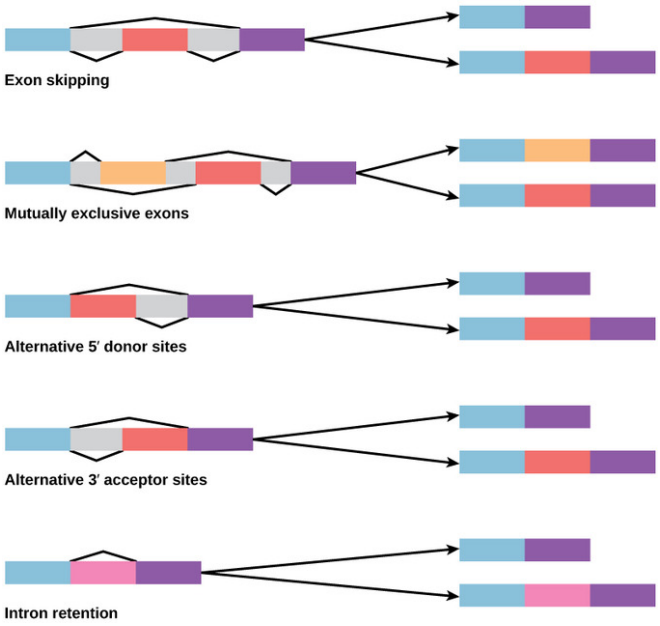


Figure **16.6.3.1**: Alternative Splicing: There are five basic modes of alternative splicing.

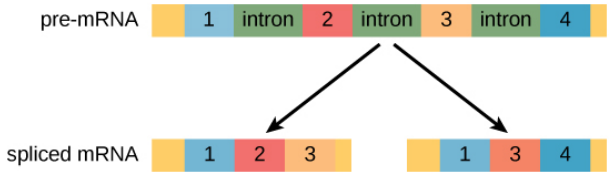


Figure **16.6.3.1**: Alternative Splicing: Pre-mRNA can be alternatively spliced to create different proteins.

Alternative Splicing

Alternative splicing is a process that occurs during gene expression and allows for the production of multiple proteins (protein isoforms) from a single gene coding. Alternative splicing can occur due to the different ways in which an exon can be excluded from or included in the messenger RNA. It can also occur if portions on an exon are excluded/included or if there is an inclusion of introns. For example, if a pre-mRNA has four exons (A, B, C, and D), these can be spliced and translated in a number of different combinations. Exons A, B, and C can be translated together or Exons A, C, and D can be translated. This results in what is called

alternative splicing. The pattern of splicing and production of alternatively-spliced messenger RNA is controlled by the binding of regulatory proteins (trans-acting proteins that contain the genes) to cis-acting sites that are found on the pre-RNA. Some of these regulatory proteins include splicing activators (proteins that promote certain splicing sites) and splicing repressors (proteins that reduce the use of certain sites). Some common splicing repressors include: heterogeneous nuclear ribonucleoprotein (hnRNP) and polypyrimidine tract binding protein (PTB). Proteins that are translated from alternatively-spliced messenger RNAs differ in the sequence of their amino acids which results in altered function of the protein. This is one reason why the human genome can encode a wide diversity of proteins. Alternative splicing is a common process that occurs in eukaryotes; most of the multi-exonic genes in humans are spliced alternatively. Unfortunately, abnormal variations in splicing are also the reason why there are many genetic diseases and disorders.

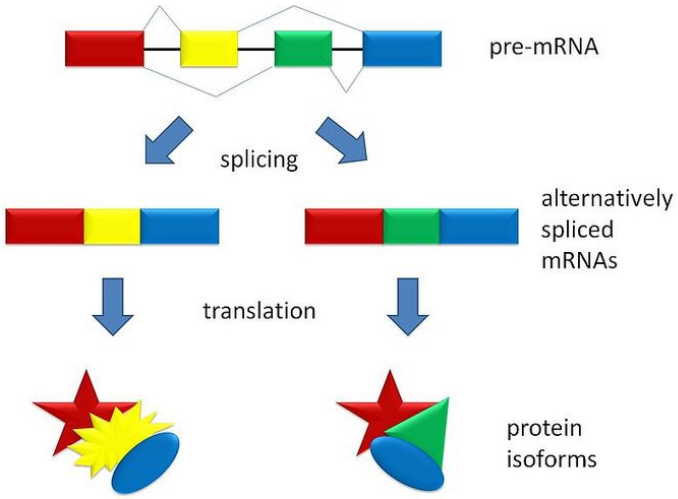


Figure **16.6.3.1**: Mechanism of Splicing: Alternative splicing can result in protein isoforms.

Spliceosome

The splicing of messenger RNA is accomplished and catalyzed by a macro-molecule complex known as the spliceosome. The areas for ligation and cleavage are determined by the many sub-units of the spliceosome which include the branch site (A) and the 5′ and 3′ splice sites. Interactions between these sub-units and the small nuclear ribonucleoproteins (snRNP) found in the spliceosome create a spliceosome A complex which helps determine which introns to leave out and which exons to keep and bind together. Once the introns are cleaved and removed, the exons are joined together by a phosphodiester bond.

Regulatory Proteins

As noted above, splicing is regulated by repressor proteins and activator proteins, which are are also known as trans-acting proteins. Equally as important are the silencers and enhancers that are found on the messenger RNAs, also known as cis-acting sites. These regulatory functions work together in order to create splicing code that determines alternative splicing.

Key Points

- Introns are intervening sequences within a pre-mRNA molecule that do not code for proteins and are removed during RNA processing by a spliceosome.
- Exons are expressing sequences within a pre-mRNA molecule that are spliced together once introns are removed to form mature mRNA molecules that are translated into proteins.
- Alternative splicing allows for the production of various protein isoforms from one single gene coding.
- A spliceosome is a complex comprised of both RNA molecules and proteins which determine which introns to leave out and which exons to keep and bind together.

Key Terms

- **intron**: a portion of a split gene that is included in pre-RNA transcripts but is removed during RNA processing and rapidly degraded
- **exon**: a region of a transcribed gene present in the final functional RNA molecule

- **spliceosome**: a dynamic complex of RNA and protein subunits that removes introns from precursor mRNA

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16.6.4: The Initiation Complex and Translation Rate

Learning Objectives

- Discuss how eukaryotes assemble ribosomes on the mRNA to begin translation

Ribosome Assembly and Translation Rate

Like transcription, translation is controlled by proteins that bind and initiate the process. In translation, before protein synthesis can begin, ribosome assembly has to be completed. This is a multi-step process.

In ribosome assembly, the large and small ribosomal subunits and an initiator tRNA ($tRNA_i$) containing the first amino acid of the final polypeptide chain all come together at the translation start codon on an mRNA to allow translation to begin. First, the small ribosomal subunit binds to the $tRNA_i$ which carries methionine in eukaryotes and archaea and carries N-formyl-methionine in bacteria. (Because the $tRNA_i$ is carrying an amino acid, it is said to be charged.) Next, the small ribosomal subunit with the charged $tRNA_i$ still bound scans along the mRNA strand until it reaches the start codon AUG, which indicates where translation will begin. The start codon also establishes the reading frame for the mRNA strand, which is crucial to synthesizing the correct sequence of amino acids. A shift in the reading frame results in mistranslation of the mRNA. The anticodon on the $tRNA_i$ then binds to the start codon via basepairing. The complex consisting of mRNA, charged $tRNA_i$, and the small ribosomal subunit attaches to the large ribosomal subunit, which completes ribosome assembly. These components are brought together by the help of proteins called initiation factors which bind to the small ribosomal subunit during initiation and are found in all three domains of life. In addition, the cell spends GTP energy to help form the initiation complex. Once ribosome assembly is complete, the charged $tRNA_i$ is positioned in the P site of the ribosome and the empty A site is ready for the next aminoacyl-tRNA. The polypeptide synthesis begins and always proceeds from the N-terminus to the C-terminus, called the N-to-C direction.

In eukaryotes, several eukaryotic initiation factor proteins (eIFs) assist in ribosome assembly. The eukaryotic initiation factor-2 (eIF-2) is active when it binds to guanosine triphosphate (GTP). With GTP bound to it, eIF-2 protein binds to the small 40S ribosomal subunit. Next, the initiatior tRNA charged with methionine (Met-$tRNA_i$) associates with the GTP-eIF-2/40S ribosome complex, and once all these components are bound to each other, they are collectively called the 43S complex.

Eukaryotic initiation factors eIF1, eIF3, eIF4, and eIF5 help bring the 43S complex to the 5′-m^7G cap of an mRNA be translated. Once bound to the mRNA's 5′ m^7G cap, the 43S complex starts travelling down the mRNA until it reaches the initiation AUG codon at the start of the mRNA's reading frame. Sequences around the AUG may help ensure the correct AUG is used as the initiation codon in the mRNA.

Once the 43S complex is at the initiation AUG, the tRNAi-Met is positioned over the AUG. The anticodon on $tRNA_i$-Met basepairs with the AUG codon. At this point, the GTP bound to eIF2 in the 43S complexx is hydrolyzed to GDP + phosphate, and energy is released. This energy is used to release the eIF2 (with GDP bound to it) from the 43S complex, leaving the 40S ribosomal subunit and the $tRNA_i$-Met at the translation start site of the mRNA.

Next, eIF5 with GTP bound binds to the 40S ribosomal subunit complexed to the mRNA and the $tRNA_i$-Met. The eIF5-GTP allows the 60S large ribosomal subunit to bind. Once the 60S ribosomal subunit arrives, eIF5 hydrolyzes its bound GTP to GDP + phosphate, and energy is released. This energy powers assembly of the two ribosomal subunits into the intact 80S ribosome, with tRNAi-Met in its P site while also basepaired to the initiation AUG codon on the mRNA. Translation is ready to begin.

The binding of eIF-2 to the 40S ribosomal subunit is controlled by phosphorylation. If eIF-2 is phosphorylated, it undergoes a conformational change and cannot bind to GTP. Therefore, the 43S complex cannot form properly and translation is impeded. When eIF-2 remains unphosphorylated, it binds the 40S ribosomal subunit and actively translates the protein.

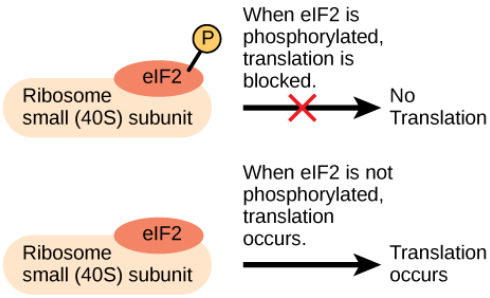


Figure **16.6.4.1**: Translation Initiation Complex: Gene expression can be controlled by factors that bind the translation initiation complex.

The ability to fully assemble the ribosome directly affects the rate at which translation occurs. But protein synthesis is regulated at various other levels as well, including mRNA synthesis, tRNA synthesis, rRNA synthesis, and eukaryotic initiation factor synthesis. Alteration in any of these components affects the rate at which translation can occur.

Key Points

- The components involved in ribosome assembly are brought together by the help of proteins called initiation factors which bind to the small ribosomal subunit.
- Initiator tRNA is used to locate the start codon AUG (the amino acid methionine) which establishes the reading frame for the mRNA strand.
- GTP carried by eIF2 is the energy source used for loading the initiator tRNA carried by the small ribosomal subunit on the correct start codon in the mRNA.
- GTP carried by eIF5 is the energy source for assembling the large and small ribosomal subunits together.

Key Terms

- **reading frame**: either of three possible triplets of codons in which a DNA sequence could be transcribed
- **phosphorylation**: the addition of a phosphate group to a compound; often catalyzed by enzymes

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16.6.5: Regulating Protein Activity and Longevity

Learning Objectives

- Explain how chemical modifications affect protein activity and longevity

Chemical Modifications, Protein Activity, and Longevity

Proteins can be chemically modified with the addition of methyl, phosphate, acetyl, and ubiquitin groups. The addition or removal of these groups from proteins regulates their activity or the length of time they exist in the cell. Sometimes these modifications can regulate where a protein is found in the cell; for example, in the nucleus, the cytoplasm, or attached to the plasma membrane.

Chemical modifications occur in response to external stimuli such as stress, the lack of nutrients, heat, or ultraviolet light exposure. These changes can alter protein function, epigenetic accessibility, transcription, mRNA stability, or translation; all resulting in changes in expression of various genes. This is an efficient way for the cell to rapidly change the abundance levels of specific proteins in response to the environment. Because proteins are involved in every stage of gene regulation, the phosphorylation of a protein (depending on the protein that is modified) can alter accessibility to the chromosome, can alter translation (by altering transcription factor binding or function), can change nuclear shuttling (by influencing modifications to the nuclear pore complex), can alter RNA stability (by binding or not binding to the RNA to regulate its stability), can modify translation (increase or decrease), or can change post-translational modifications (add or remove phosphates or other chemical modifications). All of these protein activities are affected by the phosphorylation process. The enzymes which are responsible for phosphorylation are known as protein kinases. The addition of a phosphate group to a protein can result in either activation or deactivation; it is protein dependent.

Another example of chemical modifications affecting protein activity include the addition or removal of methyl groups. Methyl groups are added to proteins via the process of methylation; this is the most common form of post-translational modification. The addition of methyl groups to a protein can result in protein-protein interactions that allows for transcriptional regulation, response to stress, protein repair, nuclear transport, and even differentiation processes. Methylation on side chain nitrogens is considered largely irreversible while methylation of the carboxyl groups is potentially reversible. Methylation in the proteins negates the negative charge on it and increases the hydrophobicity of the protein. Methylation on carboxylate side chains covers up a negative charge and adds hydrophobicity. The addition of this chemical group changes the property of the protein and, thus, affects it activity.

The addition of an ubiquitin group to a protein marks that protein for degradation. Ubiquitin acts like a flag indicating that the protein lifespan is complete. These proteins are moved to the proteasome, an organelle that functions to remove proteins to be degraded. One way to control gene expression is to alter the longevity of the protein: ubiquitination shortens a protein's lifespan.

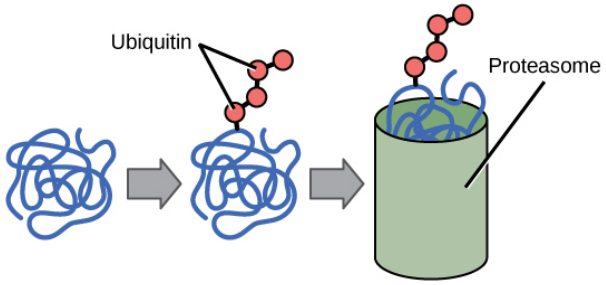


Figure **16.6.5.1**: Ubiquitin Tags: Proteins with ubiquitin tags are marked for degradation within the proteasome.

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Key Points

- Proteins can be chemically modified by adding methyl, phosphate, acetyl, and ubiquitin groups.
- Protein longevity can be affected by altering stages of gene regulation, including but not limited to altering: accessibility to chromosomal DNA for transcription, rate of translation, nuclear shuttling, RNA stability, and post-translational modifications.
- Ubiquitin is added to a protein to mark it for degradation by the proteasome.

Key Terms

- **ubiquitin**: a small polypeptide present in the cells of all eukaryotes; it plays a part in modifying and degrading proteins
- **proteasome**: a complex protein, found in bacterial, archaeal and eukaryotic cells, that breaks down other proteins via proteolysis

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16.7: Regulating Protein Activity and Longevity

Learning Objectives

- Explain how chemical modifications affect protein activity and longevity

Chemical Modifications, Protein Activity, and Longevity

Proteins can be chemically modified with the addition of methyl, phosphate, acetyl, and ubiquitin groups. The addition or removal of these groups from proteins regulates their activity or the length of time they exist in the cell. Sometimes these modifications can regulate where a protein is found in the cell; for example, in the nucleus, the cytoplasm, or attached to the plasma membrane.

Chemical modifications occur in response to external stimuli such as stress, the lack of nutrients, heat, or ultraviolet light exposure. These changes can alter protein function, epigenetic accessibility, transcription, mRNA stability, or translation; all resulting in changes in expression of various genes. This is an efficient way for the cell to rapidly change the abundance levels of specific proteins in response to the environment. Because proteins are involved in every stage of gene regulation, the phosphorylation of a protein (depending on the protein that is modified) can alter accessibility to the chromosome, can alter translation (by altering transcription factor binding or function), can change nuclear shuttling (by influencing modifications to the nuclear pore complex), can alter RNA stability (by binding or not binding to the RNA to regulate its stability), can modify translation (increase or decrease), or can change post-translational modifications (add or remove phosphates or other chemical modifications). All of these protein activities are affected by the phosphorylation process. The enzymes which are responsible for phosphorylation are known as protein kinases. The addition of a phosphate group to a protein can result in either activation or deactivation; it is protein dependent.

Another example of chemical modifications affecting protein activity include the addition or removal of methyl groups. Methyl groups are added to proteins via the process of methylation; this is the most common form of post-translational modification. The addition of methyl groups to a protein can result in protein-protein interactions that allows for transcriptional regulation, response to stress, protein repair, nuclear transport, and even differentiation processes. Methylation on side chain nitrogens is considered largely irreversible while methylation of the carboxyl groups is potentially reversible. Methylation in the proteins negates the negative charge on it and increases the hydrophobicity of the protein. Methylation on carboxylate side chains covers up a negative charge and adds hydrophobicity. The addition of this chemical group changes the property of the protein and, thus, affects it activity.

The addition of an ubiquitin group to a protein marks that protein for degradation. Ubiquitin acts like a flag indicating that the protein lifespan is complete. These proteins are moved to the proteasome, an organelle that functions to remove proteins to be degraded. One way to control gene expression is to alter the longevity of the protein: ubiquitination shortens a protein's lifespan.

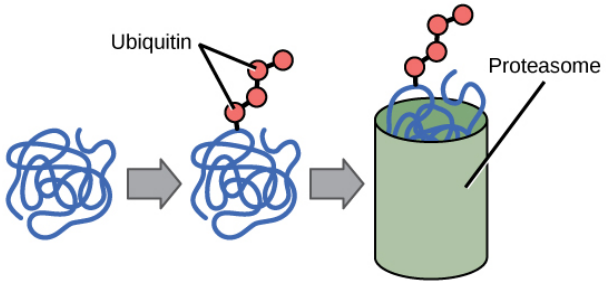


Figure **16.7.1**: Ubiquitin Tags: Proteins with ubiquitin tags are marked for degradation within the proteasome.

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17.6.5: Gene Therapy

17.7: Agricultural Applications

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SECTION OVERVIEW

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17.1.1: Overview of Recombinant DNA Technology

Recombinant DNA technology utilizes the power of microbiological selection and screening procedures to allow investigators to isolate a gene that represents as little as 1 part in a million of the genetic material in an organism. The DNA from the organism of interest is divided into small pieces that are then placed into individual cells (usually bacterial). These can then be separated as individual colonies on plates, and they can be screened through rapidly to find the gene of interest. This process is called **molecular cloning**.

Joining DNA in vitro to form recombinant molecules

Restriction endonucleasescut at defined sequences of (usually) 4 or 6 bp. This allows the DNA of interest to be cut at specific locations. The physiological function of restriction endonucleases is to serve as part of system to protect bacteria from invasion by viruses or other organisms. (See Chapter 7)

Table 3.1. List of restriction endonucleases and their cleavage sites. A ' means that the nuclease cuts between these 2 nucleotides to generate a 3' hydroxyl and a 5' phosphate.

Enzyme	Site		Enzyme	Site
*Alu*I	AG'CT		*Not*I	GC'GGCCGC
*Bam*HI	G'GATCC		*Pst*I	CTGCA'G
*Bgl*II	A'GATCT		*Pvu*II	CAG'CTG
*Eco*RI	G'AATTC		*Sal*I	G'TCGAC
*Hae*III	GG'CC		*Sau*3AI	'GATC
*Hha*I	GCG'C		*Sma*I	CCC'GGG
*Hinc*II	GTY'RAC		*Spe*I	A'CTAGT
*Hind*III	A'AGCTT		*Taq*I	T'CGA
*Hin*fI	G'ANTC		*Xba*I	T'CTAGA
*Hpa*II	C'CGG		*Xho*I	C'TCGAG
*Kpn*I	GGTAC'C		*Xma*I	C'CCGGG
*Mbo*I	'GATC			

N = A,G,C or T

R = A or G

Y = C or T

S = G or C

W = A or T

a. Sticky ends

(1) Since the recognition sequences for restriction endonucleases are pseudopalindromes, an off-center cleavage in the recognition site will generate either a 5' overhang or a 3' overhang with self-complementary (or "sticky") ends.

e.g. 5' overhang EcoRI G'AATTC

BamHI G'GATCC

3' overhangPstI CTGCA'G

(2) When the ends of the restriction fragments are complementary,

e.g. for EcoRI 5'---G AATTC---3'

3'---CTTAA G---5'

the ends can anneal to each other. **Any two fragments, regardless of their origin (animal, plant, fungal, bacterial) can be joined in vitro to form recombinant molecules** (Figure 3.3)**.**

Figure 3.3.

b. Blunt ends

(1) The restriction endonuclease cleaves in the center of the pseudopalindromic recognition site to generate blunt (or flush) ends.

(2) E.g. HaeIII GG'CC

HincII GTY'RAC

T4 DNA ligase is used to tie together fragments of DNA (Figure 3.4). Note that the annealed "sticky" ends of restriction fragments have **nicks**(usually 4 bp apart). Nicks are breaks in the phosphodiester backbone, but all nucleotides are present. **Gaps**in one strand are missing a string of nucleotides.

T4 DNA ligase uses ATP as source of adenylyl group attached to 5' end of the nick, which is a good leaving group after attack by the 3' OH. (See Chapter 5 on Replication).

At high concentration of DNA ends and of ligase, the enzyme can also ligate together blunt-ended DNA fragments. Thus any two blunt-ended fragments can be ligated together. Note: Any fragment with a 5' overhang can be readily converted to a blunt-ended molecule by fill-in synthesis catalyzed by a DNA polymerase (often the Klenow fragment of DNA polymerase I). Then it can be ligated to another blunt-ended fragment.

Figure 3.4

Linkers are short duplex oligonucleotides that contain a restriction endonuclease cleavage site. They can be ligated onto any blunt-ended molecule, thereby generating a new restriction cleavage site on the ends of the molecule. Ligation of a linker on a restriction fragment followed by cleavage with the restriction endonuclease is one of several ways to generate an end that is easy to ligate to another DNA fragment.

Annealing of **homopolymer tails** are another way to joint two different DNA molecules.

The enzyme **terminal deoxynucleotidyl transferase**will catalyze the addition of a string of nucleotides to the 3' end of a DNA fragment. Thus by incubating each DNA fragment with the appropriate dNTP and terminal deoxynucleotidyl transferase, one can add complementary homopolymers to the ends of the DNAs that one wants to combine. E.g., one can add a string of G's to the 3' ends of one fragment and a string of C's to the 3' ends of the other fragment. Now the two fragments will join together via the homopolymer tails.

Figure 3.5. Use of linkers (left) and homopolymer tails (right) to make recombinant DNA molecules.

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17.1.2: Introduction of recombinant DNA into cell and replication- Vectors

Vectors used to move DNA between species, or from the lab bench into a living cell, must meet three requirements (Figure **17.1.2.1**):

1. They must be **autonomously replicating** DNA molecules in the host cell. The most common vectors are designed for replicating in bacteria or yeast, but there are vectors for plants, animals and other species.
2. They must contain a **selectable marker** so cells containing the recombinant DNA can be distinguished from those that do not. An example is drug resistance in bacteria.
3. They must have an **insertion site** to accommodate foreign DNA. Usually a unique restriction cleavage site in a nonessential region of the vector DNA. Later generation vectors have a set of about 15 or more unique restriction cleavage sites.

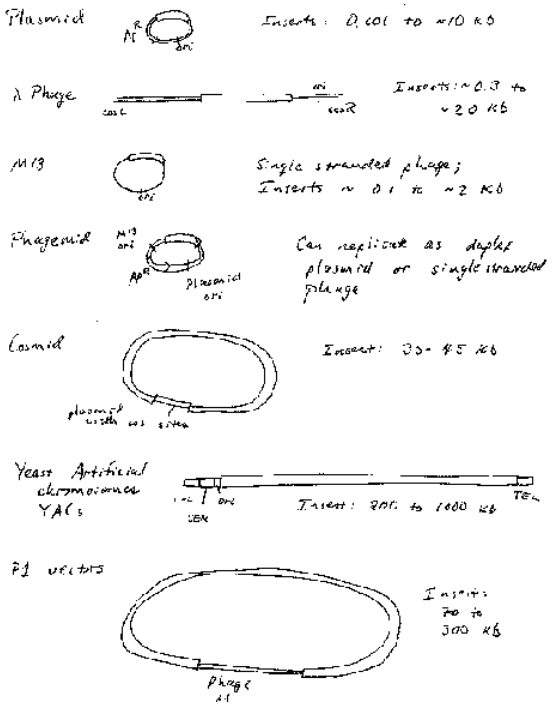


Figure **17.1.2.1**: Summary of vectors for molecular cloning

Plasmid Vectors

Plasmids are autonomously replicating circular DNA molecules found in bacteria. They have their own origin of replication, and they replicate independently of the origins on the "host" chromosome. Replication is usually dependent on host functions, such as DNA polymerases, but regulation of plasmid replication is distinct from that of the host chromosome. Plamsids, such as the *sex-factor F*, can be very large (94 kb), but others can be small (2-4 kb). Plasmids do not encode an essential function to the bacterium, which distinguishes them from chromosomes. Plasmids can be present in a single copy, such as F, or in multiple copies, like those used as most cloning vectors, such as pBR322, pUC, and pBluescript.

In nature, plasmids provide carry some useful function, such as transfer (F), or antibiotic resistance. This is what keeps the plasmids in a population. In the absence of selection, plasmids are lost from bacteria. The antibiotic resistance genes on plasmids are often carried within, or are derived from, transposons, a types of transposable element. These are DNA segments that are capable of "jumping" or moving to new locations (Chapter 9).

A plasmid that was widely used in many recombinant DNA projects is pBR322 (Figure **17.1.2.2**). It replicates from an origin derived from a colicin-resistance plasmid (ColE1). This origin allows a fairly high copy number, about 100 copies of the plasmid per cell. Plasmid pBR322 carries two antibiotic resistance genes, each derived from different transposons. These transposons were initially found in R-factors, which are larger plasmids that confer antibiotic resistance.

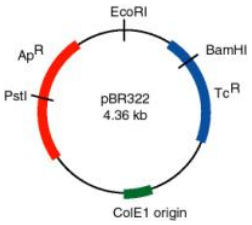


Figure 17.1.2.2: Features of plasmid pBR322. The gene conferring resistance to ampicillin (ApR) can be interrupted by insertion of a DNA fragment into the PstI site, and the gene conferring resistance to tetracycline (TcR) can be interrupted by insertion of a DNA fragment into the BamHI site. Replication is controlled by the ColE1 origin.

Use of the TcR and ApR genes allows for easy screening for recombinants carrying inserts of foreign DNA. For instance, insertion of a restriction fragment in the *Bam*HI site of the TcR gene inactivates that gene. One can still select for ApR colonies, and then screen to see which ones have lost TcR .

Exercise 17.1.2.1

What effects on drug resistance are seen when you use the *Eco*RI or *Pst*I sites in pBR322 for inserting foreign DNA?

A generation of vectors developed after pBR322 are designed for even more efficient **screening for recombinant plasmids**, i.e. those that have foreign DNA inserted. The **pUC** plasmids (named for plasmid universal cloning) and plasmids derived from them use a rapid screen for inactivation of the b-galactosidase gene to identify recombinants (Figure 17.1.2.3).

One can screen for production of functional **b-galactosidase** in a cell by using the chromogenic substrate **X-gal** (a halogenated indoyl b-galactoside). When cleaved by b-galactosidase, the halogenated indoyl compound is liberated and forms a blue precipitate. The pUC vector has the b-galactosidase gene {actually only part of it, but enough to form a functional enzyme with the rest of the gene that is encoded either on the E. coli chromosome or an F' factor}. When introduced into *E. coli*, the colonies are **blue** on plates containing X-gal.

The **multiple cloning sites** (unique restriction sites) are in the b-galactosidase gene (lacZ). When a restriction fragment is introduced into one or more of these sites, the b-galactosidase activity is lost by this insertional mutation. Thus cells containing recombinant plasmids form **white**(not blue) colonies on plates containing X-gal.

The replication origin is a modified ColE1 origin of replication that has been mutated to eliminate a negative control region. Hence the **copy number is very high**(several hundred or more plasmid molecules per cell), and one obtains an very high yield of plasmid DNA from cultures of transformed bacteria. The plasmid has ApR as a selectable marker.

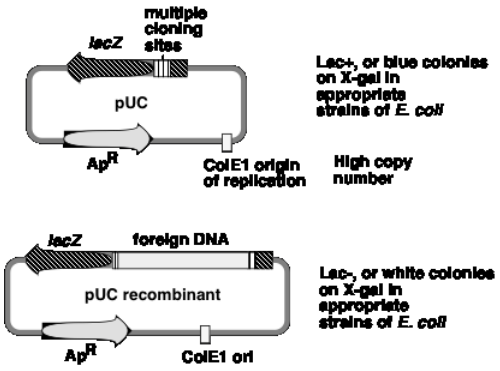


Figure 17.1.2.3: pUC-type vectors

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17.1.3: Introducting Recombinant DNA into Host Cells

Transformation in *E. coli*

E. coli does not have a natural system for taking up DNA, but when treated with $CaCl_2$, the cells will take up the added DNA (Figure **17.1.3.1**). The recombinant vectors will give a new phenotype to the cells (usually drug resistance), so this process can be considered **DNA-mediated transformation**. An average efficiency is about 10^6 transformants per mg of DNA, although some more elaborate transformation cocktails procedures can give up to about 10^8 transformants per mg of DNA.

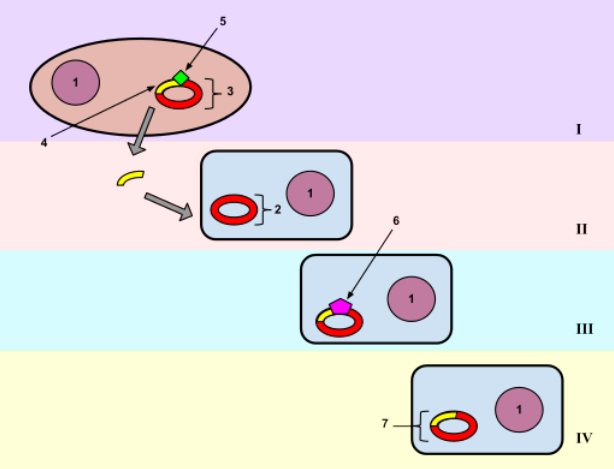


Figure **17.1.3.1**: DNA-mediated transformation of E. coli. A gene from bacterial cell 1 is moved from bacterial cell 1 to bacterial cell 2. This process of bacterial cell 2 taking up new genetic material is called transformation. Step I: The DNA of a bacterial cell is located in the cytoplasm (1), but also in the plasmid, an independent, circular loop of DNA. The gene to be transferred (4) is located on the plasmid of cell 1 (3), but not on the plasmid of bacterial cell 2 (2). In order to remove the gene from the plasmid of bacterial cell 1, a restriction enzyme (5) is used. The restriction enzyme binds to a specific site on the DNA and "cuts" it, releasing the satisfactory gene. Genes are naturally removed and released into the environment usually after a cell dies and disintegrates. Step II: Bacterial cell 2 takes up the gene. This integration of genetic material from the environment is an evolutionary tool and is common in bacterial cells. Step III: The enzyme DNA ligase (6) adds the gene to the plasmid of bacterial cell 2 by forming chemical bonds between the two segments which join them together. Step IV: The plasmid of bacterial cell 2 now contains the gene from bacterial cell 1 (7). The gene has been transferred from one bacterial cell to another, and transformation is complete. (CC BY_SA 3.0; Sprovenzano15)

Usually one will transform with a mixture of recombinant vector molecules, most of which carry a different restriction fragment. Each transformed E. coli cell will pick up only **one** plasmid molecule, so the complex mixture of plasmids in the ligation mix has been separated into a population of transformed bacteria (Figre **17.1.3.1**). The bacterial cells are then plated at a sufficiently low density that individual colonies can be identified. Each colony (or transformant) carries a single plasmid, so as one screens the colonies, one is actually screening through individual DNA molecules. A colony is a visible group of bacterial cells on a plate, all of which are derived from a single bacterial cell. A group of identical cells derived from a single cell is called a **clone**. Since each clone carries a single type of recombinant DNA molecule, the process is called **molecular cloning**.

Phage Vectors

Phase vectors are a more efficient introduction of DNA into bacteria. Phage vectors such as those derived from bacteriophage l can carry **larger inserts** and can be **introduced into bacteria more efficiently**. l phage has a duplex DNA genome of about 50 kb. The internal 20 kb can be replaced with foreign DNA and still retain the lytic functions. Hence restriction fragments up to 20 kb can replace the l sequences, allowing larger genomic DNA fragments to be cloned (Figure **17.1.3.2**).

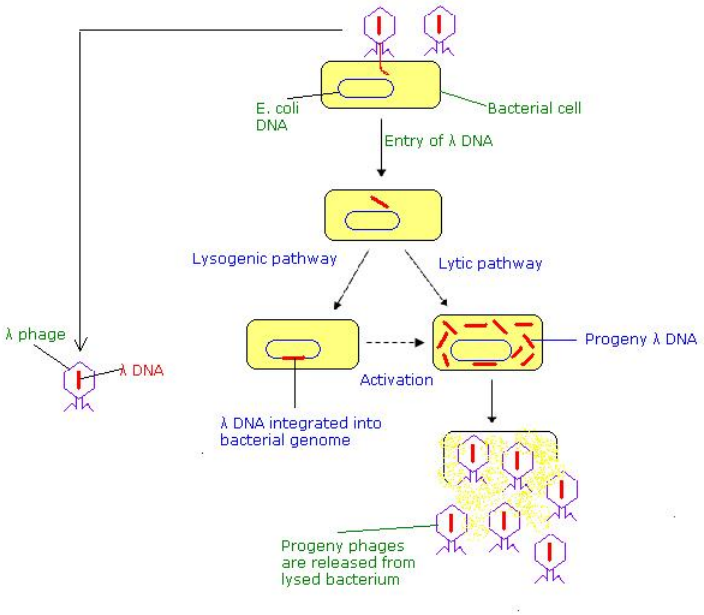


Figure 17.1.3.2: Lambda vectors for cloning. (public Domain; Tinastella).

Recombinant bacteriophage can be introduction into *E. coli* by **infection**. DNA that has the cohesive ends of l can be packaged in vitro into infective phage particles. Being in a viral particle brings the efficiency of infection reliably over 108 plaque forming units per mg of recombinant DNA.

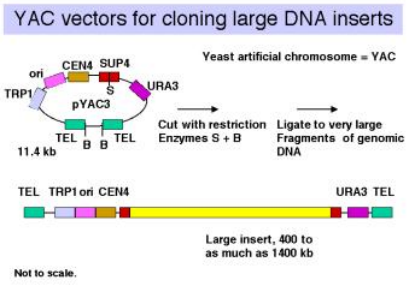
Some other bacteriphage vectors for cloning are derived from the virus M13. One can obtain **single stranded DNA** from M13 vectors and recombinants. M13 is a virus with a genome of single stranded DNA. It has a nonessential region into which foreign genes can be inserted. It has been modified to carry a gene for b-galactosidase as a way to screen for recombinants. Introduction of recombinant M13 DNA into E. coli will lead to an infection of the host, and the progeny viral particles will contain single-stranded DNA. The replicative form is duplex, allowing one to cleave with restriction enzymes and insert foreign DNA.

Some vectors are hybrids between plasmids and single-strand phage; these are called **phagemids**. One example is pBluescript. Phagemids are plasmids (with the modified, high-copy number ColE1 origin) that also have an M13 origin of replication. Infection of transformed bacteria (containing the phagemid) with a helper virus (e.g. derived from M13) will cause the M13 origin to be activated, and progeny viruses carrying single-stranded copies of the phagemid can be obtained. Hence one can easily obtain either double- or single-stranded forms of thes plasmids. {The "blue" comes from the blue-white screening for recombinants that can be done when the multiple cloning sites are in the b-galactosidase gene. The "script" refers to the ability to make RNA copies of either strand in vitro with phage RNA polymerases.}

Vectors Designed to Carry Larger Inserts

Fragments even larger than those carried in l vectors are useful for studies of longer segments of chromosomes or whole genomes. Several vectors have been designed for cloning these very large fragments, 50 to 400 kb.

- **Cosmids** are plasmids that have the cohesive ends of l phage. They can be packaged in vitro into infective phage particles to give a more efficient delivery of the DNA into the cells. They can carry about 35 to 45 kb inserts.
- **Yeast artificial chromosomes** (**YACs**) are yeast vectors with centromeres and telomeres. They can carry about 200 kb or larger fragments (in principle up to 1000 kb = 1 Mb). Thus very large fragments of DNA can be cloned in yeast (Figure 17.1.3.3). In practice, chimeric clones with fragments from different regions of the genome are obtained fairly often, and some of the inserts are unstable.



,

Figure **17.1.3.3**

Vectors derived from bacteriophage **P1** can carry fragments of about 100 kb. Fragments in a similar size range are also cloned into **bacterial artificial chromosomes** (**BACs**), which are derived from the F-factor (Figure **17.1.3.4**). These have a lower copy number (like F) but they are stable and relatively easy to work with in the laboratory. BACs have become one of the most frequently used vectors for large inserts in genome projects.

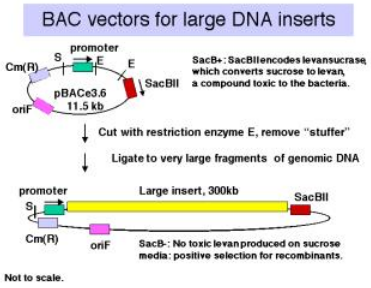


Figure **17.1.3.4**

Shuttle vectors for testing functions of isolated genes

Shuttle vectors can replicate in two different organisms, e.g. bacteria and yeast, or mammalian cells and bacteria. They have the appropriate origins of replication. Hence one can, e.g. clone a gene in bacteria, maybe modify it or mutate it in bacteria, and test its function by introducing it into yeast or animal cells.

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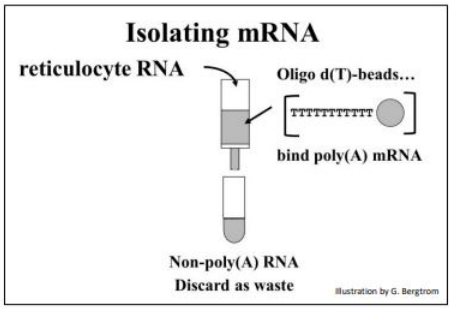
17.1.4: Make and Screen a cDNA Library

The first step in making a cDNA library is to isolate cellular mRNA. This mRNA extract should represent all of the transcripts in the cells at the time of isolation, or the cell's **transcriptome**. This term is used by analogy to genome. However, a genome is all of the genetic information of an organism. In contrast, a transcriptome (usually eukaryotic) reflects all of the genes expressed in a given cell type at a moment in time. Reversetranscribed cDNAs from an mRNA extract are also referred to as a transcriptome…, and likewise, a cDNA library. A cDNA library is a tube full of bacterial cells that have taken up (i.e., been **transformed** with) plasmids recombined with cDNAs. cDNA libraries made from mRNAs taken from different cell types or the same cells grown under different conditions are in effect, different transcriptomes. Each reflects mRNAs transcribed in cells at the moment of their extraction. When cells in a cDNA library are spread out on a nutrient agar petri dish, each cell grows into a colony of cells; each cell in the colony is a clone of a starting cell. cDNA libraries can be used isolate and sequence the DNA encoding a polypeptide that you are studying.

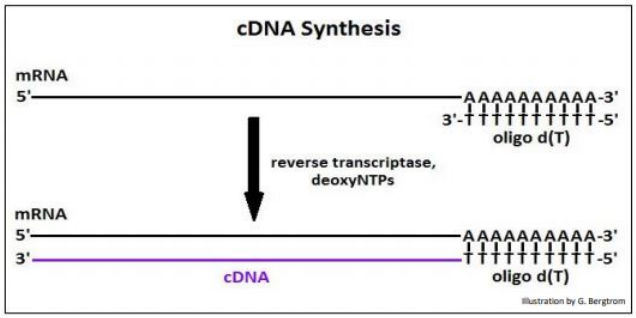
Recall that the mature mRNA in eukaryotic cells has been spliced. This means that cDNAs from eukaryotic cells do not include introns. Introns, as well as sequences of enhancers and other regulatory elements in and surrounding a gene must be studied in genomic libraries, to be discussed later. Here we look at how to make a cDNA library.

A. cDNA Construction

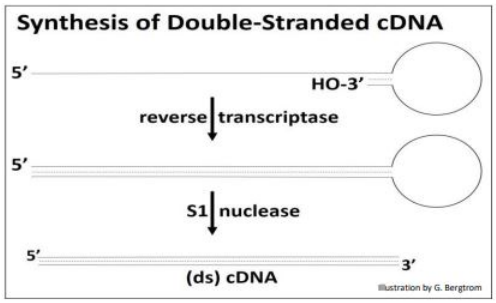
mRNA is only a few percent of a eukaryotic cell; most is rRNA. But that small amount of mRNA can be separated from other cellular RNAs by virtue of their 3' poly(A) tails. Simply pass a total RNA extract over an **oligo-d(T) column** (illustrated below).



The strings of thymidine (T) can H-bond with the poly(A) tails of mRNAs, tethering them to the column. All RNAs without a 3' poly(A) tail will flow through the column as waste. A second buffer is passed over the column to destabilize the A-T H-bonds to allow **elution** of an mRNA fraction. When free' oligo d(T) is added to the eluted mRNA, it forms H-bonds with the poly(A) tails of the mRNAs, serving as a primer for the synthesis of cDNA copies of the poly(A) mRNAs originally in the cells. Finally, four deoxynucleotide DNA precursors and **reverse transcriptase** (originally isolated from chicken retrovirus-infected cells) are added to start reverse transcription. The synthesis of a cDNA strand complementary to an mRNA is shown below.



After heating to separate the cDNAs from the mRNAs, the cDNA is replicated to produce double-stranded, or (ds)cDNA, as illustrated below.



Synthesis of the second cDNA strand is also catalyzed by reverse transcriptase! The enzyme recognizes DNA as well as RNA templates, and has the same 5'-to-3' DNA polymerizing activity as DNA polymerases. After 2nd cDNA strand synthesis, **S1 nuclease** (a *single-stranded endonuclease* originally isolated from an East Asian fungus!) is added to open the loop of the (ds) cDNA structure and trim the rest of the single-stranded DNA. What remains is the (ds) cDNA.

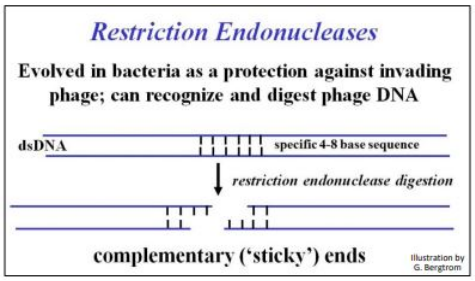
258 Isolate mRNA and Make cDNA

259 Reverse Transcriptase

B. Cloning cDNAs into Plasmid Vectors

To understand cDNA cloning and other aspects of making recombinant DNA, we need to talk a bit more about the recombinant DNA tool kit. In addition to *reverse transcriptase* and S1 nuclease, other necessary enzymes in the 'kit' include **restriction endonucleases** (*restriction enzymes*) and **DNA ligase**. The natural function of restriction enzymes in bacteria is to recognize specific restriction site sequences in phage DNA (most often **palindromic** DNA sequences), hydrolyze it and thus avoid infection.

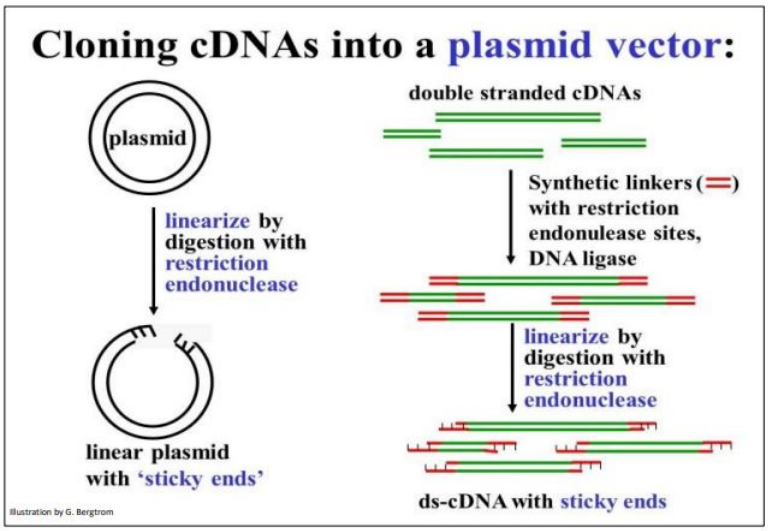
Restriction enzymes that make a scissors cut through the two strands of the double helix leaves *blunt ends*. Restriction enzymes that make a staggered cut on each strand at their restriction site leave behind *complementary* ('sticky') ends (below).



If you mix two of double-stranded DNA fragments with the same sticky ends from different sources (e.g., different species), they will form H-bonds at their complementary ends, making it easy to recombine plasmid DNA with (ds)cDNA, that have the same complementary 'sticky ends'. Using the language of recombinant DNA technologies, let's look at how plasmid vectors and cDNAs can be made to recombine.

1. Preparing Recombinant Plasmid Vectors Containing cDNA Inserts

Vectors are *carrier* DNAs engineered to recombine with foreign DNAs of interest. When a recombinant vector with its foreign **DNA insert** gets into a host cell, it can replicate many copies of itself, enough in fact for easy isolation and study. cDNAs are typically inserted into plasmid vectors that are usually purchased "off-the-shelf". They can be *cut* with a restriction enzyme at a suitable location, leaving those sticky ends. On the other hand, it would not do to digest (ds)cDNA with restriction endonucleases since the goal is not to clone cDNA fragments, but entire cDNA molecules. Therefore, it will be necessary to attach **linkers** to either end of the (ds)cDNAs. Plasmid DNAs and cDNA-linker constructs can then be digested with the same restriction enzyme to produce compatible 'sticky ends'. Steps in the preparation of vector and (ds)cDNA for recombination are shown below.

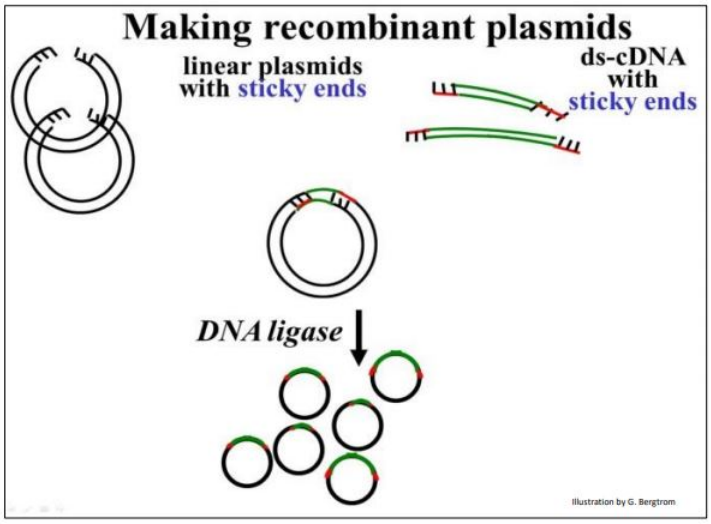


To prepare for recombination, a plasmid vector is digested with a **restriction enzyme** to open the DNA circle. To have compatible *sticky ends*, double-stranded cDNAs to be inserted are mixed with *linkers* and **DNA ligase** to put a linker DNA at both ends of the (ds) cDNA. DNA ligase is another tool in the recombinant DNA toolkit. Linkers are short, synthetic double-stranded DNA oligomers containing restriction sites recognized and cut by the same restriction enzyme as the plasmid. Once the linkers are attached to the ends of the plasmid DNAs, they are digested with the appropriate restriction enzyme. This leaves both the (ds)cDNAs and the plasmid vectors with complementary sticky ends.

260 Restriction Enzymes and Recombinant DNA

2. Recombining Plasmids and cDNA Inserts and Transforming Host Cells

The next step is to mix the cut plasmids with the digested linker-cDNAs in just the right proportions so that the most of the cDNA (linker) ends will anneal (form Hbonds) with the most of the sticky plasmid ends. Adding **DNA ligase** to the plasmid/linker-cDNA mixture forms phosphodiester bonds between plasmid and cDNA insert, completing the recombinant circle of DNA, as shown below.

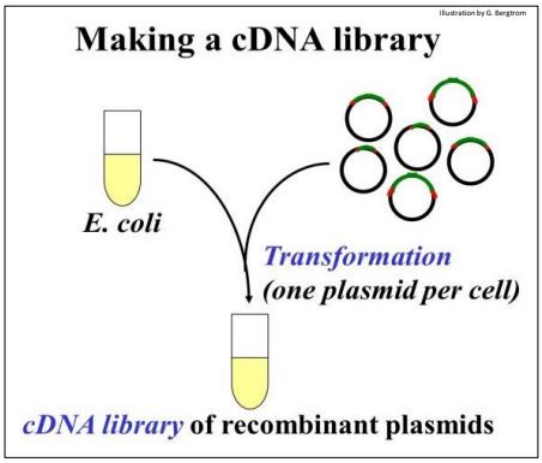


In early cloning experiments, an important consideration was to generate plasmids with only one copy of a given cDNA insert, rather than lots of re-ligated plasmids with no inserts or lots of plasmids with multiple inserts. Using betterengineered vector and linker combinations, this issue became less important.

261 Recombine a cDNA Insert with a Plasmid Vector

3. Transforming Host Cells with Recombinant Plasmids

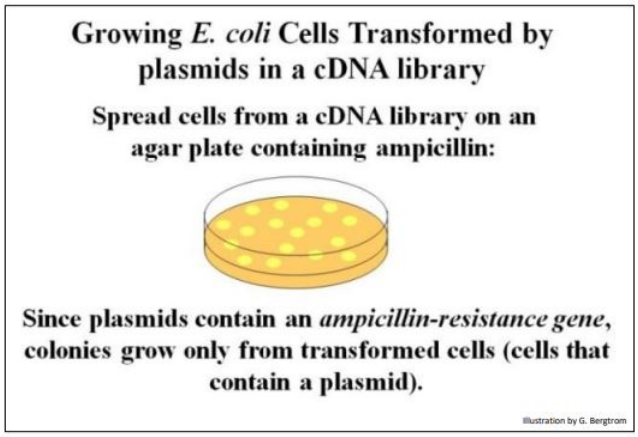
The recombinant DNA molecules are now ready for 'cloning'. They are added to E. coli (sometimes other host cells) *made permeable* so that they can be easily **transformed**. Recall that transformation as defined by Griffith is bacterial uptake of foreign DNA leading to a genetic change. The **transforming principle** in cloning is the recombinant plasmid! The transformation step is shown below.



The tube full of transformed cells is the **cDNA Library.**

262 Making the cDNA Library.

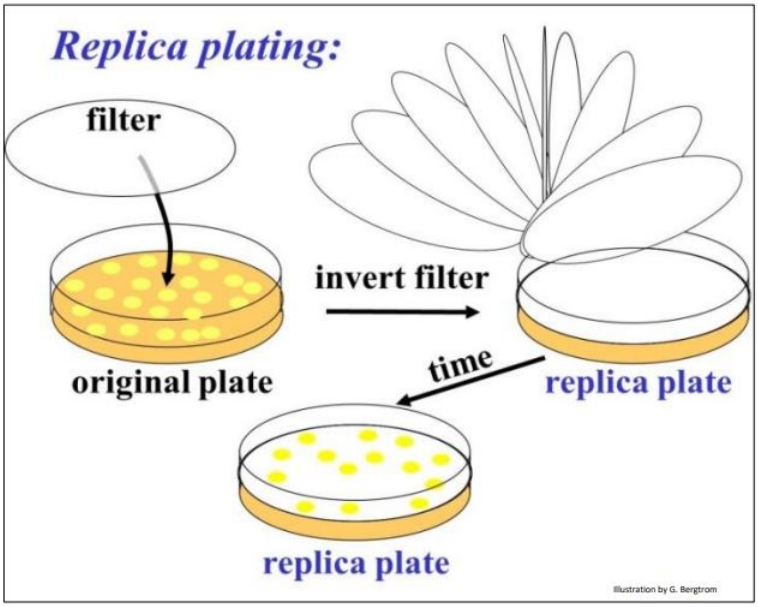
After all these treatments, not all plasmid molecules in the mix are recombinant; some cells in the mix haven't even taken up a plasmid. So when the recombinant cells are plated on agar, how do you tell which of the colonies that grow came from cells that took up a recombinant plasmid? Both the **host strain** of *E. coli* and plasmid vectors used these days were further engineered to solve this problem. One such plasmid vector carries an **antibiotic resistance gene**. In this case, ampicillin-sensitive cells would be transformed with recombinant plasmids containing the *resistance gene*. When these cells are plated on media containing **ampicillin** (a form of penicillin), they grow, as illustrated below.



Untransformed cells (cells that failed to take up a plasmid) lack the ampicillin resistance gene and thus, do not grow on ampicillin-medium. But, there is still a question. How can you tell whether the cells that grew were transformed by a recombinant plasmid containing a cDNA insert? It is possible that some of the transformants contain only non-recombinant plasmids that still have the ampicillin resistance gene!

To address this question, plasmids were further engineered with a **streptomycin resistance gene**. But this antibiotic resistance gene was also engineered to contain restriction enzyme sites in the middle of the gene. Thus, inserting a cDNA in this plasmid would disrupt and inactivate the gene. Here is how this second bit of genetic engineering enabled growth only of cells transformed with a

recombinant plasmid containing a cDNA insert. We can tell *transformants* containing recombinant plasmids apart from those containing non-recombinant plasmids by the technique of **replica plating** shown (illustrated below).

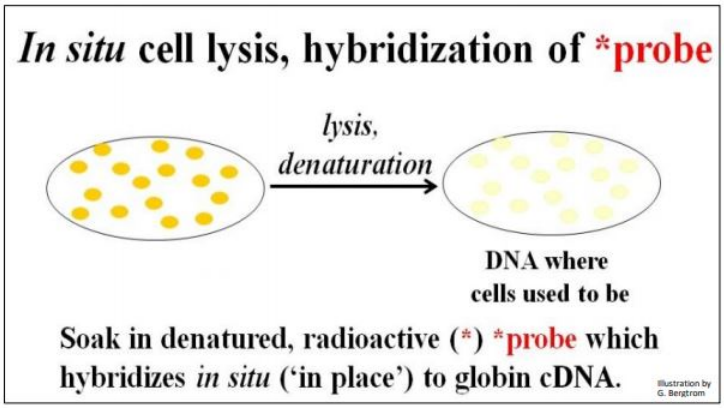


After colonies grow on the ampicillin agar plate, lay a filter over the plate. The filter will pick up a few cells from each colony, in effect becoming a replica (mirror image) of the colonies on the plate. Place the *replica filter* on a new agar plate containing streptomycin; the new colonies that grow on the filter must be streptomycin-resistant, containing only non-recombinant plasmids. Colonies containing recombinant plasmids, those that did not grow in streptomycin are easily identified on the original ampicillin agar plate. In practice, highly efficient recombination and transformation procedures typically reveal very streptomycinresistant cells (i.e., colonies) after replica plating. In this case, ampicillin-resistant cells constitute a good cDNA library, ready for screening.

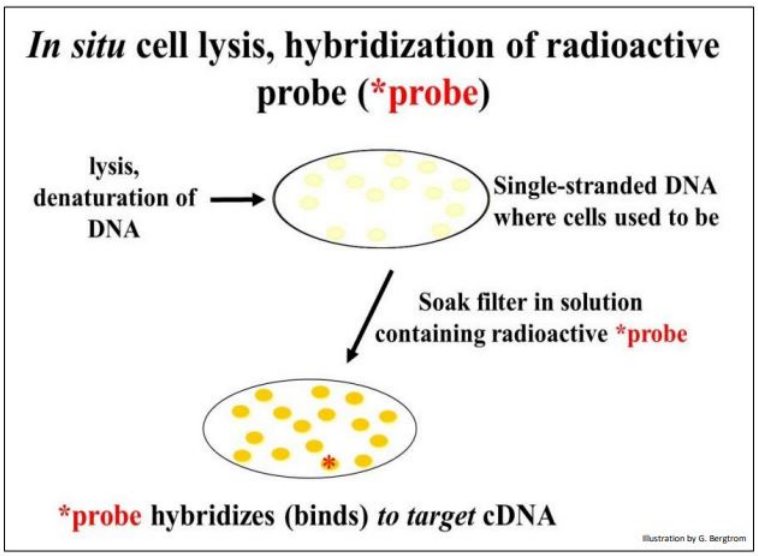
263 Making a Replica Plate Filter

4. Identifying Colonies Containing Plasmids with Inserts of Interest

The next step is to **screen** the colonies from the cDNA library for those containing the specific cDNA that you're after. This typically begins preparing multiple replica filters like the one above. Remember, these filters are replicas of bacterial cells containing recombinant plasmids that grow on ampicillin but not streptomycin. The number of replica filters that must be screened can be calculated from assumptions and formulas for estimating how many colonies must be screened to represent an entire transcriptome (i.e., the number of different mRNAs in the original cellular mRNA source). Once the requisite number of replica filters are made, they are subjected to **in situ lysis** to disrupt cell walls and membranes. The result is that the cell contents are released and the DNA is denatured (i.e., becomes single-stranded). The DNA then adheres to the filter *in place* (*in situ*, where the colonies were). The result of *in situ lysis* is a filter with faint traces of the original colony (below).

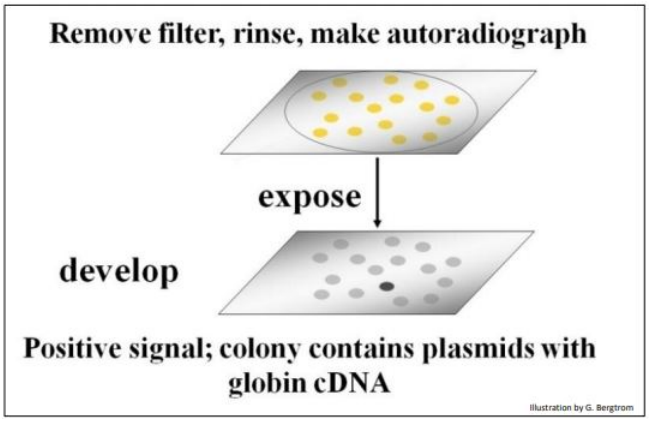


Next, a molecular **probe** is used to identify DNA containing the sequence of interest. The probe is often a **synthetic oligonucleotide** whose sequence was inferred from known amino acid sequences. These oligonucleotides are made radioactive and placed in a bag with the filter(s). DNA from cells that contained recombinant plasmids with a cDNA of interest will bind the complementary probe. The results of *in situ* lysis and **hybridization** of a radioactive probe to a replica filter are shown below.



264 Probing a Replica Plate Filter

The filters are rinsed to remove un-bound radioactive oligomer probe, and then placed on X-ray film. After a period of exposure, the film is developed. Black spots will form on the film from radioactive exposure, creating an autoradiograph of the filter. The black spots in the autoradiograph correspond to colonies on a filter that contain a recombinant plasmid with your target cDNA sequence (below).



Once a positive clone is identified on the film, the corresponding recombinant colony is located on the original plate. This colony is grown up in a liquid culture and the plasmid DNA is isolated. At that point, the cloned plasmid DNA can be sequenced and the amino acid sequence encoded by its cDNA can be inferred from the genetic code dictionary to verify that the cDNA *insert* in fact encodes the protein of interest. Once verified as the sequence of interest, a cloned plasmid cDNA can be made radioactive or fluorescent, and used to

- probe for the genes from which they originated.
- identify and quantitate the mRNA even locate the transcripts in the cells.
- quantitatively measure amounts of specific mRNAs.

Isolated plasmid cDNAs can even be expressed in suitable cells to make the encoded protein. These days, diabetics no longer receive pig insulin, but get synthetic human insulin human made from expressed human cDNAs. Moreover, while the introduction

of the *polymerase chain reaction* (**PCR**, see below) has superseded some uses of cDNAs, they still play a role in genome-level and transcriptome-level studies.

265 Pick a Clone From a Replica Filter and Play With It!

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SECTION OVERVIEW

17.2: Amplifying DNA Using the Polymerase Chain Reaction

The polymerase chain reaction is a technique for quickly "cloning" a particular piece of DNA in the test tube (rather than in living cells like *E. coli*). Thanks to this procedure, one can make virtually unlimited copies of a single DNA molecule even though it is initially present in a mixture containing many different DNA molecules.

Procedure

To perform PCR, you must know at least a portion of the sequence of the DNA molecule that you wish to replicate. You must then synthesize **primers**: short oligonucleotides (containing about two dozen nucleotides) that are precisely complementary to the sequence at the 3' end of each strand of the DNA you wish to amplify. The DNA sample is heated to separate its strands and mixed with the primers. If the primers find their complementary sequences in the DNA, they bind to them; synthesis begins (as always 5' -> 3') using the original strand as the template.

The reaction mixture must contain all four deoxynucleotide triphosphates (dATP, dCTP, dGTP, dTTP), and a DNA polymerase. It helps to use a DNA polymerase that is not denatured by the high temperature needed to separate the DNA strands. Polymerization continues until each newly-synthesized strand has proceeded far enough to contain the site recognized by the **other primer**. Now you have two DNA molecules identical to the original molecule. You take these two molecules, heat them to separate their strands, and repeat the process. Each cycle doubles the number of DNA molecules.

Using automated equipment, each cycle of replication can be completed in less than 5 minutes. After 30 cycles, what began as a single molecule of DNA has been amplified into more than a billion copies ($2^{30} = 1.02 \times 10^9$).

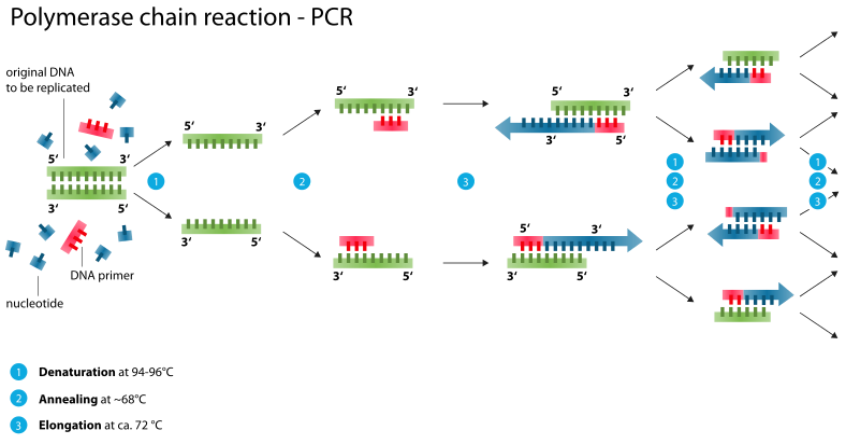


Figure 11.2.1: Schematic drawing of the Polymerase Chain Reaction (PCR) cycle. (CC-SA-BY-3.0; Enzoklop)

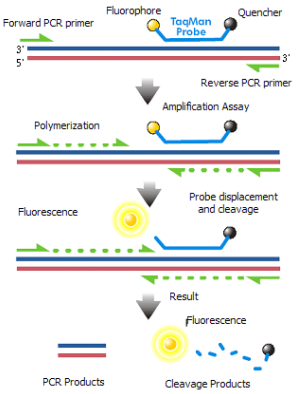
With PCR, it is routinely possible to amplify enough DNA from a single hair follicle for DNA typing. Some workers have successfully amplified DNA from a single sperm cell. The PCR technique has even made it possible to analyze DNA from microscope slides of tissue preserved years before. However, the great sensitivity of PCR makes contamination by extraneous DNA a constant problem.

17.2.1: qPCR

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17.2.1: qPCR

Quantitative PCR (qPCR)



Measurements can be made of individual genes of interest through PCR of those specific genes. A process known as Real-Time PCR or quantitative PCR (**qPCR**) is used to measure individual genes using fluorescence measurements. An intercalating agent that binds only to double-stranded DNA called **Sybr Green** is used in a qPCR machine that is measuring fluorescence after each cycle of PCR indirectly indicates the amount of amplified product. However, non-specific products of amplification may also be measured and not discriminated from the authentic amplicon.

An alternative to Sybr Green is exemplified by the TaqMan technology. With TaqMan, a third primer (**TaqMan probe**) is designed in the middle of the area to be amplified. This middle primer is designed with a hairpin self-complementarity so that the 5′ and 3′ ends are in close proximity. At one end, a **fluorescent reporter** is attached while the other terminus has a **quencher** that absorbs any fluorescence signal. Under normal circumstances, measurements of fluorescence will be very low. When PCR extension occurs, the Polymerase hydrolyzes this middle primer, thereby separating the quencher and reporter. The name TaqMan is a play on words since it is imagined that the polymerase is chewing up the probe like Pacman. With increased distance between quencher/reporter, the fluorescence signal from this probe can now be measured. This method is much more specific than Sybr Green. However, the use of specific probes increases the cost considerably.

Threshold Cycles (C_t)

File:Qpcr-cycling.png

Credit: Zuzanna K. Filutowska (CC-BY-SA 3.0)

Fluorescence measurement early during the PCR process will be very low due to the small number of dsDNA molecules (Sybr Green) or most TaqMan primers being quenched. During this exponential DNA production, a threshold will be reached in which the fluorescence will linearly increase. A specific point where the fluorescence is clearly measurable is called the **Threshold Cycle (C_t)** is used as a reference point to compare expression values.

Looking at the example of Sybr Green qPCR above, it can be observed that samples exponentially increasing at a lower cycle number (C_t) has a higher level of mRNA expression (towards the left) of that gene than samples with higher cycle number (towards the right). Notice that the fluorescence eventually plateaus and stops increasing. This is due to the depletion of raw materials for DNA production like dNTPs.

Since the PCR reactions theoretically represent a doubling of DNA after each cycle, the C_t values can be interpreted on a base 2 system. If there is a difference in C_t between two samples (**ΔC_t**) of 5 cycles, this corresponds to 2^5 or 32 fold difference. We can control for variations in the RNA preparation through comparing the fluorescence values of our gene of interest to a housekeeping gene like actin. The use of a house-keeping gene to normalize the initial input to the reactions and comparison between samples is referred to as **Relative Quantification**.

Melt Curves for Sybr Green

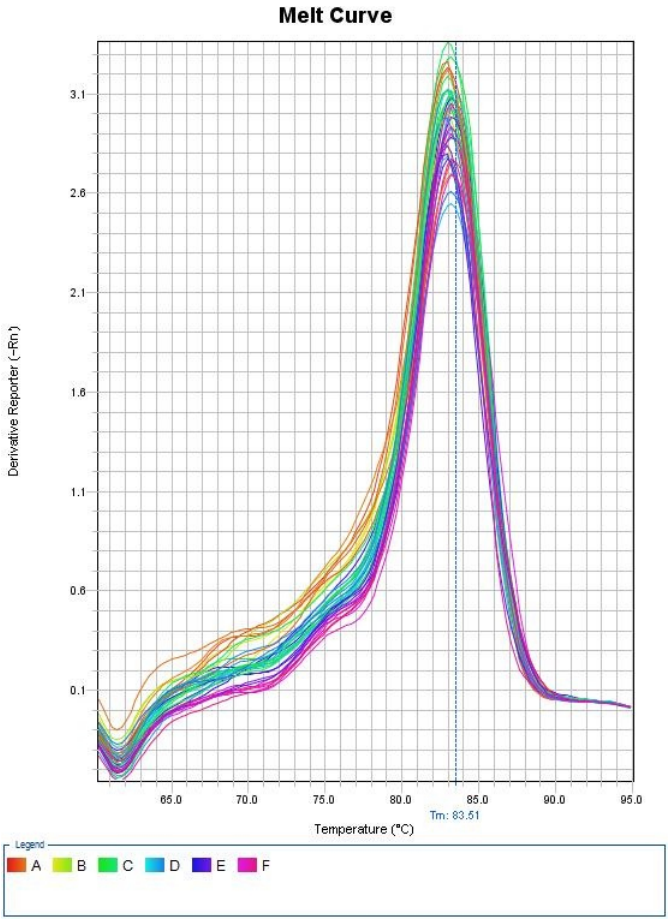
File:Melting Curve Analysis Graphs.svg

The top panel illustrates the decrease in fluorescence as the temperature increases due to the dissociation of double-stranded DNA. The bottom panel illustrates the first derivative plot. Each peak in this example illustrates a different allele. The double peaks represent the presence of the 2 distinct alleles in the amplification products.

Credit: Seans Potato Business (CC-BY-SA 3.0)

When using Sybr Green, we need to ensure that the PCR is specific so that the fluorescence measurement truly reflect amplification of our gene of interest. At the end of each qPCR run (~40 cycles), a melt curve is performed. A **melting curve** (or dissociation curve) comes from constant measurements as the temperature is increased. As temperature increases, the DNA strands start to denature and fluorescence will begin to decrease. After complete separation of DNA strands, the fluorescence will again remain

constant. The way this curve is viewed is through a derivative plot where the inflection in fluorescence reading is reported as the **melting temperature (Tm)**.



This melt curve illustrates each sample contains the same specific product with a melting temperature of 83.51°C.

Any peaks in this plot refer to a specific PCR product. If multiple peaks appear, the results will not be valid as they do not directly measure a single product.

Expression Measurements

Differential gene expression refers to transcriptional programs activated by the cell under various conditions. “Differential” refers to a comparison of two or more states or timepoints. Using mRNA as an indirect measurement of protein, one can ascertain which proteins are linked to these different states. In eukaryotes, this can be assessed by enriching total RNA for polyA-containing mature mRNA. Through the use of oligo-(dT) containing resin, mRNA can be separated from non-protein encoding RNA. Likewise, performing a reverse-transcription using an oligo-(dT) primer will create a stable complementary DNA (cDNA) molecule that can be used with PCR. Using qPCR in this way is called **RT-PCR** or reverse-transcription polymerase chain reaction where specific primer pairs are used to amplify a small portion of a known gene.

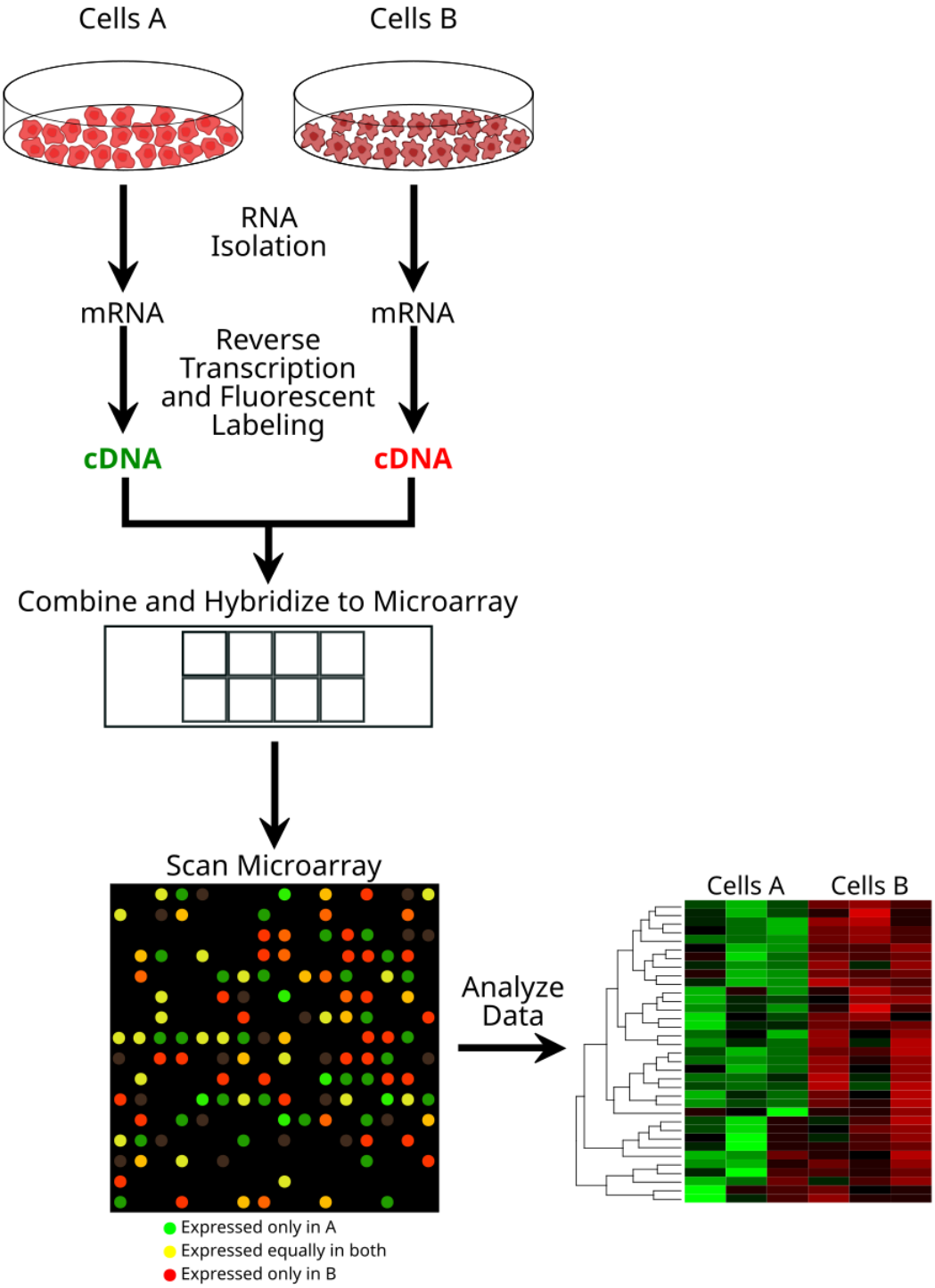
Hybridization-Based Methods and Microarrays:

File:Northern Blot.jpg

Credit: FrozenMan (CC-BY-SA 4.0)

Prior to RT-PCR, the expression of individual genes was assessed through a hybridization-based approach. This method called for running RNA on an agarose gel and transferring the size-fractionated RNAs onto a membrane through a method called “blotting”. This transferred RNA was then hybridized to a radioactively labeled probe for a specific gene (corresponding to the reverse complementary sequence) and visualized by exposure to X-ray film in a process called **Northern Blotting**. The intensity of the

band would be proportional to the amount of mRNA corresponding to the gene of interest. Re-probing with a housekeeping gene like actin would be used as a loading control to illustrate that a similar amount of total RNA was loaded into each well. Differences in sizes of the mRNA on the Northern Blot also revealed differences in splice variants of mature mRNA in the different states.



Credit: Jeremy Seto (CC-BY-NC-SA)

This technique was later adapted using non-radioactive methods. Using these non-radioactive methods, the reverse protocol was developed to measure multiple gene targets. By systematically immobilizing gene-specific probes onto a membrane or a microscope slide, an array of targets can be produced. In the simplest paradigm of having 2 states (control or experimental), cDNA

from each sample can be used to generate fluorescent RNA that can hybridize to immobilized probes. Using 2 different fluorescent markers allows for the competitive hybridization onto the array whereby the fluorescent signal in each channel can reveal the differential gene expression of the two states in a 2-color **microarray**.

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SECTION OVERVIEW

17.3: Creating, Correcting, and Analyzing Genetic Variation

17.3.1: DNA Fingerprinting

17.3.2: PCR-Based Mutagenesis

17.3.3: Genome Editing (CRISPR)

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17.3.1: DNA Fingerprinting

DNA fingerprinting is routinely used today to establish paternity, in the diagnosis of inherited disorders, and for use in criminal cases. DNA fingerprinting enables forensic investigators to determine whether two DNA samples originate from the same individual. Not all of the DNA present is used in this analysis. Restriction enzymes act as molecular scissors and are used to cleave DNA molecules at specific points. Over 2,500 different restriction enzymes have been identified. These enzymes are produced by bacteria and are used to destroy foreign DNA such as bacteriophages - viruses that infect and replicate within a bacterium.

For example the restriction enzyme EcoR1, isolated from E. coli, cuts DNA at the sequence GAATTC.



The length and the number of the fragments produced depends upon the frequency and the distance between the recognition sites. This distinct pattern is known as restriction fragment length polymorphisms (RFLP's) which are unique to each individual therefore forming a DNA fingerprint. After DNA samples are cut by restriction enzymes, the fragments are separated using gel electrophoresis. PCR, polymerase chain reaction, can be used to analysis very small or degraded samples. This enzyme amplifies even trace amounts of DNA
present. The length of the segments analyzed are much smaller and the repeat sites are called microsatellites.

The phosphate group of the DNA molecule is negatively charged which gives the fragments an overall negative charge. In an electrical current the negatively charged fragments will be attracted to the positive pole. Smaller fragments will migrate faster and further in a given time period. Therefore the fragments are separated by size. After separation radioactive markers are added which are complementary to the separated fragments. Photographic film is placed over the gel and the areas that are exposed to the radioactive markers darken. This generates a series of lines that resemble a bar code. The film then becomes the DNA fingerprint. In this experiment we will be using a mixture of dyes that will simulate the migration of DNA fragments.

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17.3.2: PCR-Based Mutagenesis

Molecular cloning was the first method available to isolate a gene of interest and make many copies of it to obtain sufficient amounts of the DNA to study. Today, there is a faster and easier way to obtain large amounts of a DNA sequence of interest -the polymerase chain reaction (PCR). PCR allows one to use the power of DNA replication to amplify DNA enormously in a short period of time. As you know, cells replicate their DNA before they divide, and in doing so, double the amount of the cell's DNA. PCR essentially mimics cellular DNA replication in the test tube, repeatedly copying the target DNA over and over, to produce large quantities of the desired DNA.

Selective Replication

In contrast to cellular DNA replication, which amplifies all of a cell's DNA during a replication cycle, PCR does targeted amplification to replicate only a segment of DNA bounded by the two primers that determine where DNA polymerase begins replication. Figure 8.34 illustrates the process. Each cycle of PCR involves three steps, denaturing, annealing and extension, each of which occurs at a different temperature.

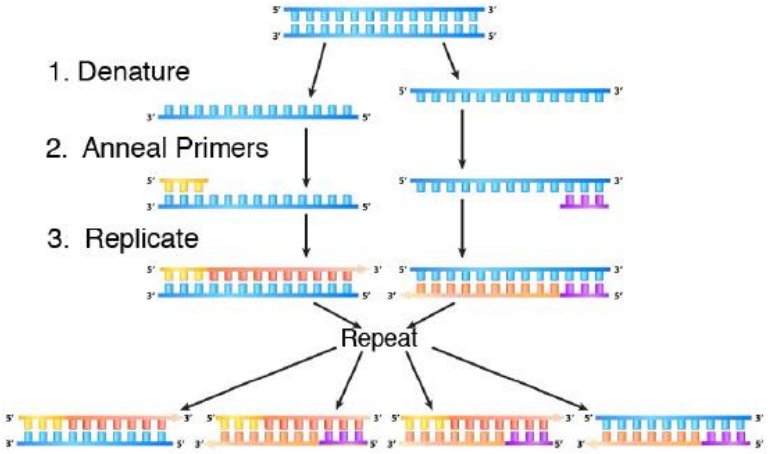


Figure 8.34 - Steps in the polymerase chain reaction. Image by Aleia Kim

The Starting Materials

Since PCR is, basically, replication of DNA in a test-tube, all the usual ingredients needed for DNA replication are required:

- A template (the DNA containing the target sequence that is being copied)
- Primers (to initiate the synthesis of the new DNA strands)
- Thermostable DNA polymerase (to carry out the synthesis). The polymerase needs to be heat stable, because heat is used to separate the template DNA strands in each cycle.
- dNTPs (DNA nucleotides to build the new DNA strands).
- The template is the DNA that contains the target you want to amplify (the "target" is the specific region of the DNA you want to amplify).

The primers are short synthetic single-stranded DNA molecules whose sequence matches a region flanking the target sequence. It is possible to chemically synthesize DNA molecules of any given base sequence, to use as primers. To make primers of the correct sequence that will bind to the template DNA, it is necessary to know a little bit of the template sequence on either side of the region of DNA to be amplified. DNA polymerases and dNTPs are commercially available from biotechnology supply companies.

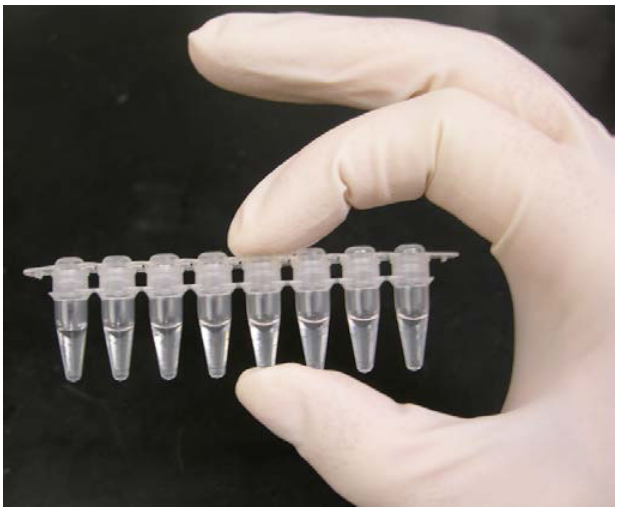


Figure 8.35 - PCR tubes with DNA samples ready for reaction. Wikipedia

First, all of the reagents are mixed together. Primers are present in millions of fold excess over the template. This is important because each newly made DNA strand starts from a primer. The first step of the process involves separating the strands of the target DNA by heating to near boiling.

Next, the solution is cooled to a temperature that favors complementary DNA sequences finding each other and making base pairs, a process called annealing. Since the primers are present in great excess, the complementary sequences they target are readily found and base-paired to the primers. These primers direct the synthesis of DNA. Only where a primer anneals to a DNA strand will replication occur, since DNA polymerases require a primer to begin synthesis of a new strand.



Figure 8.36 - A PCR thermocycler system. Wikipedia

Extension

In the third step in the process, the DNA polymerase replicates DNA by extension from the 3’ end of the primer, making a new DNA strand. At the end of the first cycle, there are twice as many DNA molecules, just as in cellular replication. But in PCR, the process is repeated, usually for between 25 and 30 cycles. At the end of the process, there is a theoretical yield of 230 (over 1 billion times) more DNA than there was to start. (This enormous amplification power is the reason that PCR is so useful for forensic investigations, where very tiny amounts of DNA may be available at a crime scene.)

The temperature cycles are controlled in a thermocycler, which repeatedly raises and lowers temperatures according to the set program. Since each cycle can be completed in a couple of minutes, the entire amplification can be completed very rapidly. The

resulting DNA is analyzed on a gel to ensure that it is of the expected size, and depending on what it is to be used for, may also be sequenced, to be certain that it is the desired fragment.

Mutagenesis

PCR is frequently used to obtain gene sequences to be cloned into vectors for protein expression, for example. Besides simplicity and speed, PCR also has other advantages. Because primers can be synthesized that differ from the template sequence at any given position, it is possible to use PCR for site-directed mutagenesis. That is, PCR can be used to mutate a gene at a desired position in the sequence. This allows the proteins encoded by the normal and mutant genes to be expressed, purified and compared.

Analysis of gene expression

PCR can also be used to measure gene expression. Where in PCR the amount of amplified product is not determined till the end of all the cycles, a variation called quantitative real-time PCR is used, in which the accumulation of product is measured at each cycle. This is possible because real-time PCR machines have a detector module that can measure the levels of a fluorescent marker in the reaction, with the amount of fluorescence proportional to the amount of amplified product. By following the accumulation of product over the cycles it is possible to calculate the amount of starting template. To measure gene expression, the template used is mRNA reverse-transcribed into cDNA (see below). This coupling of reverse transcription with quantitative real-time PCR is called qRT-PCR.

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17.3.3: Genome Editing (CRISPR)

The development of tools that would allow scientists to make specific, targeted changes in the genome has been the Holy Grail of molecular biology. An ingenious new tool that is both simple and effective in making precise changes is poised to revolutionize the field, much as PCR did in the 1980s. Known as the CRISPR/Cas9 system, and often abbreviated simply as CRISPR, it is based on a sort of bacterial immune system that allows bacteria to recognize and inactivate viral invaders.

CRSPR

CRISPR stands for Clustered Regularly Interspaced Short Palindromic Repeats, short repeated sequences found in prokaryotic DNA, separated by spacer sequences derived from past encounters with, for example, a bacteriophage. Like the glass slipper left behind by Cinderella that was later used to identify her, the pieces of the invader's sequences are a way for the bacteria to identify the virus if it attacks again. Inserted into the bacterial genome, these sequences can later be transcribed into a guide RNA that matches, and base-pairs with, sections of the viral genome if it was encountered again. A nuclease associated with the guide RNA then cleaves the sequence base-paired with the guide RNA. (The nucleases are named Cas for CRISPR-associated.)

The essential elements of this system are a guide RNA that homes in on the target sequence and a nuclease that can make a cut in the sequence that is bound by the guide RNA. By engineering guide RNAs complementary to a target gene, it is possible to target the nuclease to cleave within that gene. In the CRISPR/Cas9 system, the Cas9 endonuclease cuts both strands of the gene sequence targeted by the guide RNA (Figure **17.3.3.1**). This generates a double-strand break that the cell attempts to repair.

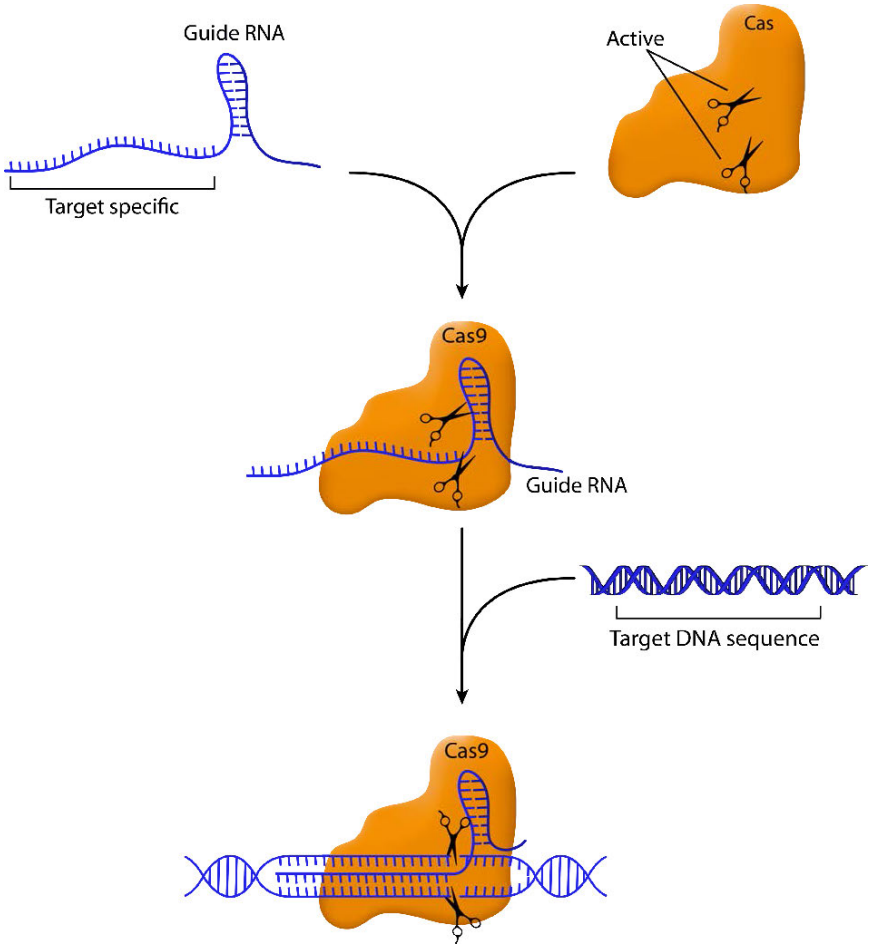


Figure **17.3.3.1**: A guide RNA directs the Cas9 nuclease to its target gene. Image by Pehr Jacobsen

As you may remember, double-strand breaks in DNA can be repaired by simple, nonhomologous end joining (NHEJ) or by homologous recombination. When a break is fixed by NHEJ, there is good chance that there will be deletions or insertions that will

inactivate the gene they are in. Thus, targeted cleavage of a site by CRISPR/Cas9 can easily and specifically inactivate a gene, making it easy to characterize the gene's function.

But, what if you wished to simply mutate the gene at a specific site to study the effect of the mutation? This, too, can be achieved. If a homologous sequence bearing the specific mutation is provided, homologous recombination can repair the break, and at the same time insert the exact mutation desired. It is obvious that if you can insert a mutation as just described, it should be possible to correct a mutation in the genome by cleaving at the appropriate spot and providing the correct sequence as a template for repair by homologous recombination. The simplicity of the system holds great promise for curing genetic diseases.

Scientists have also come up with some creative variations on the CRISPR/Cas9 system. For instance, one variant inactivates the nuclease activity of Cas9. The guide RNA in this system pairs with the target sequence, but the Cas9 does not cleave it. Instead, the Cas9 blocks the transcription of the downstream gene (Figure **17.3.3.2**) This method allows specific genes to be turned off without actually altering the DNA sequence.

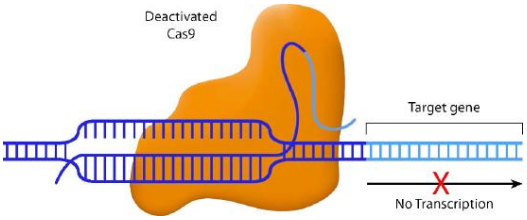


Figure **17.3.3.2**: Inactive Cas9 can block transcription of a target gene. Image by Pehr Jacobsen

Another variation also uses a disabled Cas9, but this time, the Cas9 is fused to a transcriptional activation domain. In this situation, the guide RNA positions the Cas9-activator domain in a place where it can enhance transcription from a specific promoter (Figure **17.3.3.3**). Other variations on this theme attach histone-modifying enzymes or DNA methylases to the inactive Cas9. Again, the guide RNA positions the Cas9 in the desired spot, and the enzyme attached to Cas9 can methylate the DNA or modify the histones in that region.

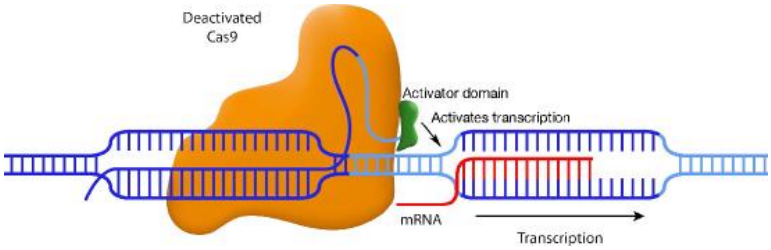


Figure **17.3.3.3**: A Cas9-activator domain fusion can activate transcription of a target gene. Image by Pehr Jacobsen

CRISPR has already been used to edit genomes in a wide variety of species (and in human cell cultures). It may not be long before the technique is approved for clinical use. In the meanwhile, CRISPR is transforming molecular biology.

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SECTION OVERVIEW

17.4: Constructing and Using Transgenic Organisms

17.4.1: Transgenic Animals

17.4.2: Transgenic Plants

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17.4.1: Transgenic Animals

A transgenic animal is one that carries a foreign gene that has been deliberately inserted into its genome. The foreign gene is constructed using recombinant DNA methodology. In addition to the gene itself, the DNA usually includes other sequences to enable it to be incorporated into the DNA of the host and to be expressed correctly by the cells of the host. Transgenic sheep and goats have been produced that express foreign proteins in their milk. Transgenic chickens are now able to synthesize human proteins in the "white" of their eggs. These animals should eventually prove to be valuable sources of proteins for human therapy.

Note

In July 2000, researchers from the team that produced Dolly reported success in producing transgenic lambs in which the transgene had been inserted at a specific site in the genome and functioned well.

Transgenic **mice** have provided the tools for exploring many biological questions.

Example

Normal mice cannot be infected with polio virus. They lack the cell-surface molecule that, in humans, serves as the receptor for the virus. So normal mice cannot serve as an inexpensive, easily-manipulated model for studying the disease. However, transgenic mice expressing the human gene for the polio virus receptor

- can be infected by polio virus and even
- develop paralysis and other pathological changes characteristic of the disease in humans.

Two methods of producing transgenic mice are widely used:

- transforming **embryonic stem cells** (**ES** cells) growing in tissue culture with the desired DNA
- injecting the desired gene into the **pronucleus** of a fertilized mouse egg

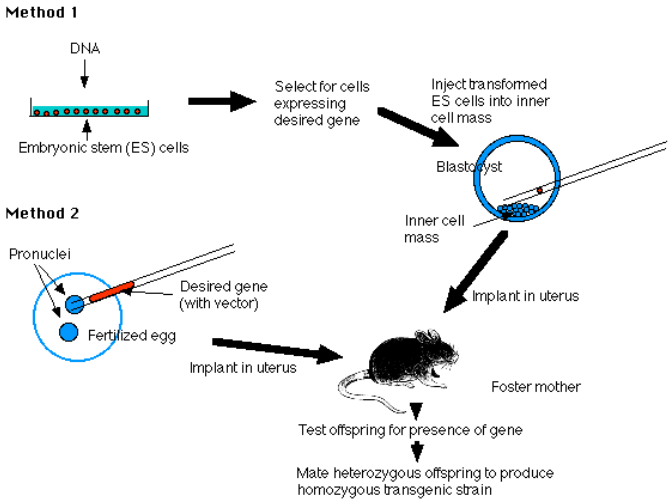


Fig.11.4.1 Methods to produce Transgenic mice

The Embryonic Stem Cell Method - Method 1

Embryonic stem cells (**ES** cells) are harvested from the **inner cell mass** (ICM) of mouse blastocysts. They can be grown in culture and retain their full potential to produce all the cells of the mature animal, **including its gametes**.

1. Make your DNA

Using recombinant DNA methods, build molecules of DNA containing

- the gene you desire (e.g., the insulin gene)

- **vector** DNA to enable the molecules to be inserted into host DNA molecules
- **promoter and enhancer sequences** to enable the gene to be expressed by host cells

2. Transform ES cells in culture

Expose the cultured cells to the DNA so that some will incorporate it.

3. Select for successfully transformed cells

4. Inject these cells into the inner cell mass (ICM) of mouse blastocysts.

5. Embryo transfer

- Prepare a **pseudopregnant** mouse (by mating a female mouse with a vasectomized male). The stimulus of mating elicits the hormonal changes needed to make her uterus receptive.
- Transfer the embryos into her uterus.
- Hope that they **implant** successfully and develop into healthy pups (no more than one-third will).

6. Test her offspring

- Remove a small piece of tissue from the tail and examine its DNA for the desired gene. No more than 10–20% will have it, and they will be heterozygous for the gene.

7. Establish a transgenic strain

- Mate two heterozygous mice and screen their offspring for the 1 in 4 that will be **homozygous** for the transgene.
- Mating these will found the transgenic strain.

The Pronucleus Method - Method 2

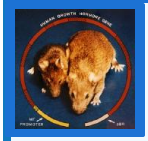
1. Prepare your DNA as in Method 1

2. Transform fertilized eggs

- Harvest freshly fertilized eggs before the sperm head has become a pronucleus.
- Inject the male pronucleus with your DNA.
- When the pronuclei have fused to form the diploid zygote nucleus, allow the zygote to divide by mitosis to form a 2-cell embryo.

3. Implant the embryos in a pseudopregnant foster mother and proceed as in Method 1.

Example



This image (courtesy of R. L. Brinster and R. E. Hammer) shows a transgenic mouse (right) with a normal littermate (left). The giant mouse developed from a fertilized egg transformed with a recombinant DNA molecule containing:

- the gene for **human growth hormone**
- a strong mouse gene **promoter**

The levels of growth hormone in the serum of some of the transgenic mice were several hundred times higher than in control mice.

Random vs. Targeted Gene Insertion

The early vectors used for gene insertion could, and did, place the gene (from one to 200 copies of it) anywhere in the genome. However, if you know some of the DNA sequence flanking a particular gene, it is possible to design vectors that replace that gene. The replacement gene can be one that

- restores function in a mutant animal or

- knocks out the function of a particular locus.

In either case, targeted gene insertion requires

- the desired gene
- ***neo*^{r}**, a gene that encodes an enzyme that inactivates the antibiotic neomycin and its relatives, like the drug G418, which is lethal to mammalian cells
- ***tk***, a gene that encodes **thymidine kinase**, an enzyme that phosphorylates the nucleoside analog **ganciclovir**. **DNA polymerase** fails to discriminate against the resulting nucleotide and inserts this nonfunctional nucleotide into freshly-replicating DNA. So ganciclovir kills cells that contain the *tk* gene

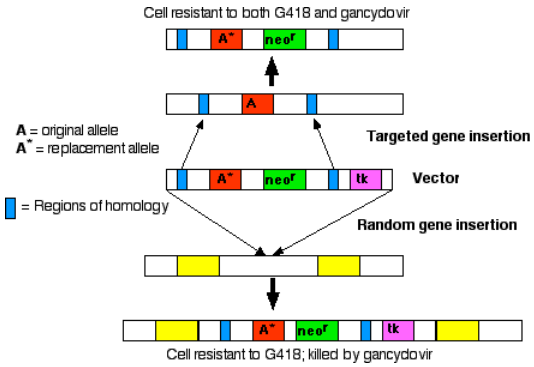


Figure 11.4.2 Neo vector

Step 1

Treat culture of ES cells with preparation of vector DNA.

Results:

- **Most cells** fail to take up the vector; these cells will be killed if exposed to G418.
- In a **few cells**: the vector is inserted randomly in the genome. In random insertion, the entire vector, including the ***tk*** gene, is inserted into host DNA. These cells are resistant to G418 but killed by gancyclovir.
- In **still fewer cells**: **homologous recombination** occurs. Stretches of DNA sequence in the vector find the homologous sequences in the host genome, and the region between these homologous sequences replaces the equivalent region in the host DNA.

Step 2

Culture the mixture of cells in medium containing both G418 and ganciclovir.

- The cells (the majority) that failed to take up the vector are killed by G418.
- The cells in which the vector was inserted randomly are killed by gancyclovir (because they contain the *tk* gene).
- This leaves a population of cells transformed by homologous recombination (enriched several thousand fold).

Step 3

Inject these into the inner cell mass of mouse blastocysts.

Knockout Mice: What do they teach us?

If the replacement gene (**A*** in the diagram) is nonfunctional (a "null" allele), mating of the heterozygous transgenic mice will produce a strain of "**knockout mice**" homozygous for the nonfunctional gene (both copies of the gene at that locus have been "knocked out"). Knockout mice are valuable tools for discovering the function(s) of genes for which mutant strains were not previously available. Two generalizations have emerged from examining knockout mice:

- Knockout mice are often surprisingly unaffected by their deficiency. Many genes turn out not to be indispensable. The mouse genome appears to have sufficient redundancy to compensate for a single missing pair of alleles.
- Most genes are **pleiotropic**. They are expressed in different tissues in different ways and at different times in development.

Tissue-Specific Knockout Mice

While "housekeeping" genes are expressed in all types of cells at all stages of development, other genes are normally expressed in only certain types of cells when turned on by the appropriate signals (e.g. the arrival of a hormone).

To study such genes, one might expect that the methods described above would work. However, it turns out that genes that are only expressed in certain adult tissues may nonetheless be vital during embryonic development. In such cases, the animals do not survive long enough for their knockout gene to be studied. Fortunately, there are now techniques with which transgenic mice can be made where a particular gene gets knocked out in only one type of cell.

The Cre/*loxP* System

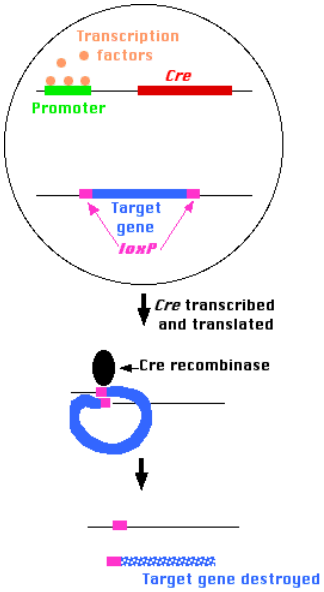


Figure 11.4.3 The Cre/loxP System

One of the bacteriophages that infects E. coli, called P1, produces an enzyme — designated Cre — that cuts its DNA into lengths suitable for packaging into fresh virus particles. Cre cuts the viral DNA wherever it encounters a pair of sequences designated *loxP*. All the DNA between the two *loxP* sites is removed, and the remaining DNA ligated together again (so the enzyme is a recombinase). Using "Method 1" above, mice can be made transgenic for

- the gene encoding Cre attached to a promoter that will be activated only when it is bound by the same transcription factors that turn on the other genes required for the unique function(s) of that type of cell;
- a "target" gene, the one whose function is to be studied, flanked by *loxP* sequences.

In the adult animal,

- those cells that
  - receive signals (e.g., the arrival of a hormone or cytokine)
  - to turn on production of the transcription factors needed
  - to activate the promoters of the genes whose products are needed by that particular kind of cell

  will also turn on transcription of the Cre gene. Its protein will then remove the "target" gene under study.
- All other cells will lack the transcription factors needed to bind to the Cre promoter (and/or any enhancers) so the target gene remains intact.

The result: a mouse with a particular gene knocked out in only certain cells.

Knock-in Mice

The Cre/*loxP* system can also be used to

- remove DNA sequences that block gene transcription. The "target" gene can then be turned **on** in certain cells or at certain times as the experimenter wishes.

- replace one of the mouse's own genes with a new gene that the investigator wishes to study.

Such transgenic mice are called "knock-in" mice.

Transgenic Sheep and Goats

Until recently, the transgenes introduced into sheep inserted randomly in the genome and often worked poorly. However, in July 2000, success at inserting a transgene into a specific gene locus was reported. The gene was the human gene for **alpha1-antitrypsin**, and two of the animals expressed large quantities of the human protein in their milk.

This is how it was done.

Sheep fibroblasts (connective tissue cells) growing in tissue culture were treated with a vector that contained these segments of DNA:

1. 2 regions homologous to the sheep *COL1A1* gene. This gene encodes Type 1 collagen. (Its absence in humans causes the inherited disease osteogenesis imperfecta.)

   This locus was chosen because fibroblasts secrete large amounts of collagen and thus one would expect the gene to be easily accessible in the chromatin.

2. A neomycin-resistance gene to aid in isolating those cells that successfully incorporated the vector.
3. The human gene encoding alpha1-antitrypsin.

   Some people inherit two non- or poorly-functioning genes for this protein. Its resulting low level or absence produces the disease **Alpha1-Antitrypsin Deficiency** (**A1AD** or **Alpha1**). The main symptoms are damage to the lungs (and sometimes to the liver).

4. Promoter sites from the **beta-lactoglobulin** gene. These promote hormone-driven gene expression in milk-producing cells.
5. Binding sites for ribosomes for efficient translation of the beta-lactoglobulin mRNAs.

Successfully-transformed cells were then

- Fused with enucleated sheep eggs and implanted in the uterus of a ewe (female sheep)
- Several embryos survived until their birth, and two young lambs lived over a year.
- When treated with hormones, these two lambs secreted milk containing large amounts of alpha1-antitrypsin (650 µg/ml; 50 times higher than previous results using random insertion of the transgene).

On June 18, 2003, the company doing this work abandoned it because of the great expense of building a facility for purifying the protein from sheep's milk. Purification is important because even when 99.9% pure, human patients can develop antibodies against the tiny amounts of sheep proteins that remain.

However, another company, GTC Biotherapeutics, has persevered and in June of 2006 won preliminary approval to market a human protein, antithrombin, in Europe. Their protein — the first made in a transgenic animal to receive regulatory approval for human therapy — was secreted in the milk of transgenic goats.

Transgenic Chickens

Chickens grow faster than sheep and goats and large numbers can be grown in close quarters. They also synthesize several grams of protein in the "white" of their eggs.Two methods have succeeded in producing chickens carrying and expressing foreign genes.

- Infecting embryos with a viral vector carrying
  - the human gene for a therapeutic protein
  - promoter sequences that will respond to the signals for making proteins (e.g. lysozyme) in egg white
- Transforming rooster sperm with a human gene and the appropriate promoters and checking for any transgenic offspring.

Preliminary results from both methods indicate that it may be possible for chickens to produce as much as 0.1 g of human protein in each egg that they lay.

Not only should this cost less than producing therapeutic proteins in culture vessels, but chickens will probably add the correct sugars to glycosylated proteins — something that E. coli cannot do.

Transgenic Pigs

Transgenic pigs have also been produced by fertilizing normal eggs with sperm cells that have incorporated foreign DNA. This procedure, called sperm-mediated gene transfer (SMGT) may someday be able to produce transgenic pigs that can serve as a source of transplanted organs for humans.

Transgenic Primates

In the 28 May 2009 issue of **Nature**, Japanese scientists reported success in creating transgenic marmosets. Marmosets are primates and thus our closest relatives (so far) to be genetically engineered. In some cases, the transgene (for green fluorescent protein) was incorporated into the germline and passed on to the animal's offspring. The hope is that these transgenic animals will provide the best model yet for studying human disease and possible therapies.

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17.4.2: Transgenic Plants

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Progress is being made on several fronts to introduce new traits into plants using recombinant DNA technology. The genetic manipulation of plants has been going on since the dawn of agriculture, but until recently this has required the slow and tedious process of cross-breeding varieties. Genetic engineering promises to speed the process and broaden the scope of what can be done.

There are several methods for introducing genes into plants, including infecting plant cells with plasmids as vectors carrying the desired gene and physically shooting microscopic pellets containing the gene directly into the cell. In contrast to animals, there is no real distinction between somatic cells and germline cells. Somatic tissues of plants (e.g., root cells grown in culture) can be transformed in the laboratory with the desired gene and can grow into mature plants with flowers. If all goes well, the transgene will be incorporated into the pollen and eggs and passed on to the next generation. In this respect, it is easier to produce transgenic plants than transgenic animals.

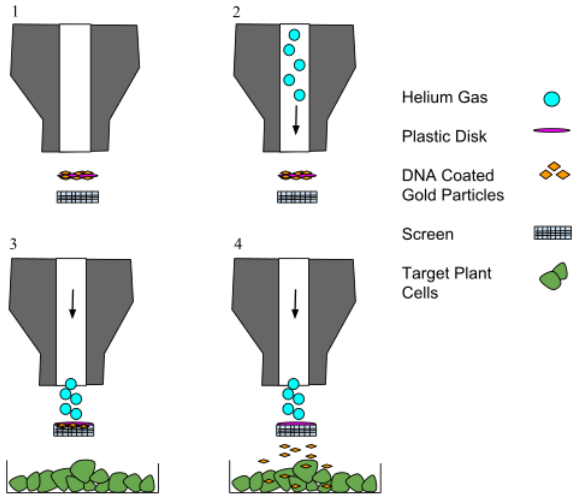


Figure 17.4.2.1: A gene gun is used for injecting cells with genetic information, it is also known as biolistic particle delivery system. Gene guns can be used effectively on most cells but are mainly used on plant cells. Step 1 The gene gun apparatus is ready to fire. Step 2 When the gun is turned on and the helium flows through. Step 3 The helium moving the disk with DNA coated particles toward the screen. Step 4 The helium having pushed the particles moving through the screen and moving to the target cells to transform the cells. (CC-SA-BY-4.0; RachelBrooks15)

Achievements

Improved Nutritional Quality

Milled rice is the staple food for a large fraction of the world's human population. Milling rice removes the husk and any beta-carotene it contained. Beta-carotene is a precursor to vitamin A, so it is not surprising that vitamin A deficiency is widespread, especially in the countries of Southeast Asia. The synthesis of beta-carotene requires a number of enzyme-catalyzed steps. In January 2000, a group of European researchers reported that they had succeeded in incorporating **three transgenes** into rice that enabled the plants to manufacture beta-carotene in their endosperm.

Insect Resistance

Bacillus thuringiensis is a bacterium that is pathogenic for a number of insect pests. Its lethal effect is mediated by a protein toxin it produces. Through recombinant DNA methods, the toxin gene can be introduced directly into the genome of the plant where it is expressed and provides protection against insect pests of the plant.

Disease Resistance

Genes that provide resistance against plant viruses have been successfully introduced into such crop plants as tobacco, tomatoes, and potatoes.

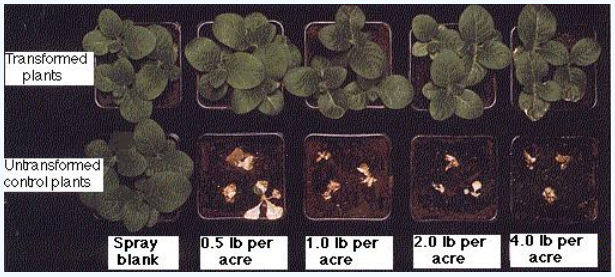
Example 17.4.2.1

Tomato plants infected with **tobacco mosaic virus** (which attacks tomato plants as well as tobacco). The plants in the back row carry an introduced gene conferring resistance to the virus. The resistant plants produced three times as much fruit as the sensitive plants and the same as control plants.

Herbicide Resistance

Questions have been raised about the safety — both to humans and to the environment — of some of the broad-leaved weed killers like 2,4-D. Alternatives are available, but they may damage the crop as well as the weeds growing in it. However, genes for resistance to some of the newer herbicides have been introduced into some crop plants and enable them to thrive even when exposed to the weed killer.

Example 17.4.2.2



Effect of the herbicide bromoxynil on tobacco plants transformed with a bacterial gene whose product breaks down bromoxynil (top row) and control plants (bottom row). "Spray blank" plants were treated with the same spray mixture as the others except the bromoxynil was left out. (Courtesy of Calgene, Davis, CA.)

Salt Tolerance

A large fraction of the world's irrigated crop land is so laden with salt that it cannot be used to grow most important crops. However, researchers at the University of California Davis campus have created transgenic tomatoes that grow well in saline soils. The transgene was a highly-expressed sodium/proton antiport pump that sequestered excess sodium in the vacuole of leaf cells. There was no sodium buildup in the fruit.

"Terminator" Genes

This term is used (by opponents of the practice) for transgenes introduced into crop plants to make them produce sterile seeds (and thus force the farmer to buy fresh seeds for the following season rather than saving seeds from the current crop). The process involves introducing three transgenes into the plant:

- A gene encoding a **toxin** which is lethal to developing seeds but not to mature seeds or the plant. This gene is normally inactive because of a stretch of DNA inserted between it and its promoter.
- A gene encoding a **recombinase** — an enzyme that can remove the spacer in the toxin gene thus allowing to be expressed.
- A **repressor** gene whose protein product binds to the promoter of the recombinase thus keeping it inactive.

How they work

When the seeds are soaked (before their sale) in a solution of tetracycline

- Synthesis of the repressor is blocked.
- The recombinase gene becomes active.
- The spacer is removed from the toxin gene and it can now be turned on.

Because the toxin does not harm the growing plant — only its developing seeds — the crop can be grown normally except that its seeds are sterile. The use of terminator genes has created much controversy. Farmers — especially those in developing countries — want to be able to save some seed from their crop to plant the next season. However, Seed companies want to be able to keep selling seeds.

Transgenes Encoding Antisense RNA

Messenger RNA (mRNA) is single-stranded. Its sequence of nucleotides is called "sense" because it results in a gene product (protein). Normally, its unpaired nucleotides are "read" by transfer RNA anticodons as the ribosome proceeds to **translate** the message.

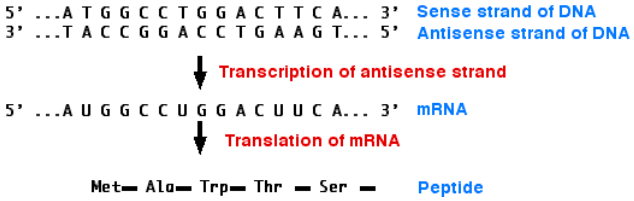


Figure 17.4.2.2: Sense Strand

The second strand is called the **antisense strand** because its sequence of nucleotides is the complement of message sense. When mRNA forms a duplex with a complementary antisense RNA sequence, translation is blocked. This may occur because the ribosome cannot gain access to the nucleotides in the mRNA or duplex RNA is quickly degraded by ribonucleases in the cell. With recombinant DNA methods, synthetic genes (DNA) encoding antisense RNA molecules can be introduced into the organism.

Biopharmaceuticals

The genes for proteins to be used in human (and animal) medicine can be inserted into plants and expressed by them.

Advantages:

- Glycoproteins can be made (bacteria like E. coli cannot do this).
- Virtually unlimited amounts can be grown in the field rather than in expensive fermentation tanks.
- It avoids the danger from using mammalian cells and tissue culture medium that might be contaminated with infectious agents.
- Purification is often easier.

Corn is the most popular plant for these purposes, but tobacco, tomatoes, potatoes, rice and carrot cells grown in tissue culture are also being used.

Some of the proteins that have been produced by transgenic crop plants:

- human growth hormone with the gene inserted into the chloroplast DNA of tobacco plants
- humanized antibodies against such infectious agents as
  - HIV
  - respiratory syncytial virus (RSV)
  - sperm (a possible contraceptive)
  - herpes simplex virus, HSV, the cause of "cold sores"
  - Ebola virus, the cause of the often-fatal Ebola hemorrhagic fever
- protein antigens to be used in vaccines
  - An example: patient-specific antilymphoma (a cancer) vaccines. B-cell lymphomas are clones of malignant B cells expressing on their surface a unique antibody molecule. Making tobacco plants transgenic for the RNA of the variable (unique) regions of this antibody enables them to produce the corresponding protein. This can then be incorporated into a vaccine in the hopes (early trials look promising) of boosting the patient's immune system — especially the cell-mediated branch — to combat the cancer.
- other useful proteins like lysozyme and trypsin
- However, as of April 2012, the only protein to receive approval for human use is glucocerebrosidase, an enzyme lacking in Gaucher's disease. It is synthesized by transgenic carrot cells grown in tissue culture.

Controversies

The introduction of transgenic plants into agriculture has been vigorously opposed by some. There are a number of issues that worry the opponents. One of them is the potential risk of transgenes in commercial crops endangering native or nontarget species.

Examples:

- A gene for herbicide resistance in, e.g. maize (corn), escaping into a weed species could make control of the weed far more difficult.
- The gene for Bt toxin expressed in pollen might endanger pollinators like honeybees.

To date, field studies on Bt cotton and maize show that the numbers of some nontarget insects are reduced somewhat but not as much as in fields treated with insecticides.

Another worry is the inadvertent mixing of transgenic crops with nontransgenic food crops. Although this has occurred periodically, there is absolutely no evidence of a threat to human health. Despite the controversies, farmers around the world are embracing transgenic crops. Currently in the United States over 80% of the corn, soybeans, and cotton grown are genetically modified (GM) — principally to provide resistance to the herbicide glyphosate ("Roundup Ready®") thus making it practical to spray the crop with glyphosate to kill weeds without harming the crop and resistance to insect attack (by expressing the toxin of *Bacillus thuringiensis*).

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SECTION OVERVIEW

17.5: Environmental Applications

17.5.1: Bioremediation

17.5.2: Water Treatment

17.5.3: Genomics and Biofuels

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17.5.1: Bioremediation

Bioremediation is a waste management technique that involves the use of organisms such as plants, bacteria, and fungi to remove or neutralize pollutants from a contaminated site. According to the United States EPA, bioremediation is a “treatment that uses naturally occurring organisms to break down hazardous substances into less toxic or non toxic substances”.

Bioremediation is widely used to treat human sewage and has also been used to remove agricultural chemicals (pesticides and fertilizers) that leach from soil into groundwater. Certain toxic metals, such as selenium and arsenic compounds, can also be removed from water by bioremediation. Mercury is an example of a toxic metal that can be removed from an environment by bioremediation. Mercury is an active ingredient of some pesticides and is also a byproduct of certain industries, such as battery production. Mercury is usually present in very low concentrations in natural environments but it is highly toxic because it accumulates in living tissues. Several species of bacteria can carry out the biotransformation of toxic mercury into nontoxic forms. These bacteria, such as *Pseudomonas aeruginosa*, can convert Hg^{2+} to Hg, which is less toxic to humans.

Probably one of the most useful and interesting examples of the use of prokaryotes for bioremediation purposes is the cleanup of oil spills. The importance of prokaryotes to petroleum bioremediation has been demonstrated in several oil spills in recent years, such as the Exxon Valdez spill in Alaska (1989) (Figure **17.5.1.1**), the Prestige oil spill in Spain (2002), the spill into the Mediterranean from a Lebanon power plant (2006,) and more recently, the BP oil spill in the Gulf of Mexico (2010). To clean up these spills, bioremediation is promoted by adding inorganic nutrients that help bacteria already present in the environment to grow. Hydrocarbon-degrading bacteria feed on the hydrocarbons in the oil droplet, breaking them into inorganic compounds. Some species, such as *Alcanivorax borkumensis*, produce surfactants that solubilize the oil, while other bacteria degrade the oil into carbon dioxide. In the case of oil spills in the ocean, ongoing, natural bioremediation tends to occur, inasmuch as there are oil-consuming bacteria in the ocean prior to the spill. Under ideal conditions, it has been reported that up to 80 percent of the nonvolatile components in oil can be degraded within 1 year of the spill. Researchers have genetically engineered other bacteria to consume petroleum products; indeed, the first patent application for a bioremediation application in the U.S. was for a genetically modified oil-eating bacterium.



(a) (b)

Figure **17.5.1.1**. (a) Cleaning up oil after the Valdez spill in Alaska, the workers hosed oil from beaches and then used a floating boom to corral the oil, which was finally skimmed from the water surface. Some species of bacteria are able to solubilize and degrade the oil. (b) One of the most catastrophic consequences of oil spills is the damage to fauna. (credit a: modification of work by NOAA; credit b: modification of work by GOLUBENKOV, NGO: Saving Taman)

There are a number of cost/efficiency advantages to bioremediation, which can be employed in areas that are inaccessible without excavation. For example, hydrocarbon spills (specifically, oil spills) or certain chlorinated solvents may contaminate groundwater, which can be easier to treat using bioremediation than more conventional approaches. This is typically much less expensive than excavation followed by disposal elsewhere, incineration, or other off-site treatment strategies. It also reduces or eliminates the need for “pump and treat”, a practice common at sites where hydrocarbons have contaminated clean groundwater. Using prokaryotes for bioremediation of hydrocarbons also has the advantage of breaking down contaminants at the molecular level, as opposed to simply chemically dispersing the contaminant.

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17.5.2: Water Treatment

Resolution of the global water pollution crisis requires multiple approaches to improve the quality of our fresh water and move towards sustainability. The most deadly form of water pollution, pathogenic microorganisms that cause waterborne diseases, kills almost 2 million people in underdeveloped countries every year. The best strategy for addressing this problem is proper sewage (wastewater) treatment. Untreated sewage is not only a major cause of pathogenic diseases, but also a major source of other pollutants, including oxygen-demanding waste, nutrients (N and P, particularly), and toxic heavy metals. Wastewater treatment is done at a sewage treatment plant in urban areas and through a septic tank system in rural areas.

The main purpose of **sewage (wastewater) treatment** is to remove organic matter (oxygen-demanding waste) and kill bacteria. Special methods also can be used to remove nutrients and other pollutants. The numerous steps at a conventional sewage treatment plant include **pretreatment** (screening and removal of sand and gravel), **primary treatment** (settling or floatation to remove organic solids, fat, and grease), **secondary treatment** (aerobic bacterial decomposition of organic solids), **tertiary treatment** (bacterial decomposition of nutrients and filtration), **disinfection** (treatment with chlorine, ozone, ultraviolet light, or bleach to kill most microbes), and either **discharge** to surface waters (usually a local river) or reuse for some other purpose, such as irrigation, habitat preservation, and artificial groundwater recharge (Figure 17.5.2.1).

The concentrated organic solid produced during primary and secondary treatment is called **sludge**, which is treated in a variety of ways including landfill disposal, incineration, use as fertilizer, and anaerobic bacterial decomposition, which is done in the absence of oxygen. Anaerobic decomposition of sludge produces methane gas, which can be used as an energy source. To reduce water pollution problems, separate sewer systems (where street runoff goes to rivers and only wastewater goes to a wastewater treatment plant) are much better than combined sewer systems, which can overflow and release untreated sewage into surface waters during heavy rain. Some cities such as Chicago, Illinois have constructed large underground caverns and also use abandoned rock quarries to hold storm sewer overflow. After the rain stops, the stored water goes to the sewage treatment plant for processing.

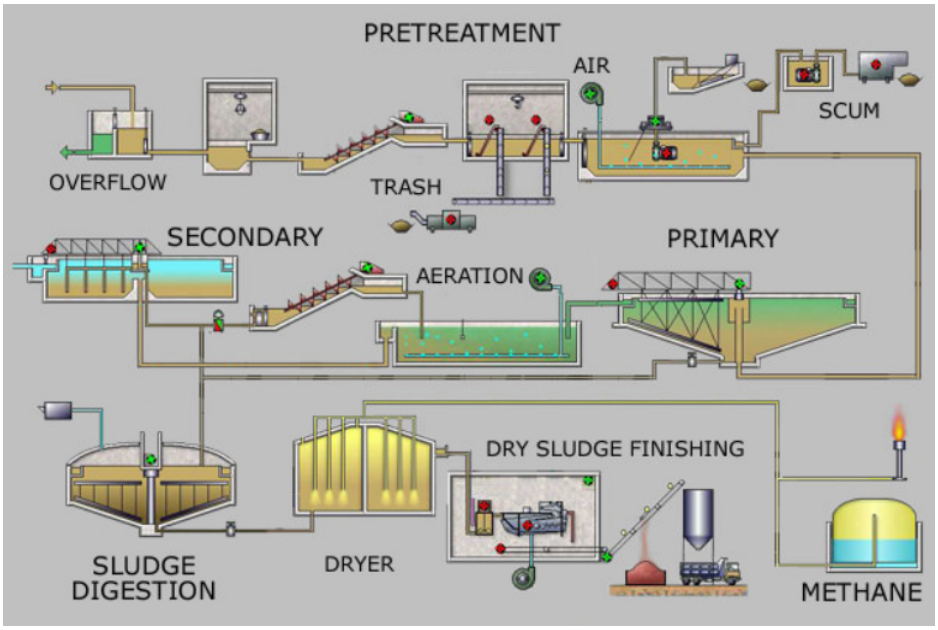


Figure 17.5.2.1. Steps at a Sewage Treatment Plant The numerous processing steps at a conventional sewage treatment plant include pretreatment (screening and removal of sand and gravel), primary treatment (settling or floatation to remove organic solids, fat, and grease), secondary treatment (aerobic bacterial decomposition of organic solids), tertiary treatment (bacterial decomposition of nutrients and filtration), disinfection (treatment with chlorine, ozone, ultraviolet light, or bleach), and either discharge to surface waters (usually a local river) or reuse for some other purpose, such as irrigation, habitat preservation, and artificial groundwater recharge. Source: Leonard G.via Wikipedia

A **septic tank system** is an individual sewage treatment system for homes in typically rural settings. The basic components of a septic tank system (Figure 17.5.2.2) include a sewer line from the house, a septic tank (a large container where sludge settles to the bottom and microorganisms decompose the organic solids anaerobically), and the drain field (network of perforated pipes where

the clarified water seeps into the soil and is further purified by bacteria). Water pollution problems occur if the septic tank malfunctions, which usually occurs when a system is established in the wrong type of soil or maintained poorly.

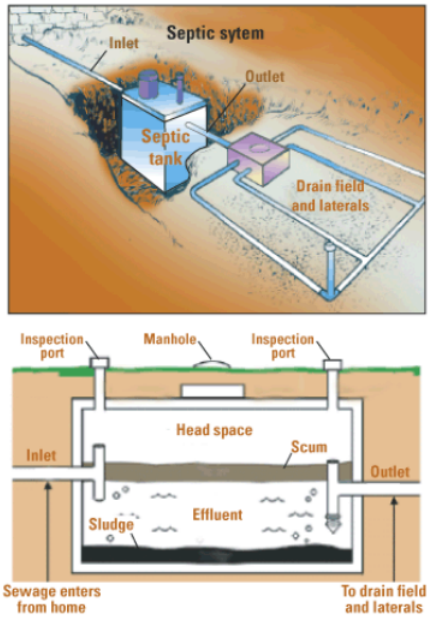


Figure **17.5.2.2**. Septic System Septic tank system for sewage treatment. Source: United States Geological Survey

For many developing countries, financial aid is necessary to build adequate sewage treatment facilities. The World Health Organization estimates an estimated cost savings of between $3 and $34 for every $1 invested in clean water delivery and sanitation. The cost savings are from health care savings, gains in work and school productivity, and prevented deaths. Simple and inexpensive techniques for treating water at home include chlorination, filters, and solar disinfection. Another alternative is to use constructed wetlands technology (marshes built to treat contaminated water), which is simpler and cheaper than a conventional sewage treatment plant.

Bottled water is not a sustainable solution to the water crisis. Bottled water is not necessarily any safer than the U.S. public water supply, it costs on average about 700 times more than U.S. tap water, and every year it uses approximately 200 billion plastic and glass bottles that have a relatively low rate of recycling. Compared to tap water, it uses much more energy, mainly in bottle manufacturing and long-distance transportation. If you don't like the taste of your tap water, then please use a water filter instead of bottled water!

CLEAN WATER ACT

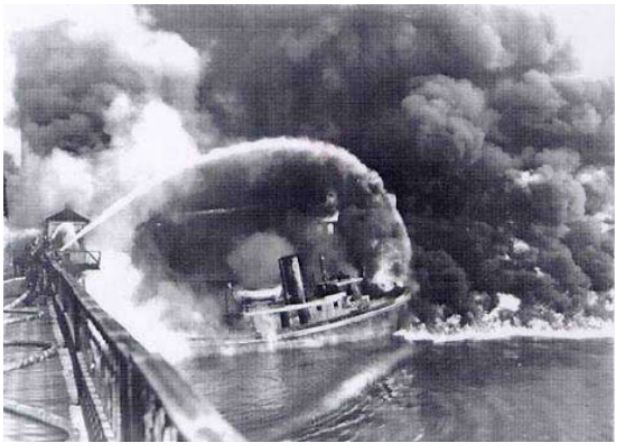


Figure **17.5.2.3**. Cuyahoga River on fire. Source: National Oceanic and Atmospheric Administration

During the early 1900s rapid industrialization in the U.S. resulted in widespread water pollution due to free discharge of waste into surface waters. The Cuyahoga River in northeast Ohio caught fire numerous times, including a famous fire in 1969 that caught the

nation’s attention. In 1972 Congress passed one of the most important environmental laws in U.S. history, the Federal Water Pollution Control Act, which is more commonly called the **Clean Water Act**. The purpose of the Clean Water Act and later amendments is to maintain and restore water quality, or in simpler terms to make our water swimmable and fishable. It became illegal to dump pollution into surface water unless there was formal permission and U.S. water quality improved significantly as a result. More progress is needed because currently the EPA considers over 40,000 U.S. water bodies as impaired, most commonly due to pathogens, metals, plant nutrients, and oxygen depletion. Another concern is protecting groundwater quality, which is not yet addressed sufficiently by federal law.

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17.5.3: Genomics and Biofuels

Learning Objectives

- Explain the process of creating new biofuels by using microbial genomics

Knowledge of the genomics of microorganisms is being used to find better ways to harness biofuels from algae and cyanobacteria. The primary sources of fuel today are coal, oil, wood, and other plant products, such as ethanol. Although plants are renewable resources, there is still a need to find more alternative renewable sources of energy to meet our population ‘s energy demands. The microbial world is one of the largest resources for genes that encode new enzymes and produce new organic compounds, and it remains largely untapped.

For microbial biomass breakdown, many candidates have already been identified. These include Clostridia species for their ability to degrade cellulose, and fungi that express genes associated with the decomposition of the most recalcitrant features of the plant cell wall, lignin, the phenolic “glue” that imbues the plant with structural integrity and pest resistance. The white rot fungus *Phanerochaete chrysosporium* produces unique extracellular oxidative enzymes that effectively degrade lignin by gaining access through the protective matrix surrounding the cellulose microfibrils of plant cell walls.

Another fungus, the yeast *Pichia stipitis*, ferments the five-carbon “wood sugar” xylose abundant in hardwoods and agricultural harvest residue. *Pichia*‘s recently-sequenced genome has revealed insights into the metabolic pathways responsible for this process, guiding efforts to optimize this capability in commercial production strains. Pathway engineering promises to produce a wider variety of organisms able to ferment the full repertoire of sugars derived from cellulose and hemicellulose and tolerate higher ethanol concentrations to optimize fuel yields. For instance, the hindgut contents of nature’s own bioreactor, the termite, has yielded more than 500 genes related to the enzymatic deconstruction of cellulose and hemicellulose.



Figure 17.5.3.1: Termites: Nature's Bioreactors: The hindgut of the termite has yielded more than 500 genes of microbes related to the enzymatic deconstruction of cellulose.

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Key Points

- Microorganisms can encode new enzymes and produce new organic compounds that can be used as biofuels.
- Genomic analysis of the fungus *Pichia* will allow optimization of its use in fermenting ethanol fuels.
- Analysis of the microbes in the hindgut of termites have found 500 genes that may be useful in enzymatic destruction of cellulose.
- Genetic markers have been used in forensic analysis, like in 2001 when the FBI used microbial genomics to determine a specific strain of anthrax that was found in several pieces of mail.
- Genomics is used in agriculture to develop plants with more desirable traits, such as drought and disease resistance.

Key Terms

- **renewable resource**: a natural resource such that it is replenished by natural processes at a rate comparable to its rate of consumption by humans or other users
- **biofuel**: any fuel that is obtained from a renewable biological resource

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SECTION OVERVIEW

17.6: Medical Applications

17.6.1: Recombinant Protein Production

17.6.2: Fluorescence In Situ Hybridization

17.6.3: Microarrays

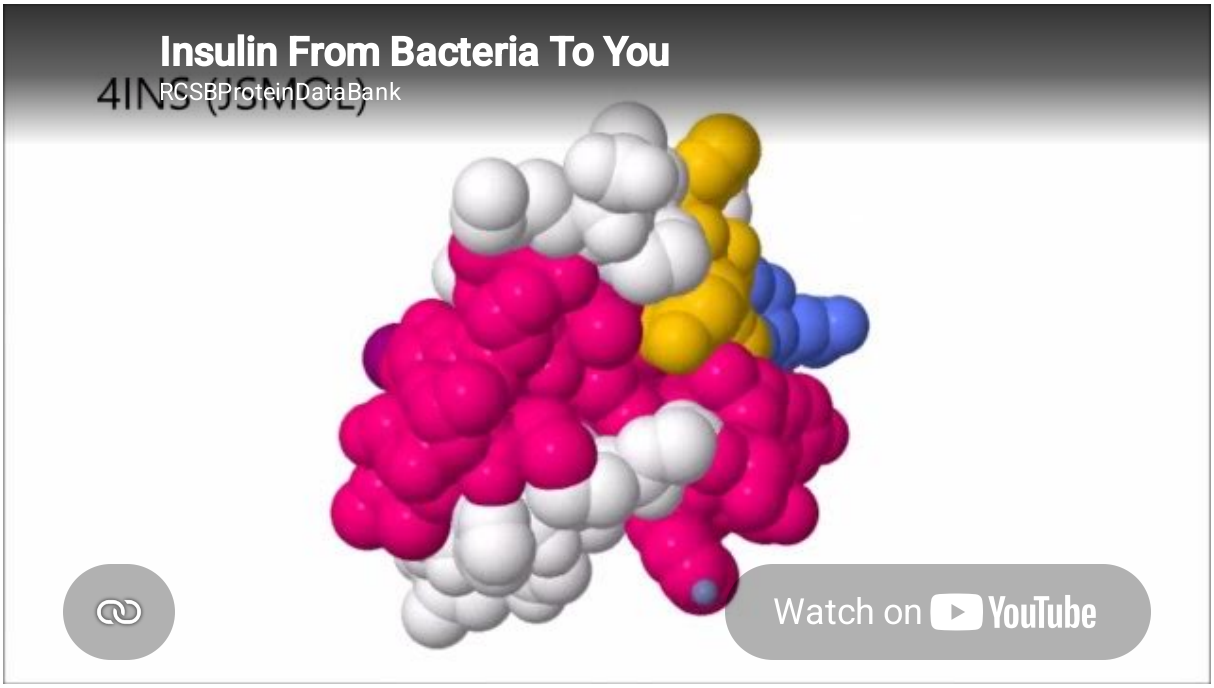
17.6.4: Immunoassays

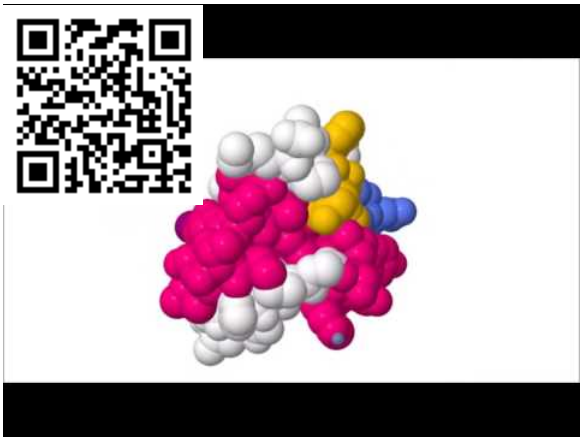
17.6.5: Gene Therapy

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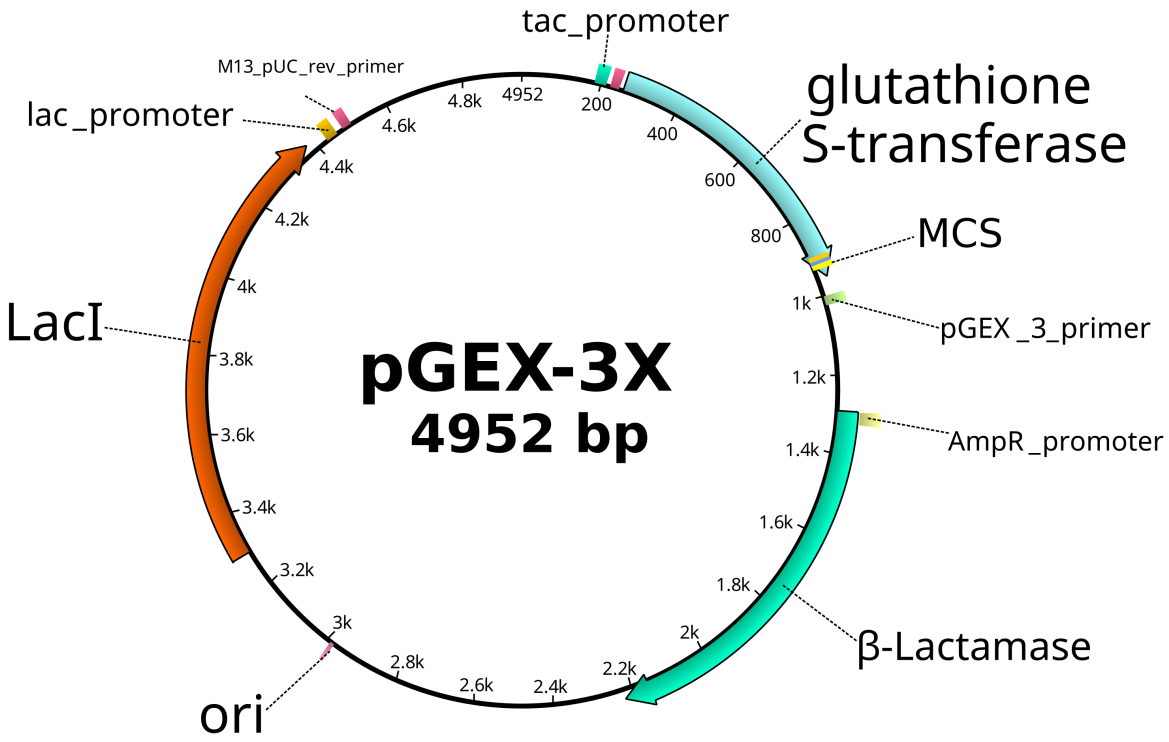
17.6.1: Recombinant Protein Production

Protein Expression





Recombinant DNA technology has many uses in basic scientific research to better understand the nature of living things. As a tool, recombinant DNA technology can be used to express proteins towards medical applications. Prior to biotechnology, type I diabetes (insulin-dependent) was treated by injection of insulin isolated from the pancreas of pigs. With the ability to express human proteins inside bacteria, yeast, and other cells, sacrificing pigs for porcine insulin is no longer necessary.



*Bacterial expression vector **pGEX-3X** contains the AmpR gene, the origin of replication, MCS downstream of the hybrid lac/trp promoter (tac) and the coding sequence for glutathione-S-transferase (GST). GST acts as a tag that is fused directly with the protein from the gene of interest and used to purify the protein with a glutathione resin.*

Bacteria or other cells can be engineered to express proteins through the process of cloning and transformation. Bacteria are advantageous because of their rapid life cycle and ease of growth. A bacterial expression vector contains the basic plasmid features: the origin of replication as well as antibiotic resistance gene. Often, an **affinity tag** will be used to aid in the purification of the protein. An example in the vector above shows the **GST** (glutathione-s-transferase) tag that can be purified with glutathione resin. Expression is only the first problem since bacteria are also synthesizing proteins that are required for the bacteria to grow and divide. Injecting these proteins in addition to insulin would cause an immune reaction that could be deadly. Therefore, it is required that overexpressed proteins be purified and isolated from other undesirable proteins.



Credit: Stewart EJ, Madden R, Paul G, Taddei F (CC-SA 3.0).

Criteria for Choosing an Expression System

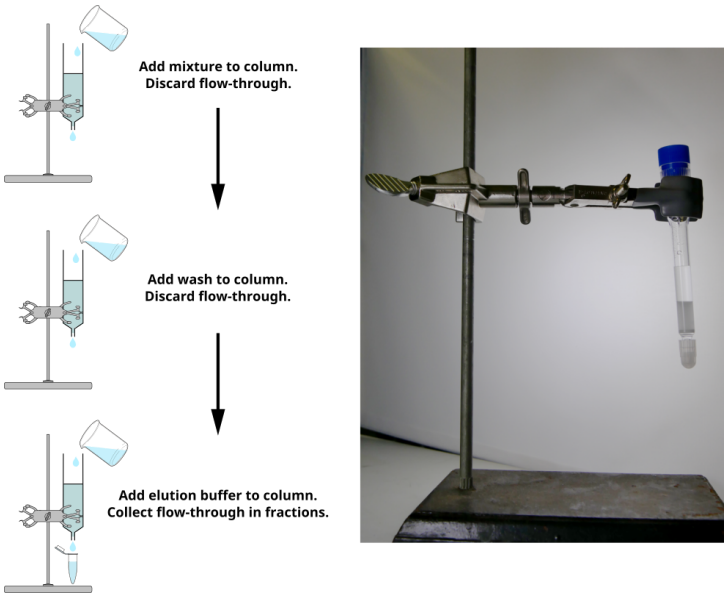
Desired characteristics	Bacteria	Yeast	Insect (baculovirus)	Mammalian cell culture (COS, CHO, HEK)
Cell growth	Rapid	Rapid	Slow	Slow
Complexity of growth medium	Minimum	Minimum	Complex	Complex
Cost of growth medium	Low	Low	High	High
Expression level	High	Low to high	Low to high	Low to moderate
Extracellular expression	Secretion to periplasm	Secretion to medium	Secretion to medium	Secretion to medium
Protein folding	Refolding usually required	Refolding may be required	Proper	Proper
Glycosylation	No	Yes	Some	Yes

Gene Expression Systems. Using nature for the art of expression (Fernandez, J.M. & Hoeffler, J.P., eds), Academic Press, San Diego, 1999.

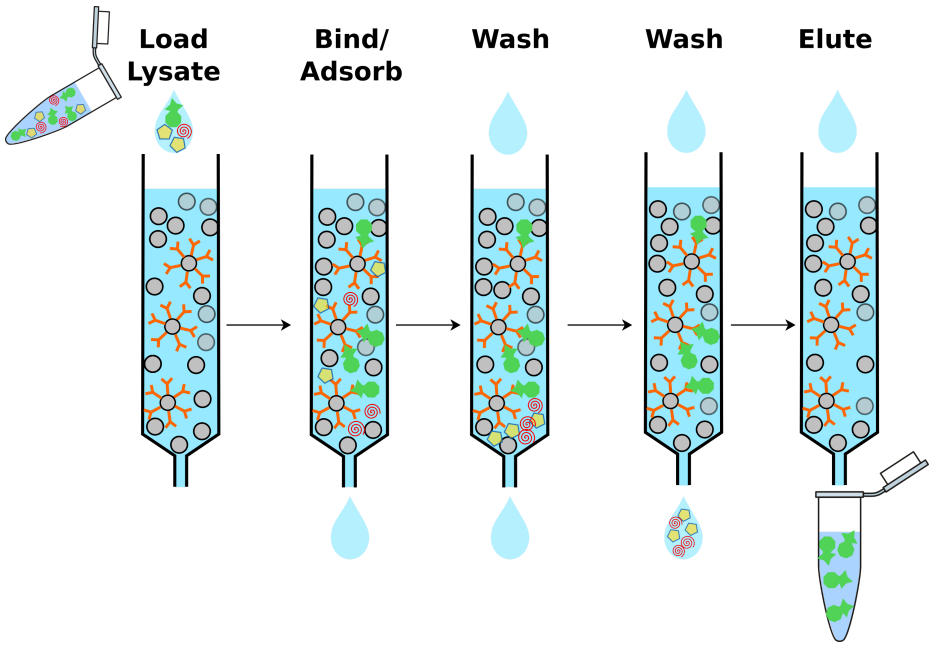
Protein expression systems have inherent advantages and disadvantages. The table above summarizes the comparison of the various cellular systems of production (Fernandez & Hoeffler, 1999).

Purification

Different methods of isolation can be applied depending on the properties of the protein. **Ion exchange chromatography** is useful if the protein of interest has a specific charge that will interact with a resin packed with the opposite charge.



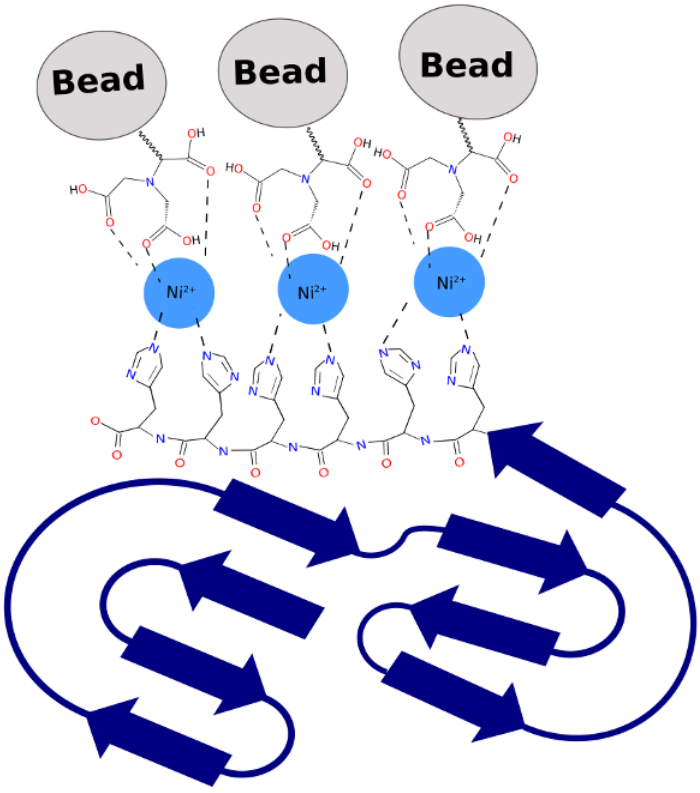
Immunoprecipitation



Immunoprecipitation: Column is packed with Protein-A agarose which binds to antibodies. Cell lysates are then loaded onto the columns where they flow through and are allowed to interact with the antibody. Washes are performed to remove the non-specifically bound proteins. An elution buffer is used to disrupt the interaction of the antibody to the protein target.

Affinity Purification

Affinity purification employs the use of specific antibodies that bind to the protein of interest very tightly to retain it on a column. With these techniques, the protein retained on the resin is washed numerous times to remove other proteins that are non-specifically sticking. A change in pH or ionic conditions then is used to disrupt the interaction with the resin and **elute** the proteins from the column. Proteins that are engineered to contain tags can be purified by antibodies specific to those tags. Also, the addition of 6 or more consecutive Histidine residues to the end of a protein makes them susceptible to purification with Nickel-NTA resin or Cobalt purification. In these cases, the 6XHis tag associates with these metal ions on the resin are selectively adhered.



Nickel NTA resin coordinating the capture of a 6His tagged protein.

Size Exclusion

File:Activated Charcoal.jpg

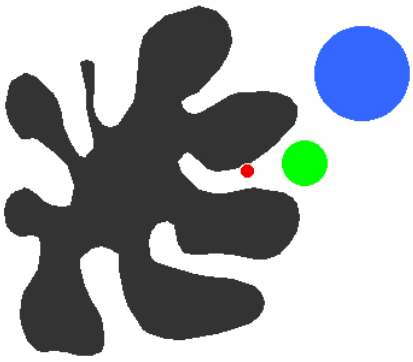
Credit: Mydriatic (CC-BY-SA 3.0)

File:SizeExChrom.png

Credit: Takometer(CC-BY 2.5)

Most of you are familiar with water purification filters. Before using these filters, you soak them in water and dark residue leaks out. This dark residue is activated charcoal. The activated charcoal has tiny microscopic pores that trap small items like ions and other particles. The primary goal of these filters is to remove metals and chlorine that are found in tap water. The porous nature of activated charcoal renders it useful for trapping molecules in water purification systems.

The process used to trap these small particles is called **size exclusion**. Unlike agarose gel electrophoresis where the smaller particles navigate through the matrix faster, size exclusion resins trap the smaller molecules.



The smaller the molecule, the longer they spend within the pores as they traverse through the matrix.

Significance of Purification

File:Limulus polyphemus (aq.).jpg

Credit: Hans Hillewaert (CC-BY)

All injectable drugs must be clean of endotoxins from bacteria. Purification of the protein of interest from bacterial lysates removes the dangerous pathogenic materials from that would otherwise activate host immune reactivity.

The horseshoe crab (*Limulus polyphemus*) performs a special function in the ecosystem by providing eggs for migratory birds to feed on. This organism also houses a special cell type in its hemolymph. The Limulus amoebocyte lysate (**LAL**) test is the most sensitive assay of detecting endotoxins from bacteria. Amoebocytes are collected from these organisms for use on testing batches of injectable drugs to ensure proper purification and safety.

References

- Joseph M. Fernandez and James P. Hoeffler. Introduction: SO MANY POSSIBILITIES: HOW TO CHOOSE A SYSTEM TO ACHIEVE YOUR SPECIFIC GOAL, In Gene Expression Systems. Academic Press, San Diego. 1999, Pages 1-5, ISBN 9780122538407. http://dx.doi.org/10.1016/B978-012253840-7/50001-8.

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17.6.2: Fluorescence In Situ Hybridization

Bright Field Microscopy

How can we confirm that a person has a specific chromosomal abnormality? The first method was simply to obtain a sample of their cells, stain the chromosomes with **Giemsa** dye, and examine the results with a light microscope (Figure **17.6.2.1**). Each chromosome can be recognized by its length, the location of its centromere, and the characteristic pattern of purple bands produced by the Giemsa. For example, if mitotic cells from a person consistently contained forty seven chromosomes in total with three chromosome 21s this would be indicative of Down syndrome. Bright field microscopy does has its limitations though - it only works with mitotic chromosomes and many chromosome rearrangements are either too subtle or too complex for even a skilled cytogeneticist to discern.

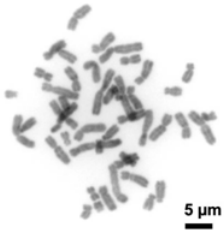


Figure **17.6.2.1**: Human chromosomes. One way to obtain chromosomes is to take a blood sample, culture the cells for three days in the presence of a T-cell growth factor, arrest the cells in metaphase with a microtubule inhibitor, and then drop the cells onto a slide. The cells burst and the chromosomes stick to the slide. The chromosomes can then be stained or probed. Because the cells are in metaphase it is possible to see 46 replicated chromosomes here. There will be dozens of collections of chromosomes like this over the entire slide. (Wikipedia-Steffen Dietzel-CC:AS)

Fluorescence In Situ Hybridization

The solution to these problems was **fluorescence in situ hybridization** (FISH). The technique is similar to a Southern blot in that a single stranded **DNA probe** is allowed to hybridize to denatured target DNA (see Section 8.6). However, instead of the probe being radioactive it is fluorescent and instead of the target DNA being restriction fragments on a nylon membrane it is denatured chromosomes on a glass slide. Because there are several fluorescent colours available it is common to use more than one probe at the same time. Typically the chromosomes are also labeled with a fluorescent stain called **DAPI** which gives them a uniform blue colour. If the chromosomes have come from a mitotic cell it is possible to see all forty six of them spread out in a small area. Alternatively, if the chromosomes are within the nucleus of an interphase cell they appear together within a large blue circle.

Using FISH to Diagnose Down Syndrome

Most pregnancies result in healthy children. However in some cases there is an elevated chance that the fetus has trisomy-21. Older women are at a higher risk because the non-disjunction events that lead to trisomy become more frequent with age. The second consideration is what the fetus looks like during an ultrasound examination. Fetuses with trisomy-21 and some other chromosome abnormalities have a swelling in the back of the neck called a nuchal translucency. If either or both factors is present the woman may choose amniocentesis. In this test some amniotic fluid is withdrawn so that the fetal cells within it can be examined. Figure **17.6.2.2** shows a positive result for trisomy-21. Based upon this image the fetus has two X chromosomes and three chromosome 21s and therefore has a karyotype of 47,XX,+21.

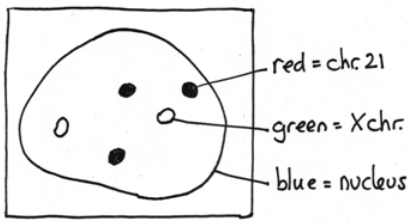


Figure **17.6.2.2**: Confirmation of Down syndrome in a fetal cell. This diagram is based upon actual results. The DNA has been stained blue with DAPI. A red fluorescent probe is binding to the centromeres of chromosome 21 (shown here as filled circles). A green fluorescent probe is binding to the centromeres of the X chromosome (open circles). Source: Figure 4 in Antonarakis, S. E. et al. 2004. Chromosome 21 and Down syndrome: From genomics to pathophysiology. Nature Reviews Genetics 5:725-738 PubMed ID: 15510164.

Using FISH to Diagnose Cri-du-Chat Syndrome

A physician may suspect that a patient has a specific genetic condition based upon the patient's physical appearance, mental abilities, health problems, and other factors. FISH can be used to confirm the diagnosis. For example, Figure **17.6.2.3** shows a positive result for cri-du-chat syndrome. The probes are binding to two long arms of chromosome 5 but only one short arm. One of the chromosome 5s must therefore be missing part of its short arm.

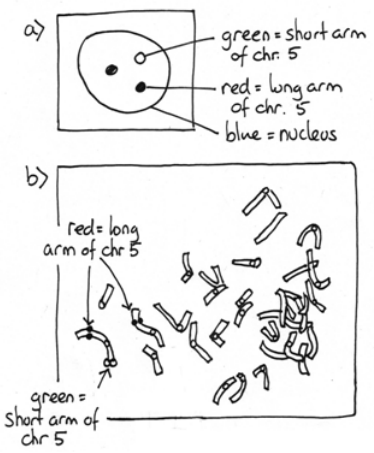


Figure **17.6.2.3**: A positive result for cri-du-chat syndrome. This diagram is based upon actual results. Cells from a patient's blood were prepared to show an interphase nucleus (a) and mitotic chromosomes (b). The DNA has been coloured blue with DAPI. The green fluorescent probe is binding to the tip of the short arm of chromosome 5 (shown here as open circles). This is the region absent in cri-du-chat. The red fluorescent probe is binding to the middle of the long arm of the same chromosome (filled circles). This probe is used as a control. Source: Figure 1 in Fang J.-S. et al. 2008 Cytogenetic and molecular characterization of three-generation family with chromosome 5p terminal deletion. Clinical Genetics 73:585-590 PubMed ID: 18400035.

Newer Techniques

FISH is an elegant technique that produces dramatic images of our chromosomes. Unfortunately, FISH is also expensive, time consuming, and requires a high degree of skill. For these reasons, FISH is slowly being replaced with PCR and DNA chip based methods. Versions of these techniques have been developed that can accurately quantify a person's DNA. For example a sample of DNA from a person with Down syndrome will contain 150% more DNA from chromosome 21 than the other chromosomes. Likewise DNA from a person with cri-du-chat syndrome will contain 50% less DNA from the end of chromosome 5. These techniques are very useful if the suspected abnormality is a deletion, a duplication, or a change in chromosome number. They are less useful for diagnosing chromosome inversions and translocations because these rearrangements often involve no net loss or gain of genes.

In the future all of these techniques will likely be replaced with DNA sequencing. Each new generation of genome sequencing machines can sequence more DNA in less time. Eventually it will be cheaper just to sequence a patient's entire genome than to use FISH or PCR to test for specific chromosome defects.

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17.6.3: Microarrays

2D gels are one way of surveying a broad spectrum of molecules simultaneously. Other approaches to doing the same thing involve what are called microarrays. DNA microarrays, for example, can be used to determine all of the genes that are being expressed in a given tissue, simultaneously. Microarrays employ a grid (or array) made of rows and columns on a glass slide, with each box of the grid containing many copies of a specific molecule, say a single-stranded DNA molecule corresponding to the sequence of a single unique gene. As an example, consider scanning the human genome for all of the known mRNA sequences and then synthesizing single stranded DNAs complementary to each mRNA. Each complementary DNA sequence would have its own spot on the matrix. The position of each unique gene sequence on the grid is known and the entire grid would represent all possible genes that are expressed. Then for a simple gene expression analysis, one could take a tissue (say liver) and extract the mRNAs from it. These mRNAs represent all the genes that are being expressed in the liver at the time the extract was made.

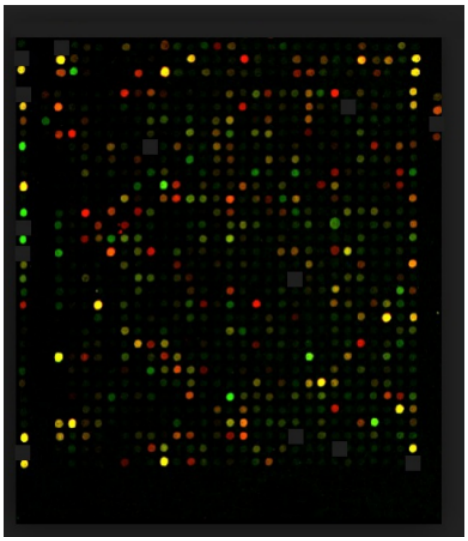


Figure 9.10.1: *Microarray*

The mRNAs can easily be tagged with a colored dye (say blue). The mixture of tagged mRNAs is then added to the array and base-pairing conditions are created to allow complementary sequences to find each other. When the process is complete, each liver mRNA should have bound to its corresponding gene on the array, creating a blue spot in that box on the grid. Since it is known which genes are in which box, a blue spot in a box indicates that the gene in that box was expressed in the liver. The presence and abundance of each mRNA may then readily determined by measuring the amount of blue dye at each box of the grid. A more powerful analysis could be performed with two sets of mRNAs, each with a different colored tag (say blue and yellow). One set of mRNAs could come from the liver of a vegetarian (tagged blue) and the other from a meat eater (tagged yellow), for example. The mRNAs are mixed and then added to the array and complementary sequences are once again allowed to form duplexes. After unhybridized mRNAs are washed away, the plate is analyzed. Blue spots in grid boxes correspond to mRNAs present in the vegetarian liver, but not in that of the meat eater. Green spots (blue plus yellow) would correspond to mRNAs present in equal abundance in the two livers. The intensity of each spot would also give information about the relative amounts of each mRNA in the tissues. Similar analyses could be done, using cDNAs instead of mRNA. Peptide microarrays have peptides bonded to the glass slide instead of DNA and can be used to study the binding of proteins or other molecules to the peptides.

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17.6.4: Immunoassays

Learning Objectives

- Describe how the Enzyme-linked immunosorbent assay (ELISA) can be used to detect and quantitate antigens, antibodies and allergens

Enzyme-linked immunosorbent assay (ELISA) is a method of quantifying an antigen immobilized on a solid surface. ELISA uses a specific antibody with a covalently coupled enzyme. The amount of antibody that binds the antigen is proportional to the amount of antigen present, which is determined by spectrophotometrically measuring the conversion of a clear substance to a colored product by the coupled enzyme.

Several variations of ELISA, seen in, exist but the most commonly used method is the sandwich ELISA. The sandwich assay uses two different antibodies that are reactive with different epitopes on the antigen with a concentration that needs to be determined. A fixed quantity of one antibody is attached to a series of replicate solid supports, such as plastic microtiter multi-well plate. Test solutions containing antigen at an unknown concentration are added to the wells and allowed to bind. Unbound antigen is removed by washing, and a second antibody which is linked to an enzyme is allowed to bind. This second antibody-enzyme complex constitutes the indicator system of the test. The antigen serves as bridge, so the more antigen in the test solution, the more enzyme-linked antibody will bind. The test solution is used in parallel with a series of standard solutions with known concentrations of antigen that serve as control and reference. The results obtained from the standard solutions are used to construct a binding curve of the second antibody as a function of antigen concentration. The concentration of antigens can be inferred from absorbance readings of standard solutions.

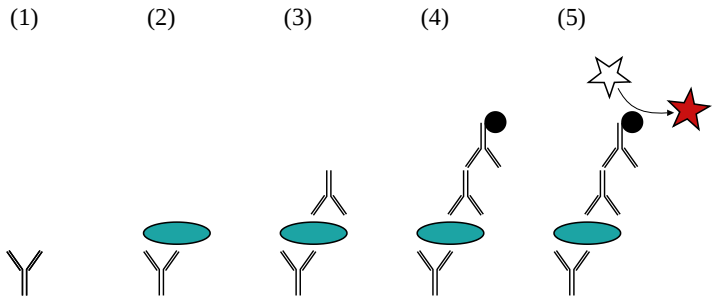


Figure: **Sandwich ELISA**: Two antibodies recognize different epitopes on same antigen.

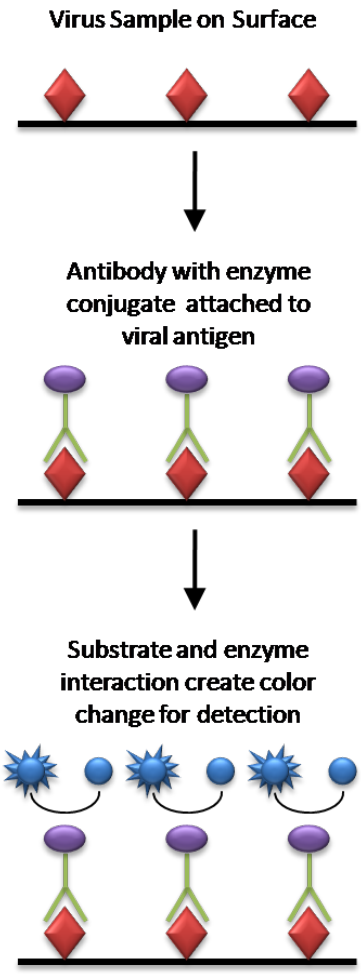


Figure: **ELISA**: Direct ELISA diagram using a viral antigen as an example.

Key Points

- ELISA is a quantitative technique that measures serum concentration of antigens, antibodies, and allergens.
- Standard ELISA uses antibody-antigen-antibody trapping principle with the second antibody coupled to an enzyme. If the complex is formed, the enzyme converts a clear solution into a colored one that can be measured with a spectrophotometer.
- ELISA is performed in a muti-well microtiter plate. In addition to the test solution, standard solutions are added with known antigen concentration. These solutions will be used to infer the concentration of the antigen being tested.

Key Terms

- **spectrophotometrically**: By using spectrophotometry.
- **epitope**: That part of a biomolecule (such as a protein) that is the target of an immune response.

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17.6.5: Gene Therapy

It is easy to see how biotechnology can be used for medicinal purposes. Knowledge of the genetic makeup of our species, the genetic basis of heritable diseases, and the invention of technology to manipulate and fix mutant genes provides methods to treat the disease.

Genetic Diagnosis and Gene Therapy

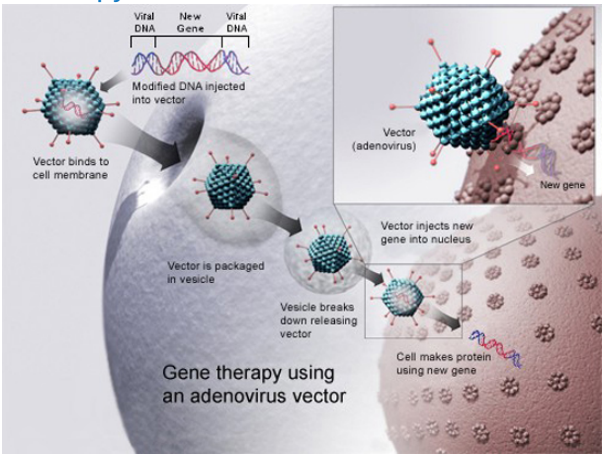


Figure 1. Gene therapy using an adenovirus vector can be used to cure certain genetic diseases in which a person has a defective gene. (credit: NIH)

The process of testing for suspected genetic defects before administering treatment is called **genetic diagnosis** by **genetic testing**. Depending on the inheritance patterns of a disease-causing gene, family members are advised to undergo genetic testing. For example, women diagnosed with breast cancer are usually advised to have a biopsy so that the medical team can determine the genetic basis of cancer development. Treatment plans are based on the findings of genetic tests that determine the type of cancer. If the cancer is caused by inherited gene mutations, other female relatives are also advised to undergo genetic testing and periodic screening for breast cancer. Genetic testing is also offered for fetuses (or embryos with *in vitro* fertilization) to determine the presence or absence of disease-causing genes in families with specific debilitating diseases.

Gene therapy is a genetic engineering technique used to cure disease. In its simplest form, it involves the introduction of a good gene at a random location in the genome to aid the cure of a disease that is caused by a mutated gene. The good gene is usually introduced into diseased cells as part of a vector transmitted by a virus that can infect the host cell and deliver the foreign DNA (Figure 1). More advanced forms of gene therapy try to correct the mutation at the original site in the genome, such as is the case with treatment of severe combined immunodeficiency (SCID).

Here's a website to help you learn more information on SCID and its gene therapy trials.

Production of Vaccines, Antibiotics, and Hormones

Traditional vaccination strategies use weakened or inactive forms of microorganisms to mount the initial immune response. Modern techniques use the genes of microorganisms cloned into vectors to mass produce the desired antigen. The antigen is then introduced into the body to stimulate the primary immune response and trigger immune memory. Genes cloned from the influenza virus have been used to combat the constantly changing strains of this virus.

Antibiotics are a biotechnological product. They are naturally produced by microorganisms, such as fungi, to attain an advantage over bacterial populations. Antibiotics are produced on a large scale by cultivating and manipulating fungal cells.

Recombinant DNA technology was used to produce large-scale quantities of human insulin in *E. coli* as early as 1978. Previously, it was only possible to treat diabetes with pig insulin, which caused allergic reactions in humans because of differences in the gene product. In addition, human growth hormone (HGH) is used to treat growth disorders in children. The HGH gene was cloned from a cDNA library and inserted into *E. coli* cells by cloning it into a bacterial vector.

Learning Objectives

Transgenic organisms possess DNA from a different species, usually generated by molecular cloning techniques. Vaccines, antibiotics, and hormones are examples of products obtained by recombinant DNA technology. Transgenic plants are usually created to improve characteristics of crop plants.

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17.7: Agricultural Applications

Agricultural biotechnology is a range of tools, including traditional breeding techniques, that alter living organisms, or parts of organisms, to make or modify products; improve plants or animals; or develop microorganisms for specific agricultural uses. Modern biotechnology today includes the tools of genetic engineering. **Genetic engineering** is the name for certain methods that scientists use to introduce new traits or characteristics to an organism (known also as **genetically modified organism** or **GMO**). For example, plants may be genetically modified to produce characteristics to enhance the growth or nutritional profile of food crops.

Benefits of Genetic Engineering

Advocates of modern biotechnology and generic engineering say that the application of biotechnology in agriculture has resulted in benefits to farmers, producers, and consumers.

Enhanced nutrition. Advances in biotechnology may provide consumers with foods that are nutritionally-enriched (Figure below) or longer-lasting, or that contain lower levels of certain naturally occurring toxicants present in some food plants. Developers are using biotechnology to try to reduce saturated fats in cooking oils, reduce allergens in foods, and increase disease-fighting nutrients in foods. Biotechnology may also be used to conserve natural resources, enable animals to more effectively use nutrients present in feed, decrease nutrient runoff into rivers and bays, and help meet the increasing world food and land demands.



Figure 17.7.1: White rice and Golden rice. Genetically engineered “Golden Rice” contains up to 35 µg β-carotene per gram of rice.

Cheaper and more manageable production. Biotechnology may provide farmers with tools that can make production cheaper and more manageable. For example, some biotechnology crops can be engineered to tolerate specific herbicides, which make weed control simpler and more efficient. Other crops have been engineered to be resistant to specific plant diseases and insect pests, which can make pest control more reliable and effective, and/or can decrease the use of synthetic pesticides. These crop production options can help countries keep pace with demands for food while reducing production costs.

Improved pest control. Biotechnology has helped to make both insect pest control and weed management safer and easier while safeguarding crops against disease. For example, genetically engineered insect-resistant cotton has allowed for a significant reduction in the use of persistent, synthetic pesticides that may contaminate groundwater and the environment. In terms of improved weed control, herbicide-tolerant soybeans, cotton, and corn enable the use of reduced-risk herbicides that break down more quickly in soil and are non-toxic to wildlife and humans.

Concerns about Genetically modified Organisms

The complexity of ecological systems presents considerable challenges for experiments to assess the risks and benefits and inevitable uncertainties of GMOs. Assessing such risks is extremely difficult, because both natural and human-modified systems are highly complex, and fraught with uncertainties that may not be clarified until long after an experimental introduction has been concluded. Critics of GMOs warn that the cultivation of GMOs, with their potential benefits and hazards to the environment, should be carefully considered within broader ecosystems.

Interbreeding with native species. When the genetically modified organisms are allowed to breed with the organisms which are not genetically engineered, then these organisms may affect the genetic of non-genetically engineered organisms. Due to this reason the whole ecological system might get affected. The main concern is that genetically modified organisms might lead the non-GM organisms to extinction and reduce biodiversity.

GM food labeling. In order to verify whether people have been harmed over the years by consuming GMF, specifically in countries like the US where people's dietary are mainly composed of such products, the law for mandatory labeling is highly required. However, the labeling is not just about health issue rather, it is about consumer rights to make an informed choice. Although a consensual system on GMO labeling is crucial, it seems unlikely that an internationally agreed labeling system can be set up in proximate future. Nevertheless, different GMO labeling schemes have been established in different countries, ranging from stringent to extremely lenient or even non existent legislations. While the EU has established strict labeling regulations, in the US, Canada and Argentina, three big producers of GMO food, such laws have been put forward but not enacted by these governments. A proper labeling represents the “GM” word, along with additional information on changed characteristics and the external source of the inserted gene. Negative labeling such as “GM free” is not suggested, because it might give the wrong impression to the consumers. The law for compulsory labeling of genetically modified food products has been established in more than 40 countries. Surveys commissioned by different organizations have shown that people across the world are seeking for transparency and consumer choice and believe that compulsory labeling scheme on GM ingredients is highly required: 88% Canadians, 92% Americans and 93% French.

Consumers right to choose. The International Federation of Organic Agriculture Movement has made stringent efforts to keep GMOs out of organic production, yet some US organic farmers have found their corn (maize) crops, including seeds, to contain detectable levels of genetically engineered DNA. The organic movement is firm in its opposition to any use of GMOs in agriculture, and organic standards explicitly prohibit their use. The farmers, whose seed is contaminated, have been under rigid organic certification, which assures that they did not use any kind of genetically modified materials on their farms. Any trace of GMOs must have come from outside their production areas. While the exact origin is unclear at this time, it is most likely that the pollution has been caused by pollen drift from GMO-fields in surrounding areas. However, the contamination may have also come from the seed supply. Seed producers, who intended to supply GMO-free seed, have also been confronted with genetic contamination and cannot guarantee that their seed is 100% GMO-free.

Ecological long-term effects. The Bt corn produces wind-borne pollen that kills the caterpillars of the Monarch butterfly. If the life cycles of this butterfly are disrupted, the Monarch butterflies might be endangered. Agriculture might be affected as the weeds acquire the modified genes to become more competitive. The risk of the evolution of common plant viruses to become more resistant or form new strains will be greatly increased. If genetic modification is carried out extensively, new viruses with greater potential to harm humankind may evolve, and the probability of this occurring can be quite high.

Human health risk. At least some of the genes used in GMOs may not have been used in the food supply before, so GM foods may pose a potential risk for human health. Much of the GM production currently grown worldwide is destined for animal feed. The FAO has concluded that risks to human and animal health from the use of GM crops and enzymes derived from GM microorganisms as animal feed are negligible. But scientists acknowledge that little is known about the long-term safety of consuming food made from GM products. WHO recognizes the need for continued safety assessments on genetically modified foods before they are marketed to prevent risks to human health and for continued monitoring.

The potential of GM crops to be allergenic is one of the main suspected adverse health effects. Many scientific data indicate that animals fed by GMO crops have been harmed or even died. Rats exposed to transgenic potatoes or soy had abnormal young sperm; cows, goats, buffalo, pigs and other livestock grazing on Bt-maize, GM cottonseed and certain biotech corn showed complications including early deliveries, abortions, infertility and also many died. However, this is a controversial subject as studies conducted by company producing the biotech crops did not show any negative effects of GM crops on mice.

Although Agri-biotech companies do not accept the direct link between the GMOs consumption and human health problems, there are some examples given by the opponents. For example: The foodborne diseases such as soy allergies have increased over the past 10 years in USA and UK and an epidemic of Morgellons disease in the US. There are also reports on hundreds of villagers and cotton handlers who developed skin allergy in India. Recent studies have revealed that Bacillus thuringiensis corn expresses an allergenic protein which alters overall immunological reactions in the body. The aforementioned reports performed by independent GMO researchers have lead to a concern about the risks of GMOs and the inherent risks associated with the genetic technology.

Intellectual property rights are one of the important factors in the current debate on GMOs. The GM crops are patented by Agri-business companies leading to monopolization of the global agricultural food and controlling distribution of the world food supply. Social activists believe that the hidden reason why biotech companies are eager to produce GMO crops is because they can be privatized, unlike ordinary crops which are the natural property of all humanity. It is argued for example that to achieve this monopoly, the large Agri-biotech company, Monsanto, has taken over small seed companies in the past 10 years and has become the biggest Agri-biotech Corporation in the world. The patent right for vegetable forms of life also affect the livelihoods of family farmers as they are required to sign a contract preventing them from saving and re-planting the seeds, thus they have to pay for seeds each year.

Critics, thus advise that the risks for the introduction of a GMOs into each new ecosystem need to be examined on a case-by-case basis, alongside appropriate risk management measures, such as through the precautionary principle in the Cartagena Protocol and the IPPC's Pest Risk Assessment (PRA).

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CHAPTER OVERVIEW

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18.1: Mapping Genomes

The study of nucleic acids began with the discovery of DNA, progressed to the study of genes and small fragments, and has now exploded to the field of genomics. Genomics is the study of entire genomes, including the complete set of genes, their nucleotide sequence and organization, and their interactions within a species and with other species. The advances in genomics have been made possible by DNA sequencing technology. Just as information technology has led to Google Maps that enable us to get detailed information about locations around the globe, genomic information is used to create similar maps of the DNA of different organisms.

Mapping Genomes

Genome mapping is the process of finding the location of genes on each chromosome. The maps that are created are comparable to the maps that we use to navigate streets. A genetic map is an illustration that lists genes and their location on a chromosome. Genetic maps provide the big picture (similar to a map of interstate highways) and use genetic markers (similar to landmarks). A genetic marker is a gene or sequence on a chromosome that shows genetic linkage with a trait of interest. The genetic marker tends to be inherited with the gene of interest, and one measure of distance between them is the recombination frequency during meiosis. Early geneticists called this linkage analysis.

Physical maps get into the intimate details of smaller regions of the chromosomes (similar to a detailed road map) (Figure 18.1.1). A physical map is a representation of the physical distance, in nucleotides, between genes or genetic markers. Both genetic linkage maps and physical maps are required to build a complete picture of the genome. Having a complete map of the genome makes it easier for researchers to study individual genes. Human genome maps help researchers in their efforts to identify human disease-causing genes related to illnesses such as cancer, heart disease, and cystic fibrosis, to name a few. In addition, genome mapping can be used to help identify organisms with beneficial traits, such as microbes with the ability to clean up pollutants or even prevent pollution. Research involving plant genome mapping may lead to methods that produce higher crop yields or to the development of plants that adapt better to climate change.

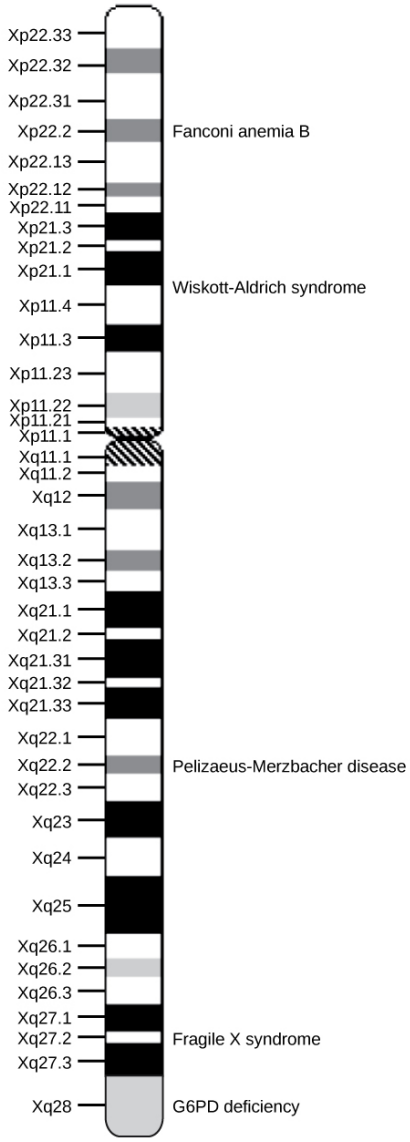


Figure 18.1.1: This is a physical map of the human X chromosome. (credit: modification of work by NCBI, NIH)

Genetic maps provide the outline, and physical maps provide the details. It is easy to understand why both types of genome-mapping techniques are important to show the big picture. Information obtained from each technique is used in combination to study the genome. Genomic mapping is used with different model organisms that are used for research. Genome mapping is still an ongoing process, and as more advanced techniques are developed, more advances are expected. Genome mapping is similar to completing a complicated puzzle using every piece of available data. Mapping information generated in laboratories all over the world is entered into central databases, such as the National Center for Biotechnology Information (NCBI). Efforts are made to make the information more easily accessible to researchers and the general public. Just as we use global positioning systems instead of paper maps to navigate through roadways, NCBI allows us to use a genome viewer tool to simplify the data mining process.

CONCEPT IN ACTION

Online Mendelian Inheritance in Man (OMIM) is a searchable online catalog of human genes and genetic disorders. This website shows genome mapping, and also details the history and research of each trait and disorder. Click the link to search for traits (such as handedness) and genetic disorders (such as diabetes).

Whole Genome Sequencing

Although there have been significant advances in the medical sciences in recent years, doctors are still confounded by many diseases and researchers are using whole genome sequencing to get to the bottom of the problem. Whole genome sequencing is a process that determines the DNA sequence of an entire genome. Whole genome sequencing is a brute-force approach to problem solving when there is a genetic basis at the core of a disease. Several laboratories now provide services to sequence, analyze, and interpret entire genomes.

In 2010, whole genome sequencing was used to save a young boy whose intestines had multiple mysterious abscesses. The child had several colon operations with no relief. Finally, a whole genome sequence revealed a defect in a pathway that controls apoptosis (programmed cell death). A bone marrow transplant was used to overcome this genetic disorder, leading to a cure for the boy. He was the first person to be successfully diagnosed using whole genome sequencing.

The first genomes to be sequenced, such as those belonging to viruses, bacteria, and yeast, were smaller in terms of the number of nucleotides than the genomes of multicellular organisms. The genomes of other model organisms, such as the mouse (*Mus musculus*), the fruit fly (*Drosophila melanogaster*), and the nematode (*Caenorhabditis elegans*) are now known. A great deal of basic research is performed in model organismsbecause the information can be applied to other organisms. A model organism is a species that is studied as a model to understand the biological processes in other species that can be represented by the model organism. For example, fruit flies are able to metabolize alcohol like humans, so the genes affecting sensitivity to alcohol have been studied in fruit flies in an effort to understand the variation in sensitivity to alcohol in humans. Having entire genomes sequenced helps with the research efforts in these model organisms (Figure 18.1.2).

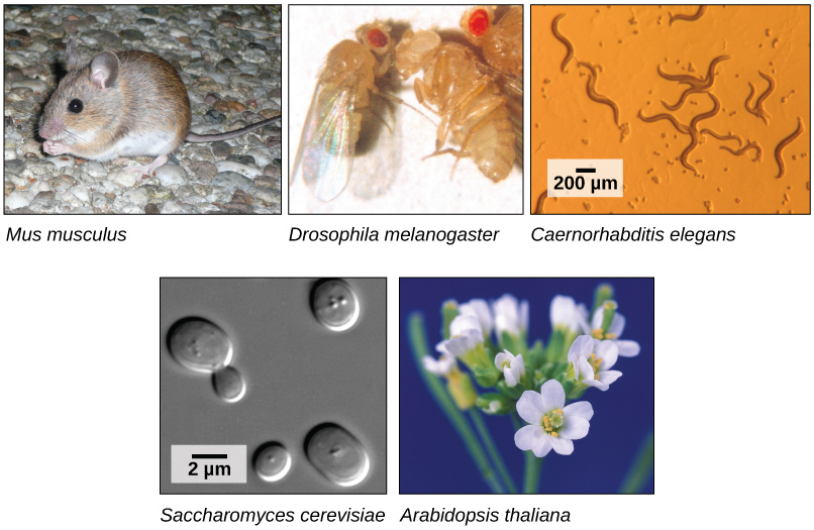


Figure 18.1.2: Much basic research is done with model organisms, such as the mouse, Mus musculus; the fruit fly, Drosophila melanogaster; the nematode Caenorhabditis elegans; the yeast Saccharomyces cerevisiae; and the common weed, Arabidopsis thaliana. (credit "mouse": modification of work by Florean Fortescue; credit "nematodes": modification of work by "snickclunk"/Flickr; credit "common weed": modification of work by Peggy Greb, USDA; scale-bar data from Matt Russell)

The first human genome sequence was published in 2003. The number of whole genomes that have been sequenced steadily increases and now includes hundreds of species and thousands of individual human genomes.

Applying Genomics

The introduction of DNA sequencing and whole genome sequencing projects, particularly the Human Genome Project, has expanded the applicability of DNA sequence information. Genomics is now being used in a wide variety of fields, such as metagenomics, pharmacogenomics, and mitochondrial genomics. The most commonly known application of genomics is to understand and find cures for diseases.

Predicting Disease Risk at the Individual Level

Predicting the risk of disease involves screening and identifying currently healthy individuals by genome analysis at the individual level. Intervention with lifestyle changes and drugs can be recommended before disease onset. However, this approach is most applicable when the problem arises from a single gene mutation. Such defects only account for about 5 percent of diseases found in developed countries. Most of the common diseases, such as heart disease, are multifactorial or polygenic, which refers to a phenotypic characteristic that is determined by two or more genes, and also environmental factors such as diet. In April 2010, scientists at Stanford University published the genome analysis of a healthy individual (Stephen Quake, a scientist at Stanford University, who had his genome sequenced); the analysis predicted his propensity to acquire various diseases. A risk assessment was done to analyze Quake's percentage of risk for 55 different medical conditions. A rare genetic mutation was found that showed him to be at risk for sudden heart attack. He was also predicted to have a 23 percent risk of developing prostate cancer and a 1.4 percent risk of developing Alzheimer's disease. The scientists used databases and several publications to analyze the genomic data. Even though genomic sequencing is becoming more affordable and analytical tools are becoming more reliable, ethical issues surrounding genomic analysis at a population level remain to be addressed. For example, could such data be legitimately used to charge more or less for insurance or to affect credit ratings?

Genome-wide Association Studies

Since 2005, it has been possible to conduct a type of study called a genome-wide association study, or GWAS. A GWAS is a method that identifies differences between individuals in single nucleotide polymorphisms (SNPs) that may be involved in causing diseases. The method is particularly suited to diseases that may be affected by one or many genetic changes throughout the genome. It is very difficult to identify the genes involved in such a disease using family history information. The GWAS method relies on a genetic database that has been in development since 2002 called the International HapMap Project. The HapMap Project sequenced the genomes of several hundred individuals from around the world and identified groups of SNPs. The groups include SNPs that are located near to each other on chromosomes so they tend to stay together through recombination. The fact that the group stays together means that identifying one marker SNP is all that is needed to identify all the SNPs in the group. There are several million SNPs identified, but identifying them in other individuals who have not had their complete genome sequenced is much easier because only the marker SNPs need to be identified.

In a common design for a GWAS, two groups of individuals are chosen; one group has the disease, and the other group does not. The individuals in each group are matched in other characteristics to reduce the effect of confounding variables causing differences between the two groups. For example, the genotypes may differ because the two groups are mostly taken from different parts of the world. Once the individuals are chosen, and typically their numbers are a thousand or more for the study to work, samples of their DNA are obtained. The DNA is analyzed using automated systems to identify large differences in the percentage of particular SNPs between the two groups. Often the study examines a million or more SNPs in the DNA. The results of GWAS can be used in two ways: the genetic differences may be used as markers for susceptibility to the disease in undiagnosed individuals, and the particular genes identified can be targets for research into the molecular pathway of the disease and potential therapies. An offshoot of the discovery of gene associations with disease has been the formation of companies that provide so-called "personal genomics" that will identify risk levels for various diseases based on an individual's SNP complement. The science behind these services is controversial.

Because GWAS looks for associations between genes and disease, these studies provide data for other research into causes, rather than answering specific questions themselves. An association between a gene difference and a disease does not necessarily mean there is a cause-and-effect relationship. However, some studies have provided useful information about the genetic causes of diseases. For example, three different studies in 2005 identified a gene for a protein involved in regulating inflammation in the body that is associated with a disease-causing blindness called age-related macular degeneration. This opened up new possibilities for research into the cause of this disease. A large number of genes have been identified to be associated with Crohn's disease using GWAS, and some of these have suggested new hypothetical mechanisms for the cause of the disease.

Pharmacogenomics

Pharmacogenomics involves evaluating the effectiveness and safety of drugs on the basis of information from an individual's genomic sequence. Personal genome sequence information can be used to prescribe medications that will be most effective and least toxic on the basis of the individual patient's genotype. Studying changes in gene expression could provide information about

the gene transcription profile in the presence of the drug, which can be used as an early indicator of the potential for toxic effects. For example, genes involved in cellular growth and controlled cell death, when disturbed, could lead to the growth of cancerous cells. Genome-wide studies can also help to find new genes involved in drug toxicity. The gene signatures may not be completely accurate, but can be tested further before pathologic symptoms arise.

Metagenomics

Traditionally, microbiology has been taught with the view that microorganisms are best studied under pure culture conditions, which involves isolating a single type of cell and culturing it in the laboratory. Because microorganisms can go through several generations in a matter of hours, their gene expression profiles adapt to the new laboratory environment very quickly. On the other hand, many species resist being cultured in isolation. Most microorganisms do not live as isolated entities, but in microbial communities known as biofilms. For all of these reasons, pure culture is not always the best way to study microorganisms. Metagenomics is the study of the collective genomes of multiple species that grow and interact in an environmental niche. Metagenomics can be used to identify new species more rapidly and to analyze the effect of pollutants on the environment (Figure 18.1.3). Metagenomics techniques can now also be applied to communities of higher eukaryotes, such as fish.

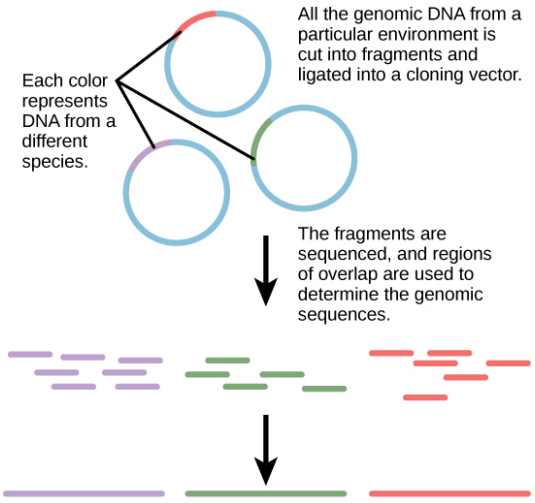


Figure 18.1.3: Metagenomics involves isolating DNA from multiple species within an environmental niche. The DNA is cut up and sequenced, allowing entire genome sequences of multiple species to be reconstructed from the sequences of overlapping pieces.

Creation of New Biofuels

Knowledge of the genomics of microorganisms is being used to find better ways to harness biofuels from algae and cyanobacteria. The primary sources of fuel today are coal, oil, wood, and other plant products such as ethanol. Although plants are renewable resources, there is still a need to find more alternative renewable sources of energy to meet our population's energy demands. The microbial world is one of the largest resources for genes that encode new enzymes and produce new organic compounds, and it remains largely untapped. This vast genetic resource holds the potential to provide new sources of biofuels (Figure 18.1.4).

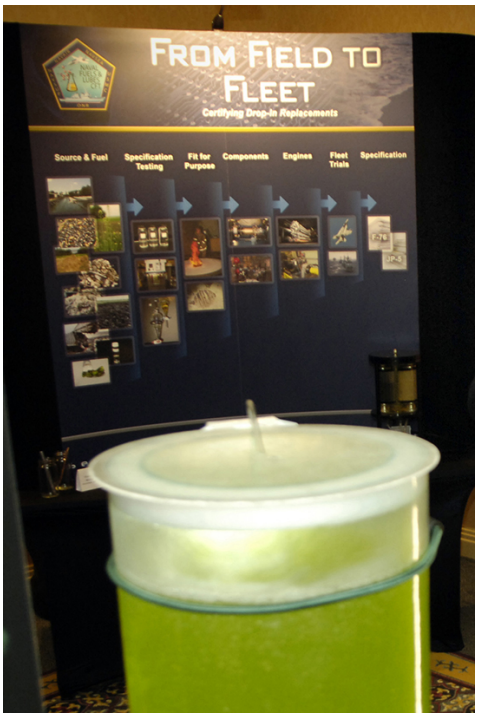


Figure 18.1.4: Renewable fuels were tested in Navy ships and aircraft at the first Naval Energy Forum. (credit: modification of work by John F. Williams, US Navy)

Mitochondrial Genomics

Mitochondria are intracellular organelles that contain their own DNA. Mitochondrial DNA mutates at a rapid rate and is often used to study evolutionary relationships. Another feature that makes studying the mitochondrial genome interesting is that in most multicellular organisms, the mitochondrial DNA is passed on from the mother during the process of fertilization. For this reason, mitochondrial genomics is often used to trace genealogy.

Genomics in Forensic Analysis

Information and clues obtained from DNA samples found at crime scenes have been used as evidence in court cases, and genetic markers have been used in forensic analysis. Genomic analysis has also become useful in this field. In 2001, the first use of genomics in forensics was published. It was a collaborative effort between academic research institutions and the FBI to solve the mysterious cases of anthrax (Figure 18.1.5) that was transported by the US Postal Service. Anthrax bacteria were made into an infectious powder and mailed to news media and two U.S. Senators. The powder infected the administrative staff and postal workers who opened or handled the letters. Five people died, and 17 were sickened from the bacteria. Using microbial genomics, researchers determined that a specific strain of anthrax was used in all the mailings; eventually, the source was traced to a scientist at a national biodefense laboratory in Maryland.

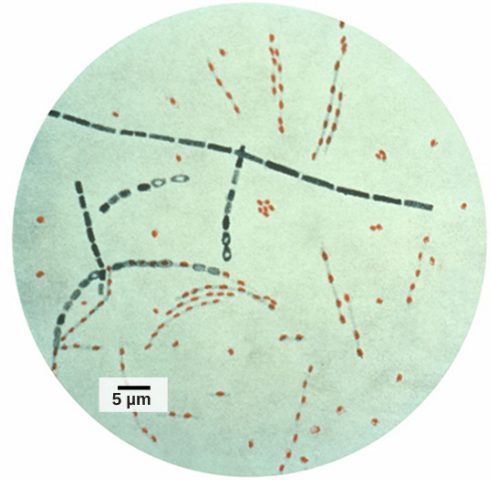


Figure 18.1.5: Bacillus anthracis is the organism that causes anthrax. (credit: modification of work by CDC; scale-bar data from Matt Russell)

Genomics in Agriculture

Genomics can reduce the trials and failures involved in scientific research to a certain extent, which could improve the quality and quantity of crop yields in agriculture (Figure 18.1.6). Linking traits to genes or gene signatures helps to improve crop breeding to generate hybrids with the most desirable qualities. Scientists use genomic data to identify desirable traits, and then transfer those traits to a different organism to create a new genetically modified organism, as described in the previous module. Scientists are discovering how genomics can improve the quality and quantity of agricultural production. For example, scientists could use desirable traits to create a useful product or enhance an existing product, such as making a drought-sensitive crop more tolerant of the dry season.



Figure 18.1.6: Transgenic agricultural plants can be made to resist disease. These transgenic plums are resistant to the plum pox virus. (credit: Scott Bauer, USDA ARS)

Proteomics

Proteins are the final products of genes that perform the function encoded by the gene. Proteins are composed of amino acids and play important roles in the cell. All enzymes (except ribozymes) are proteins and act as catalysts that affect the rate of reactions. Proteins are also regulatory molecules, and some are hormones. Transport proteins, such as hemoglobin, help transport oxygen to various organs. Antibodies that defend against foreign particles are also proteins. In the diseased state, protein function can be impaired because of changes at the genetic level or because of direct impact on a specific protein.

A proteome is the entire set of proteins produced by a cell type. Proteomes can be studied using the knowledge of genomes because genes code for mRNAs, and the mRNAs encode proteins. The study of the function of proteomes is called proteomics. Proteomics complements genomics and is useful when scientists want to test their hypotheses that were based on genes. Even though all cells in a multicellular organism have the same set of genes, the set of proteins produced in different tissues is different and dependent on gene expression. Thus, the genome is constant, but the proteome varies and is dynamic within an organism. In addition, RNAs

can be alternatively spliced (cut and pasted to create novel combinations and novel proteins), and many proteins are modified after translation. Although the genome provides a blueprint, the final architecture depends on several factors that can change the progression of events that generate the proteome.

Genomes and proteomes of patients suffering from specific diseases are being studied to understand the genetic basis of the disease. The most prominent disease being studied with proteomic approaches is cancer (Figure 18.1.7). Proteomic approaches are being used to improve the screening and early detection of cancer; this is achieved by identifying proteins whose expression is affected by the disease process. An individual protein is called a biomarker, whereas a set of proteins with altered expression levels is called a protein signature. For a biomarker or protein signature to be useful as a candidate for early screening and detection of a cancer, it must be secreted in body fluids such as sweat, blood, or urine, so that large-scale screenings can be performed in a noninvasive fashion. The current problem with using biomarkers for the early detection of cancer is the high rate of false-negative results. A false-negative result is a negative test result that should have been positive. In other words, many cases of cancer go undetected, which makes biomarkers unreliable. Some examples of protein biomarkers used in cancer detection are CA-125 for ovarian cancer and PSA for prostate cancer. Protein signatures may be more reliable than biomarkers to detect cancer cells. Proteomics is also being used to develop individualized treatment plans, which involves the prediction of whether or not an individual will respond to specific drugs and the side effects that the individual may have. Proteomics is also being used to predict the possibility of disease recurrence.



Figure 18.1.7: This machine is preparing to do a proteomic pattern analysis to identify specific cancers so that an accurate cancer prognosis can be made. (credit: Dorie Hightower, NCI, NIH)

The National Cancer Institute has developed programs to improve the detection and treatment of cancer. The Clinical Proteomic Technologies for Cancer and the Early Detection Research Network are efforts to identify protein signatures specific to different types of cancers. The Biomedical Proteomics Program is designed to identify protein signatures and design effective therapies for cancer patients.

Summary

Genome mapping is similar to solving a big, complicated puzzle with pieces of information coming from laboratories all over the world. Genetic maps provide an outline for the location of genes within a genome, and they estimate the distance between genes and genetic markers on the basis of the recombination frequency during meiosis. Physical maps provide detailed information about the physical distance between the genes. The most detailed information is available through sequence mapping. Information from all mapping and sequencing sources is combined to study an entire genome.

Whole genome sequencing is the latest available resource to treat genetic diseases. Some doctors are using whole genome sequencing to save lives. Genomics has many industrial applications, including biofuel development, agriculture, pharmaceuticals, and pollution control.

Imagination is the only barrier to the applicability of genomics. Genomics is being applied to most fields of biology; it can be used for personalized medicine, prediction of disease risks at an individual level, the study of drug interactions before the conduction of clinical trials, and the study of microorganisms in the environment as opposed to the laboratory. It is also being applied to the generation of new biofuels, genealogical assessment using mitochondria, advances in forensic science, and improvements in agriculture.

Proteomics is the study of the entire set of proteins expressed by a given type of cell under certain environmental conditions. In a multicellular organism, different cell types will have different proteomes, and these will vary with changes in the environment. Unlike a genome, a proteome is dynamic and under constant flux, which makes it more complicated and more useful than the knowledge of genomes alone.

Glossary

biomarker
: an individual protein that is uniquely produced in a diseased state

genetic map
: an outline of genes and their location on a chromosome that is based on recombination frequencies between markers

genomics
: the study of entire genomes, including the complete set of genes, their nucleotide sequence and organization, and their interactions within a species and with other species

metagenomics
: the study of the collective genomes of multiple species that grow and interact in an environmental niche

model organism
: a species that is studied and used as a model to understand the biological processes in other species represented by the model organism

pharmacogenomics
: the study of drug interactions with the genome or proteome; also called toxicogenomics

physical map
: a representation of the physical distance between genes or genetic markers

protein signature
: a set of over- or under-expressed proteins characteristic of cells in a particular diseased tissue

proteomics
: study of the function of proteomes

whole genome sequencing
: a process that determines the nucleotide sequence of an entire genome

Contributors and Attributions

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18.2: Sequencing Genomes

Skills to Develop

- Describe three types of sequencing
- Define whole-genome sequencing

Although there have been significant advances in the medical sciences in recent years, doctors are still confounded by some diseases, and they are using whole-genome sequencing to get to the bottom of the problem. Whole-genome sequencing is a process that determines the DNA sequence of an entire genome. Whole-genome sequencing is a brute-force approach to problem solving when there is a genetic basis at the core of a disease. Several laboratories now provide services to sequence, analyze, and interpret entire genomes.

For example, whole-exome sequencing is a lower-cost alternative to whole genome sequencing. In exome sequencing, only the coding, exon-producing regions of the DNA are sequenced. In 2010, whole-exome sequencing was used to save a young boy whose intestines had multiple mysterious abscesses. The child had several colon operations with no relief. Finally, whole-exome sequencing was performed, which revealed a defect in a pathway that controls apoptosis (programmed cell death). A bone-marrow transplant was used to overcome this genetic disorder, leading to a cure for the boy. He was the first person to be successfully treated based on a diagnosis made by whole-exome sequencing. Today, human genome sequencing is more readily available and can be completed in a day or two for about $1000.

Strategies Used in Sequencing Projects

The basic sequencing technique used in all modern day sequencing projects is the chain termination method (also known as the dideoxy method), which was developed by Fred Sanger in the 1970s. The chain termination method involves DNA replication of a single-stranded template with the use of a primer and a regular deoxynucleotide (dNTP), which is a monomer, or a single unit, of DNA. The primer and dNTP are mixed with a small proportion of fluorescently labeled dideoxynucleotides (ddNTPs). The ddNTPs are monomers that are missing a hydroxyl group (–OH) at the site at which another nucleotide usually attaches to form a chain (Figure 18.2.1).

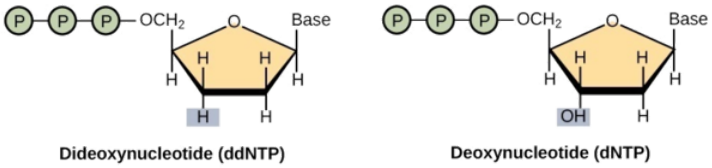


Figure 18.2.1: A dideoxynucleotide is similar in structure to a deoxynucleotide, but is missing the 3' hydroxyl group (indicated by the box). When a dideoxynucleotide is incorporated into a DNA strand, DNA synthesis stops.

Each ddNTP is labeled with a different color of fluorophore. Every time a ddNTP is incorporated in the growing complementary strand, it terminates the process of DNA replication, which results in multiple short strands of replicated DNA that are each terminated at a different point during replication. When the reaction mixture is processed by gel electrophoresis after being separated into single strands, the multiple newly replicated DNA strands form a ladder because of the differing sizes. Because the ddNTPs are fluorescently labeled, each band on the gel reflects the size of the DNA strand and the ddNTP that terminated the reaction. The different colors of the fluorophore-labeled ddNTPs help identify the ddNTP incorporated at that position. Reading the gel on the basis of the color of each band on the ladder produces the sequence of the template strand (Figure 18.2.2).

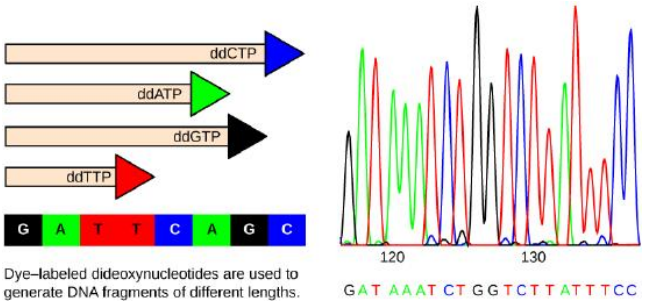


Figure **18.2.2**: Frederick Sanger's dideoxy chain termination method is illustrated. Using dideoxynucleotides, the DNA fragment can be terminated at different points. The DNA is separated on the basis of size, and these bands, based on the size of the fragments, can be read.

Early Strategies: Shotgun Sequencing and Pair-Wise End Sequencing

In shotgun sequencing method, several copies of a DNA fragment are cut randomly into many smaller pieces (somewhat like what happens to a round shot cartridge when fired from a shotgun). All of the segments are then sequenced using the chain-sequencing method. Then, with the help of a computer, the fragments are analyzed to see where their sequences overlap. By matching up overlapping sequences at the end of each fragment, the entire DNA sequence can be reformed. A larger sequence that is assembled from overlapping shorter sequences is called a contig. As an analogy, consider that someone has four copies of a landscape photograph that you have never seen before and know nothing about how it should appear. The person then rips up each photograph with their hands, so that different size pieces are present from each copy. The person then mixes all of the pieces together and asks you to reconstruct the photograph. In one of the smaller pieces you see a mountain. In a larger piece, you see that the same mountain is behind a lake. A third fragment shows only the lake, but it reveals that there is a cabin on the shore of the lake. Therefore, from looking at the overlapping information in these three fragments, you know that the picture contains a mountain behind a lake that has a cabin on its shore. This is the principle behind reconstructing entire DNA sequences using shotgun sequencing.

Originally, shotgun sequencing only analyzed one end of each fragment for overlaps. This was sufficient for sequencing small genomes. However, the desire to sequence larger genomes, such as that of a human, led to the development of double-barrel shotgun sequencing, more formally known as pairwise-end sequencing. In pairwise-end sequencing, both ends of each fragment are analyzed for overlap. Pairwise-end sequencing is, therefore, more cumbersome than shotgun sequencing, but it is easier to reconstruct the sequence because there is more available information.

Next-generation Sequencing

Since 2005, automated sequencing techniques used by laboratories are under the umbrella of next-generation sequencing, which is a group of automated techniques used for rapid DNA sequencing. These automated low-cost sequencers can generate sequences of hundreds of thousands or millions of short fragments (25 to 500 base pairs) in the span of one day. These sequencers use sophisticated software to get through the cumbersome process of putting all the fragments in order.

Evolution Connection: Comparing Sequences

A sequence alignment is an arrangement of proteins, DNA, or RNA; it is used to identify regions of similarity between cell types or species, which may indicate conservation of function or structures. Sequence alignments may be used to construct phylogenetic trees. The following website uses a software program called BLAST (basic local alignment search tool).

Under “Basic Blast,” click “Nucleotide Blast.” Input the following sequence into the large "query sequence" box: ATTGCTTCGATTGCA. Below the box, locate the "Species" field and type "human" or "Homo sapiens". Then click “BLAST” to compare the inputted sequence against known sequences of the human genome. The result is that this sequence occurs in over a hundred places in the human genome. Scroll down below the graphic with the horizontal bars and you will see short description of each of the matching hits. Pick one of the hits near the top of the list and click on "Graphics". This will bring you to a page that shows where the sequence is found within the entire human genome. You can move the slider that looks like a green flag back and forth to view the sequences immediately around the selected gene. You can then return to your selected sequence by clicking the "ATG" button.

Use of Whole-Genome Sequences of Model Organisms

The first genome to be completely sequenced was of a bacterial virus, the bacteriophage fx174 (5368 base pairs); this was accomplished by Fred Sanger using shotgun sequencing. Several other organelle and viral genomes were later sequenced. The first organism whose genome was sequenced was the bacterium *Haemophilus influenzae*; this was accomplished by Craig Venter in the 1980s. Approximately 74 different laboratories collaborated on the sequencing of the genome of the yeast *Saccharomyces cerevisiae*, which began in 1989 and was completed in 1996, because it was 60 times bigger than any other genome that had been sequenced. By 1997, the genome sequences of two important model organisms were available: the bacterium *Escherichia coli* K12 and the yeast *Saccharomyces cerevisiae*. Genomes of other model organisms, such as the mouse *Mus musculus*, the fruit fly *Drosophila melanogaster*, the nematode *Caenorhabditis elegans*, and humans *Homo sapiens* are now known. A lot of basic research is performed in model organisms because the information can be applied to genetically similar organisms. A model organism is a species that is studied as a model to understand the biological processes in other species represented by the model organism. Having entire genomes sequenced helps with the research efforts in these model organisms. The process of attaching biological information to gene sequences is called genome annotation. Annotation of gene sequences helps with basic experiments in molecular biology, such as designing PCR primers and RNA targets.

Link to Learning

Click through each step of HHMI genome sequencing site.

Uses of Genome Sequences

DNA microarrays are methods used to detect gene expression by analyzing an array of DNA fragments that are fixed to a glass slide or a silicon chip to identify active genes and identify sequences. Almost one million genotypic abnormalities can be discovered using microarrays, whereas whole-genome sequencing can provide information about all six billion base pairs in the human genome. Although the study of medical applications of genome sequencing is interesting, this discipline tends to dwell on abnormal gene function. Knowledge of the entire genome will allow future onset diseases and other genetic disorders to be discovered early, which will allow for more informed decisions to be made about lifestyle, medication, and having children. Genomics is still in its infancy, although someday it may become routine to use whole-genome sequencing to screen every newborn to detect genetic abnormalities.

In addition to disease and medicine, genomics can contribute to the development of novel enzymes that convert biomass to biofuel, which results in higher crop and fuel production, and lower cost to the consumer. This knowledge should allow better methods of control over the microbes that are used in the production of biofuels. Genomics could also improve the methods used to monitor the impact of pollutants on ecosystems and help clean up environmental contaminants. Genomics has allowed for the development of agrochemicals and pharmaceuticals that could benefit medical science and agriculture.

It sounds great to have all the knowledge we can get from whole-genome sequencing; however, humans have a responsibility to use this knowledge wisely. Otherwise, it could be easy to misuse the power of such knowledge, leading to discrimination based on a person's genetics, human genetic engineering, and other ethical concerns. This information could also lead to legal issues regarding health and privacy.

Summary

Whole-genome sequencing is the latest available resource to treat genetic diseases. Some doctors are using whole-genome sequencing to save lives. Genomics has many industrial applications including biofuel development, agriculture, pharmaceuticals,

and pollution control. The basic principle of all modern-day sequencing strategies involves the chain termination method of sequencing.

Although the human genome sequences provide key insights to medical professionals, researchers use whole-genome sequences of model organisms to better understand the genome of the species. Automation and the decreased cost of whole-genome sequencing may lead to personalized medicine in the future.

Glossary

chain termination method
: method of DNA sequencing using labeled dideoxynucleotides to terminate DNA replication; it is also called the dideoxy method or the Sanger method

contig
: larger sequence of DNA assembled from overlapping shorter sequences

deoxynucleotide
: individual monomer (single unit) of DNA

dideoxynucleotide
: individual monomer of DNA that is missing a hydroxyl group (–OH)

DNA microarray
: method used to detect gene expression by analyzing an array of DNA fragments that are fixed to a glass slide or a silicon chip to identify active genes and identify sequences

genome annotation
: process of attaching biological information to gene sequences

model organism
: species that is studied and used as a model to understand the biological processes in other species represented by the model organism

next-generation sequencing
: group of automated techniques used for rapid DNA sequencing

shotgun sequencing
: method used to sequence multiple DNA fragments to generate the sequence of a large piece of DNA

whole-genome sequencing
: process that determines the DNA sequence of an entire genome

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CHAPTER OVERVIEW

18.3: Genome Projects

18.3.1: The Human Genome Project

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18.3.1: THE HUMAN GENOME PROJECT

VITRUVIAN MAN

The drawing in Figure **18.3.1.2**, named *Vitruvian Man*, was created by Leonardo da Vinci in 1490. It was meant to show normal human body proportions. *Vitruvian Man* is used today to represent a different approach to the human body. It symbolizes a scientific research project that began in 1990, exactly 500 years after da Vinci created the drawing. That project, named the Human Genome Project, is the largest collaborative biological research project ever undertaken.

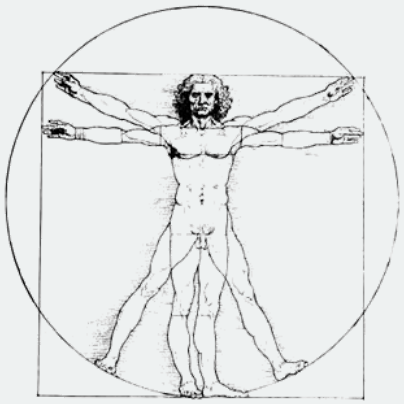


Figure **18.3.1.1**: Vitruvian man

WHAT IS THE HUMAN GENOME?

The **human genome** refers to all the DNA of the human species. Human DNA consists of 3.3 billion base pairs and is divided into more than 20,000 genes onto 23 pairs of chromosomes. The human genome also includes noncoding sequences (e.g. intergenic region) of DNA, as shown in Figure **18.3.1.2**.

DISCOVERING THE HUMAN GENOME

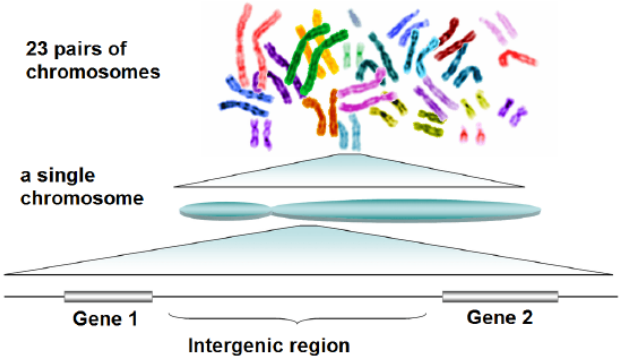


Figure **18.3.1.2**: Human Genome, Chromosomes, and Genes. Each chromosome of the human genome contains many genes as well as noncoding intergenic (between genes) regions. Each pair of chromosomes is shown here in a different color.

Scientists now know the sequence of all the DNA base pairs in the entire human genome. This knowledge was attained by the **Human Genome Project (HGP),** a $3 billion, international scientific research project that was formally launched in 1990. The project was completed in 2003, two years ahead of its 15-year projected deadline.

Determining the sequence of the billions of base pairs that make up human DNA was the main goal of the HGP. Another goal was mapping the location and determining the function of all the genes in the human genome. There are only about 20,500 genes in human beings.

A COLLABORATIVE EFFORT

Funding for the HGP came from the U.S. Department of Energy and the National Institutes of Health as well as from foreign institutions. The actual research was undertaken by scientists in 20 universities in the U.S., United Kingdom, Australia, France, Germany, Japan, and China. A private U.S. company named Celera also contributed to the effort. Although Celera had hoped to patent some of the genes it discovered, this was later denied.

REFERENCE GENOME OF THE HUMAN GENOME PROJECT

In 2003, the HGP published the results of its sequencing of DNA as a human reference genome. Figure **18.3.1.4** illustrates the process of DNA sequencing. The details of this image are out of the scope of this concept and book. The sequence of the human DNA is stored in databases available to anyone on the Internet. The U.S. National Center for Biotechnology Information (NCBI), part of the NIH, as well as comparable organizations in Europe and Japan, maintain the genomic sequences in a database known as Genbank. Protein sequences are also maintained in this database. The sequences in these databases are the combined sequences of anonymous donors, and as such do not yet address the individual differences that make us unique. However, the known sequence does lay the foundation to identify the unique differences among all of us. Most of the currently identified variations among individuals will be single nucleotide polymorphisms or SNPs. An SNP (pronounced "snip") is a DNA sequence variation occurring at a single nucleotide in the genome. For example, two sequenced DNA fragments from different individuals, GGATCTA to GGATTTA, contain a difference in a single nucleotide. If this, base change occurs in a gene, the base change then results in two alleles: the C allele and the T allele. Remember an allele is an alternative form of a gene. Almost all common SNPs have only two alleles. The effect of these SNPs on protein structure and function and any effect on the resulting phenotype are an extensive field of study.

BENEFITS OF THE HUMAN GENOME PROJECT

The sequencing of the human genome holds benefits for many fields, including molecular medicine and human evolution.

- Knowing the human DNA sequence can help us understand many human diseases. For example, it is helping researchers identify mutations linked to different forms of cancer. It is also yielding insights into the genetic basis of cystic fibrosis, liver

diseases, blood-clotting disorders, and Alzheimer's disease, among others.

- The human DNA sequence can also help researchers tailor medications to individual genotypes. This is called personalized medicine, and it has led to an entirely new field called pharmacogenomics. **Pharmacogenomics**, also called pharmacogenetics, is the study of how our genes affect the way we respond to drugs. You can read more about pharmacogenomics in the Feature below.
- The analysis of similarities between DNA sequences from different organisms is opening new avenues in the study of evolution. For example, analyses are expected to shed light on many questions about the similarities and differences between humans and our closest relatives the nonhuman primates.

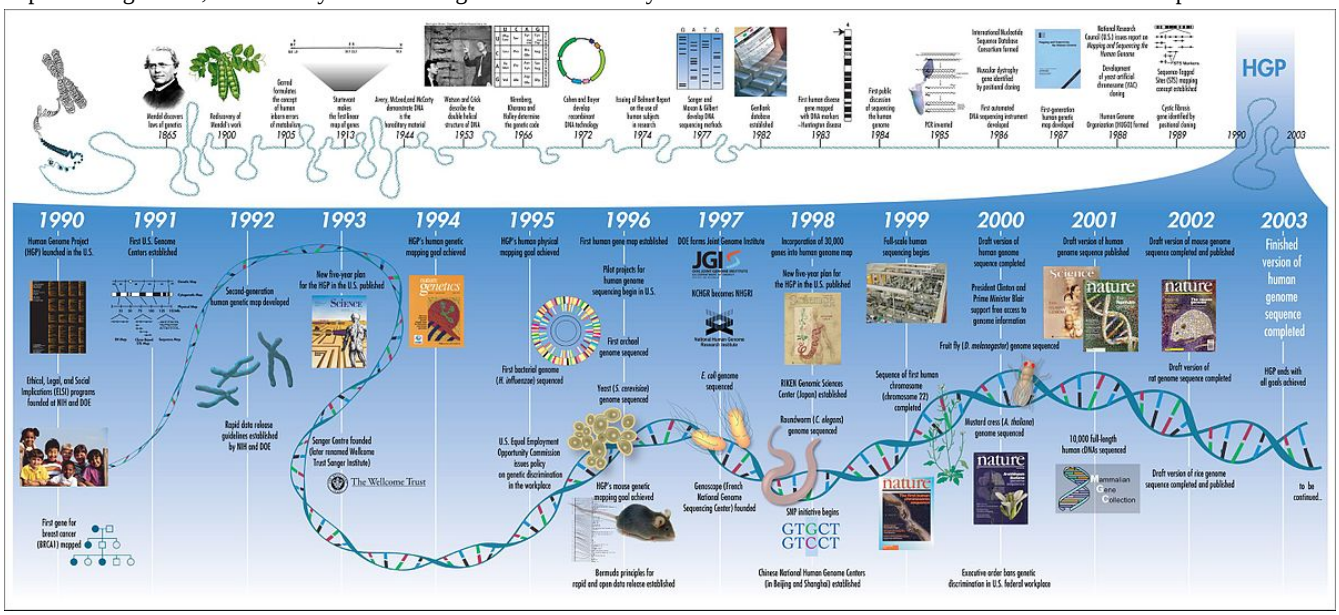


Figure **18.3.1.3**: Timeline of the human genome project from 1990 to 2003. The details of this timeline are more than we need here. You can see all the details at the NIH site.

ETHICAL, LEGAL, AND SOCIAL ISSUES OF THE HUMAN GENOME PROJECT

From its launch in 1990, the HGP proactively established and funded a separate committee to oversee potential ethical, legal, and social issues associated with the project. A major concern was the possible use of the knowledge generated by the project to discriminate against people. One issue was the fear that employers and health insurance companies would refuse to hire or insure people based on their genetic makeup, for instance, if they had genes that increased their risk of getting certain diseases. In response, in 1996, the U.S. passed the Health Insurance Portability and Accountability Act (HIPAA). It protects against unauthorized, nonconsensual release of individually identifiable health information to any entity not actively engaged in providing healthcare to a patient. This was followed in 2008 by the Genetic Information Nondiscrimination Act (GINA), which specifically prohibits genetic discrimination by health insurance companies and workplaces.

REVIEW

1. Describe the human genome.
2. What is the Human Genome Project?
3. Identify two main goals of the Human Genome Project.
4. What is the reference genome of the Human Genome Project? What is it based on?
5. Explain how knowing the sequence of DNA bases in the human genome is beneficial for molecular medicine.
6. What was one surprising finding of the Human Genome Project?
7. Why do you think scientists didn't just sequence the DNA from a single person for the Human Genome Project? Along those lines, why do you think it is important to include samples from different ethnic groups and genders in genome sequencing efforts?
8. *True or False.* The sequenced human genome does not include noncoding regions — it only includes actual genes.
9. *True or False.* Knowing the sequence of the human genome can give insight into human evolution.
10. What is pharmacogenomics?
    A. If a patient were to have pharmacogenomics done to optimize their medication, what do you think the first step would be?
    B. List one advantage and one disadvantage of pharmacogenomics.
11. There are approximately 20,000 human
    A. base pairs
    B. nucleotides
    C. alleles
    D. genes
12. Explain how the sequencing of the human genome relates to ethical concerns about genetic discrimination.

EXPLORE MORE

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SECTION OVERVIEW

18.4: Genome Annotation and Databases

18.4.1: Genome Annotation

18.4.2: Non-Coding Elements

18.4.3: The ENCODE Project

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18.4.1: Genome Annotation

Genome annotation is the identification and understanding of the genetic elements of a sequenced genome.

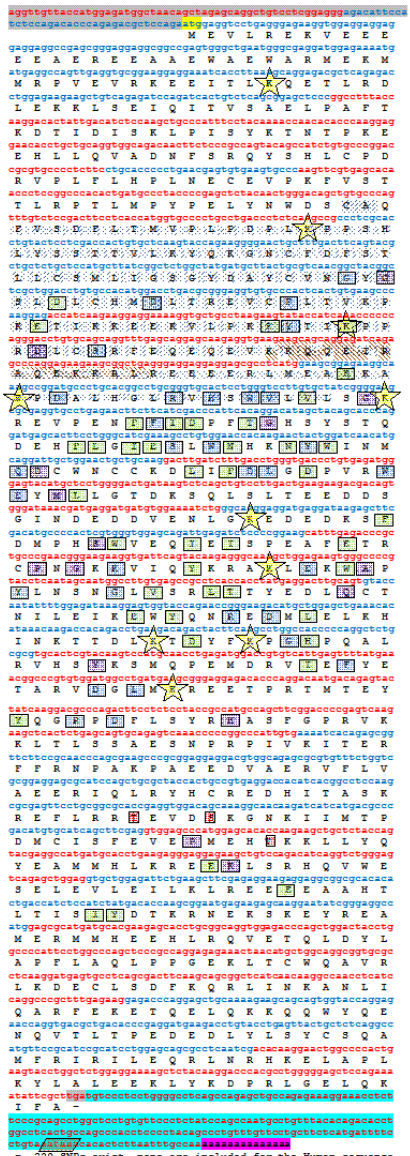
LEARNING OBJECTIVES

Define genome annotation

Key Takeaways

Genome projects are scientific endeavors that ultimately aim to determine the complete genome sequence of an organism (be it an animal, a plant, a fungus, a bacterium, an archaean, a protist, or a virus). They annotate protein-coding genes and other important genome-encoded features. The genome sequence of an organism includes the collective DNA sequences of each chromosome in the organism. For a bacterium containing a single chromosome, a genome project will aim to map the sequence of that chromosome.

Once a genome is sequenced, it needs to be annotated to make sense of it. An annotation (irrespective of the context) is a note added by way of explanation or commentary. Since the 1980's, molecular biology and bioinformatics have created the need for DNA annotation. DNA annotation or genome annotation is the process of identifying the locations of genes and all of the coding regions in a genome and determining what those genes do.



- 230 SNPs exist, none are included for the Human sequence.
- 4 isoforms present, the table below indicates which isoform form from the splicing of different exon numbers:



[1]

- The domain containing Transglutaminase-like family and Nuclear localization sequence are shaded in with a positive slope and negative slope, respectively[2].
- Amino acids that were predicted by Phosphosite to be possible phosphorylation sites are shaded in red.
- Highly conserved amino acids are shaded in blue.
- Conservation of strong amino acids are shaded in green.
- Conservation of weak amino acids are shaded in purple.

NOTE: these results are based on CLUSTALW of all 20 orthologs

[3]Letters in star represents amino acid with high probability for sumoylation.

One alternative poly-A signal was obtained in this mRNA sequence, however, [4]8 total poly-A signals were obtained when the complete genomic sequence [introns and exons was analyzed]. The following positions were where signals were obtained when NC_000016.9, Homo sapiens chromosome 16, GRCh37 primary reference assembly, was obtained from NCBI; 333, 4598, 15655, 15849, 17699, 18806, 20829, and 22379. In must be noted that these predictions do not contain a G/U rich element downstream which might limit the poly-A addition. Also, 7 of the positions 333, 4598, 15655, 15849, 17699, 18806, and 20829, are located within the introns of mRNA, hence, they may cause a defect in the amino acid sequence.

[1] Isoform information obtained from GeneCard, http://www.genecards.org/cgi-bin/carddisp.pl?gene=CCDC135&search=ccdc135
[2] Domain information obtained from Kegg, http://www.genome.jp/kegg/
[3] http://www.abgent.com/tools/sumoplot, with scores above 0.67.
[4] Polyadq output, http://rulai.cshl.org/cgi-bin/tools/polyadq/polyadq4.cgi

https://bio.libretexts.org/@go/page/75286

Figure: **Genome Annotation**: Here a small region of genome is annotated, with various elements identified. The annotation of an entire genome would entail a similar in depth analysis of thousand even millions of such DNA sequences.

Genome annotation is the process of attaching biological information to sequences. It consists of two main steps: identifying elements on the genome, a process called gene prediction, and attaching biological information to these elements. Automatic annotation tools try to perform all of this by computer analysis, as opposed to manual annotation (a.k.a. curation) which involves human expertise. Ideally, these approaches co-exist and complement each other in the same annotation pipeline (process). The basic level of annotation is using BLAST for finding similarities, and then annotating genomes based on that. However, nowadays more and more additional information is added to the annotation platform. The additional information allows manual annotators to deconvolute discrepancies between genes that are given the same annotation. Some databases use genome context information, similarity scores, experimental data, and integrations of other resources to provide genome annotations through their Subsystems approach. Other databases rely on both curated data sources as well as a range of different software tools in their automated genome annotation pipeline.

Structural annotation consists of the identification of genomic elements: ORFs and their localization, gene structure, coding regions, and the location of regulatory motifs. Functional annotation consists of attaching biological information to genomic elements: biochemical function, biological function, involved regulation and interactions, and expression.

These steps may involve both biological experiments and in silico analysis. Proteogenomics based approaches utilize information from expressed proteins, often derived from mass spectrometry, to improve genomics annotations. A variety of software tools have been developed to permit scientists to view and share genome annotations. Genome annotation is the next major challenge for the Human Genome Project, now that the genome sequences of human and several model organisms are largely complete. Identifying the locations of genes and other genetic control elements is often described as defining the biological “parts list” for the assembly and normal operation of an organism. Scientists are still at an early stage in the process of delineating this parts list and in understanding how all the parts “fit together. ”

Key Points

- Once a genome is sequenced, all of the sequencings must be analyzed to understand what they mean.
- Critical to annotation is the identification of the genes in a genome, the structure of the genes, and the proteins they encode.
- Once a genome is annotated, further work is done to understand how all the annotated regions interact with each other.

Key Terms

- **BLAST**: In bioinformatics, Basic Local Alignment Search Tool, or BLAST, is an algorithm for comparing primary biological sequence information, such as the amino-acid sequences of different proteins or the nucleotides of DNA sequences.
- **in silico**: In computer simulation or in virtual reality

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18.4.2: Non-Coding Elements

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Introduction

For many years, scientists wondered about the nature of the information that directed the activities of cells. What kind of molecules carried the information, and how was the information passed on from one generation to the next? Key experiments, done between the 1920s and the 1950s, established convincingly that this genetic information was carried by DNA. In 1953, with the elucidation of the structure of DNA, it was possible to begin investigating how this information is passed on, and how it is used.

Genomes

We use the word “genome” to describe all of the genetic material of the cell. That is, a genome is the entire sequence of nucleotides in the DNA that is in all of the chromosomes of a cell. When we use the term genome without further qualification, we are generally referring to the chromosomes in the nucleus of a eukaryotic cell. As you know, eukaryotic cells have organelles like mitochondria and chloroplasts that have their own DNA (Figure 7.1 & 7.2). These are referred to as the mitochondrial or chloroplast genomes to distinguish them from the nuclear genome.

Starting in the 1980s, scientists began to determine the complete sequence of the genomes of many organisms, in the hope of better understanding how the DNA sequence specifies cellular functions. Today, the complete genome sequences have been determined for thousands of species from all domains of life, and many more are in the process of being worked out by groups of scientists across the world.

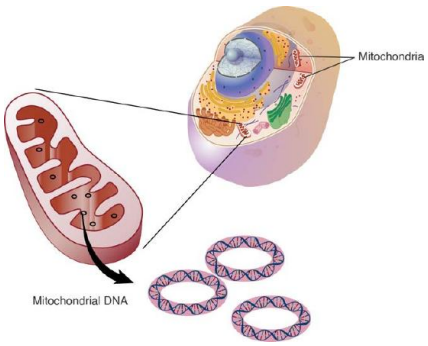


Figure 7.1 - Mitochondria carry their own genome

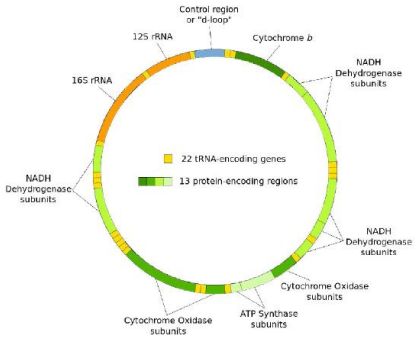


Figure 7.2 - The human mitochondrial genome - Wikipedia

Global genome initiative

The Global Genome Initiative, a collaborative effort to sequence at least one species from each of the 9,500 described invertebrate, vertebrate, and plant families is one of many such ventures. The information from these various efforts is collected in enormous online repositories, so that it is freely available to scientists. As the sequence databases compile ever more information, the fields of computational biology and bioinformatics have arisen, to analyze and organize the data in a way that helps biologists understand what the information in DNA means in the cellular context.

Genes

It has been known for many years that phenotypic traits are controlled by specific regions of the DNA that were termed “genes”. Thus, DNA was envisioned as a long string of nucleotides, in which certain regions, the genes, were separated by non-coding regions that were simply referred to as intergenic sequences (inter=between; genic=of genes). Early experiments in molecular biology suggested a simple relationship between the DNA sequence of a gene and its product, and led scientists to believe that each gene carried the information for a single protein. Changes, or mutations in the base sequence of a gene would be reflected in changes in the gene product, which in turn, would manifest itself in the phenotype or observable trait. This simple picture, while still useful, has been modified by subsequent discoveries that demonstrated that the use of genetic information by cells is somewhat more complicated. Our definition of a gene is also evolving to take new knowledge into consideration.

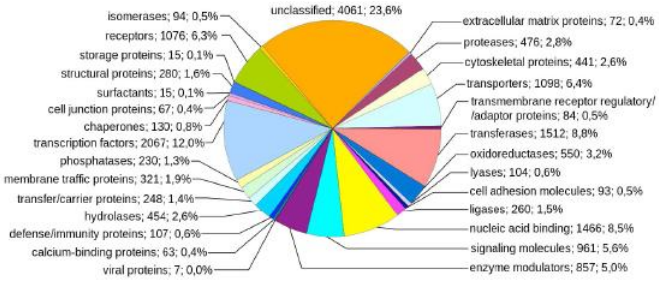


Figure 7.3 - From genomes to genes - Wikipedia

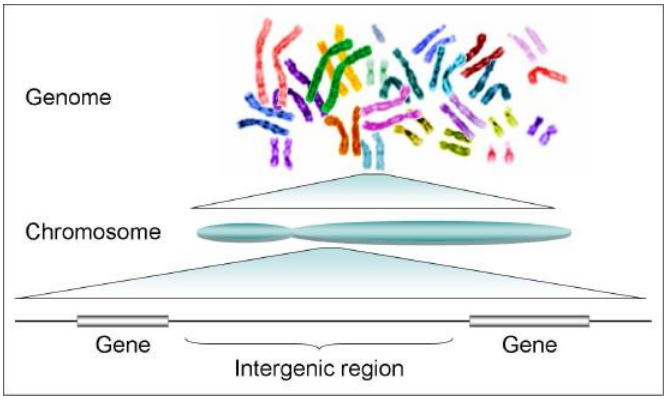


Figure 7.4 - Human genes sorted by class

Matters of size

A common-sense assumption about genomes would be that if genes specify proteins, then the more proteins an organism made, the more genes it would need to have, and thus, the larger its genome would be. Comparison of various genomes shows, surprisingly, that there is not necessarily a direct relationship between the complexity of an organism and the size of its genome (Figure 7.5). To understand how this could be true, it is necessary to recognize that while genes are made up of DNA, all DNA does not consist of genes (for purposes of our discussion, we define a gene as a section of DNA that encodes an RNA or protein product). In the human genome, less than 2% of the total DNA seems to be the sort of coding sequence that directs the synthesis of proteins. For many years, non-coding DNA in genomes was believed to be useless, and was described as "junk DNA" although it was perplexing that there seemed to be so much "useless" sequence. Recent discoveries have, however, demonstrated that much of this so-called junk DNA may play important roles in evolution, as well as in regulation of gene expression.

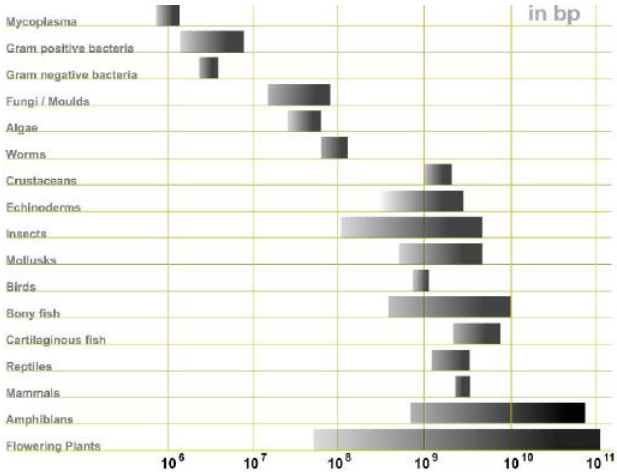


Figure 7.5 - Sizes of various genomes - Wikipedia

Introns

So, what is all the non-coding DNA doing there? We know that even coding regions in our DNA are interrupted by non-coding sequences called introns. This is true of most eukaryotic genomes. An examination of genes in eukaryotes shows that non-coding intron sequences can be much longer than the coding sections of the gene, or exons. Most exons are relatively small, and code for fewer than a hundred amino acids, while introns can vary in size from several hundred base-pairs to many kilobase-pairs (thousands of base-pairs) in length. For many genes in humans, there is much more of intron sequence than coding (a.k.a. exon) sequence. Intron sequences account for roughly a quarter of the genome in humans.

Other non-coding sequences

What other kinds of non-coding sequences are there? One function for some DNA sequences that do not encode RNA or proteins is in specifying when and to what extent a gene is used, or expressed. Such regions of DNA are called regulatory regions and each gene has one or more regulatory sequences that control its expression. However, regulatory sequences do not account for all the rest of the DNA in our genomes, either.

Transposable sequences

Surprisingly, almost half of the human genome appears to consist of several kinds of repetitive sequences. Many of the repetitive sequences are known to be transposable elements (transposons), sections of DNA that can move around within the genome. Sometimes referred to as "jumping genes" these transposable elements can move from one chromosomal location to another, either through a simple "cut and paste" mechanism that cuts the sequence out of one region of the DNA and inserts it into another location, or through a process called retrotransposition involving an RNA intermediate.

LINES & SINES

There are millions of copies of each of two major classes of such transposable elements, the LINEs (Long Interspersed Elements) and SINEs (Short Interspersed Elements) in our genomes.

LINEs and SINEs are both a kind of transposable element called retrotransposons, sequences that are copied into RNA, then reverse transcribed back into DNA before being inserted into new locations. This movement is typically not sequence specific, meaning that the transposons can be inserted randomly in the genome, in many cases within coding regions. As might be expected, this can disrupt the function of the gene. Transposons may also insert within regulatory regions, and change the expression of the genes they control. As a major cause of mutation in genomes, transposons play an important role in evolution.

Finally, recent findings have shown that much of the genome is transcribed into RNAs, even though only about 2% encodes proteins. What are the RNAs that do not encode proteins? Ribosomal RNAs (Figure 7.7) and transfer RNAs, together with the small nuclear RNAs that function in splicing, account for some of these non-translated transcripts, but not all. The remaining RNAs are regulatory RNAs, small molecules that play an important role in regulating gene expression. As we understand more about genomes, it is becoming evident that the so-called “junk” DNA is anything but.

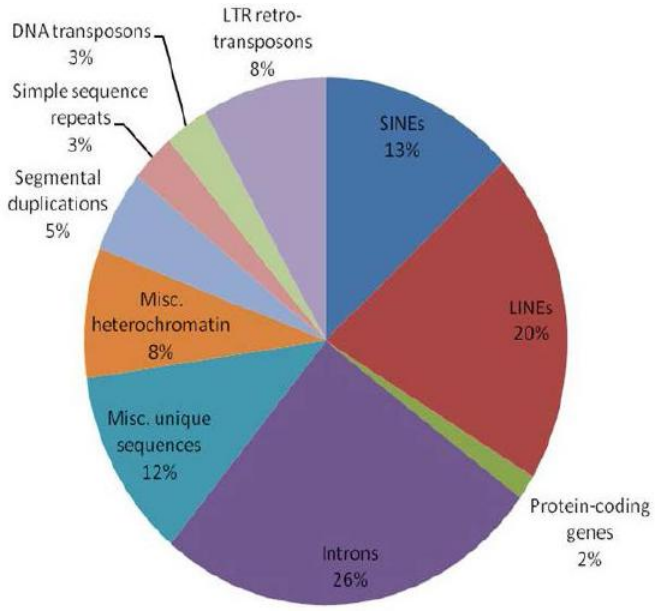


Figure 7.6 - Components of the human genome - Wikipedia

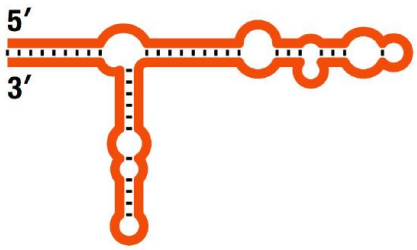


Figure 7.7 - 5S rRNA structure

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18.4.3: The ENCODE Project

The human genome was sequenced in 2003, an important step in understanding the blueprint of life. However, before this information can be fully utilized, the location, identity, and function of all protein- encoding and non-protein-encoding genes must be determined. Moreover, the human genome has many other functional elements, ranging from promotors, regulatory sequences, and other factors that determine chromatin structure. These must also be determined to fully understand the human genome.

The ENCODE (Encyclopedia of DNA Elements) project aims to solve these problems by delineating all functional elements of the human genome. To accomplish this goal, a consortium was formed to guide the project. The consortium aimed to advance and develop technologies for annotating the human genome with higher accuracy, completeness, and cost-effectiveness, along with more standardization.They also aimed to develop a series of computational techniques to parse and analyze the data obtained.

To accomplish this goal, a pilot project was launched. The ENCODE pilot project aimed to study 1% of the human genome in depth, roughly from 2003 to 2007. From 2007 to 2012, the ENCODE project ramped up to annotate the entire genome. Finally, from 2012 onwards, the ENCODE project aims further increases in all dimensions: deeper sequencing, more assays, more transcription factors, etc.

This chapter will describe some of the experimental and computational techniques used in the ENCODE project.

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SECTION OVERVIEW

18.5: Comparative and Functional Genomics

18.5.1: Comparative Genomics

18.5.2: Transcriptomics

18.5.3: Basic Techniques in Protein Analysis

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18.5.1: Comparative Genomics

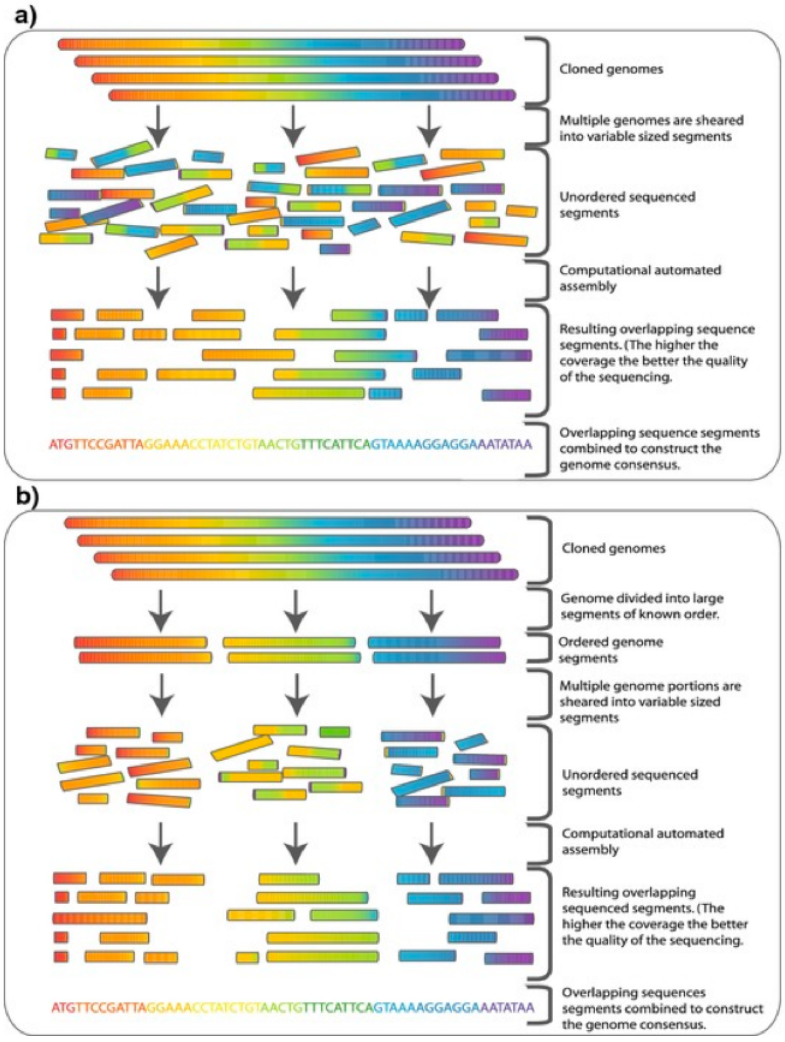
Genomics is a field that studies the entire collection of an organism's DNA or genome. It involves sequencing, analyzing, and comparing the information contained within genomes. Since sequencing has become much less expensive and more efficient, vast amounts of genomic information is now available about a wide variety of organisms, but particularly microbes, with their smaller genome size. In fact, the biggest bottleneck currently is not the lack of information but the lack of computing power to process the information!

Sequencing

Sequencing, or determining the base order of an organism's DNA or RNA, is often one of the first steps to finding out detailed information about an organism. A bacterial genome can range from 130 kilobase pairs (kbp) to over 14 Megabase pairs (Mbp), while a viral genome ranges from 0.859 to 2473 kbp. For comparison, the human genome contains about 3 billion base pairs.

Shotgun sequencing

Shotgun sequencing initially involves construction of a **genomic library**, where the genome is broken into randomly sized fragments that are inserted into vectors to produce a library of clones. The fragments are sequenced and then analyzed by a computer, which searches for overlapping regions to form a longer stretch of sequence. Eventually all the sequences are aligned to give the complete genome sequence. Errors are reduced because many of the clones contain identical or near identical sequences, resulting in good "coverage" of the genome.



Shotgun Sequencing. By Commins, J., Toft, C., Fares, M. A. [CC BY-SA 2.5], via Wikimedia Commons

Second generation DNA sequencing

Second-generation DNA sequencing uses **massively parallel methods**, where multiple samples are sequenced side-by-side. DNA fragments of a few hundred bases each are amplified by PCR and then attached to small bead, so that each bead carries several copies of the same section of DNA. The beads are put into a plate containing more than a million wells, each with one bead, and the DNA fragments are sequenced.

Third- and fourth-generation DNA sequencing

Third-generation DNA sequencing involves the sequencing of single molecules of DNA. Fourth-generation DNA sequencing, also known as “post light sequencing,” utilizes methods other than optical detection for sequencing.

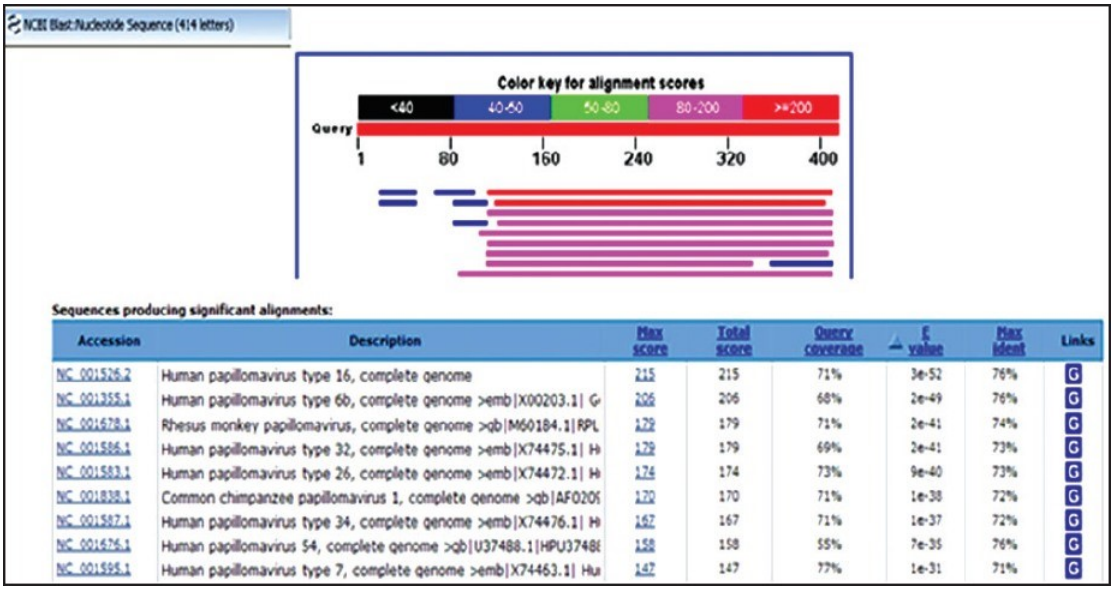
Bioinformatics

After sequencing, it is time to make sense of the information. The field of **bioinformatics** combines many fields together (i.e. biology, computer science, statistics) to use the power of computers to analyze information contained in the genomic sequence. Locating specific genes within a genome is referred to as **genome annotation**.

Open Reading Frames (ORFS)

An **open reading frame** or **ORF** denotes a possible protein-coding gene. For double-stranded DNA, there are six reading frames to be analyzed, since the DNA is read in sets of three bases at a time and there are two strands of DNA. An ORF typically has at least 100 codons before a stop codon, with 3’ terminator sequences. A **functional ORF** is one that is actually used by the organism to encode a protein. Computers are used to search the DNA sequence looking for ORFs, with those presumed to encode protein further analyzed by a bioinformaticist.

It is often helpful for the sequence to be compared against a database of sequences coding for known proteins. GenBank is a database of over 200 billion base pairs of sequences that scientists can access, to try and find matches to the sequence of interest. The database search tool **BLAST** (**basic local alignment search tool**) has programs for comparing both nucleotide sequences and amino acid sequences, providing a ranking of results in order of decreasing similarity.



BLAST Results.

Comparative Genomics

Once the sequences of organisms have been obtained, meaningful information can be gathered using **comparative genomics**. For this genomes are assessed for information regarding size, organization, and gene content.

Comparison of the genome of microbial strains has given scientists a better picture regarding the genes that organisms pick up. A group of multiple strains share a **core genome**, genes coding for essential cellular functions that they all have in common. The **pan**

genome represents all the genes found in all the members of species, so provides a good idea of the diversity of a group. Most of these "extra" genes are probably picked up by horizontal gene transfer.

Comparative genomics also shows that many genes are derived as a result of gene duplication. Genes within a single organism that likely came about because of gene duplication are referred to as **paralogs**. In many cases one of the genes might be altered to take on a new function. It is also possible for gene duplication to be found in different organisms, as a result of acquiring the original gene from a common ancestor. These genes are called **orthologs**.

Functional Genomics

The sequence of a genome and the location of genes provide part of the picture, but in order to fully understand an organism we need an idea of what the cell is doing with its genes. In other words, what happens when the genes are expressed? This is where **functional genomics** comes in – placing the genomic information in context.

The first step in gene expression is transcription or the manufacture of RNA. **Transcriptome** refers to the entire complement of RNA that a cell can make from its genome, while **proteome** refers to all the proteins encoded by an organisms' genome, in the final step of gene expression.

Microarrays

Microarrays or **gene chips** are solid supports upon which multiple spots of DNA are placed, in a grid-like fashion. Each spot of DNA represents a single gene or ORF. Known fragments of nucleic acid are labeled and used as **probes**, with a signal produced if binding occurs. Microarrays can be used to determine what genes might be turned on or off under particular conditions, such as comparing the growth of a bacterial pathogen inside the host versus outside of the host.

Proteomics

The study of the proteins of an organism (or the proteome) is referred to as **proteomics**. Much of the interest focuses on **functional proteomics**, which examines the functions of the cellular proteins and the ways in which they interact with one another.

One common technique used in the study of proteins is **two-dimensional gel electrophoresis**, which first separates proteins based on their isoelectric points. This is accomplished by using a pH gradient, which separates the proteins based on their amino acid content. The separated proteins are then run through a polyacrylamide gel, providing the second dimension as proteins are separated by size.

Structural proteomics focuses on the three-dimensional structure of proteins, which is often determined by protein modeling, using computer algorithms to predict the most likely folding of the protein based on amino acid information and known protein patterns.

Metabolomics

Metabolomics strives to identify the complete set of metabolic intermediates produced by an organism. This can be extremely complicated, since many metabolites are used by cells in multiple pathways.

Metagenomics

Metagenomics or **environmental genomics** refers to the extraction of pooled DNA directly from a specific environment, without the initial isolation and identification of organisms within that environment. Since many microbial species are difficult to culture in the laboratory, studying the **metagenome** of an environment allows scientists to consider all organisms that might be present. Taxa can even be identified in the absence of organism isolation using nucleic acid sequences alone, where the taxon is known as **phylotype**.

Key Words

genomics, sequencing, shotgun sequencing, genomic library, second generation DNA sequencing, massively parallel methods, third- and fourth-generation DNA sequencing, bioinformatics, genome annotation, open reading frame/ORF, functional ORF, GenBank, BLAST/basic local alignment search tool, comparative genomics, core genome, pan genome, paralog, ortholog, functional genomics, transcriptome, proteome, microarray/gene chips, probe, proteomics, functional proteomics, two-dimensional gel electrophoresis, structural proteomics, metabolomics, metagenomics/environmental genomics, metagenome, phylotype.

Study Questions

1. What does the field of genomics encompass?
2. What is shotgun sequencing and how does this allow for the complete sequencing of an organism's genome?
3. What are the basic differences among 2nd, 3rd, and 4th generation sequencing?
4. What is an open reading frame and how can scientists use it to determine information about a genome and its products?
5. How does functional genomics differ from comparative genomics? What are the tools used in functional genomics and what information can be obtained from each?

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18.5.2: Transcriptomics

Consider a matrix containing all of the known gene sequences in a genome. To make such a matrix for analysis, one would need to make copies of every gene, either by chemical synthesis or by using the polymerase chain reaction. The strands of the resulting DNAs would then be separated to obtain single-stranded sequences that could be attached to the chip. Each box of the grid would contain sequence from one gene. With this grid, one could analyze the transcriptome - all of the mRNAs being made in selected cells at a given time. For a simple analysis, one could take a tissue (say liver) and extract all the mRNAs from it. This mRNA population represents all the genes that were being expressed in the liver cells at the time the RNA was extracted. These RNAs should be able to hybridize (base-pair) with their corresponding genes on the microarray. Genes that were not being expressed would have no mRNAs to bind to their corresponding genes on the grid.

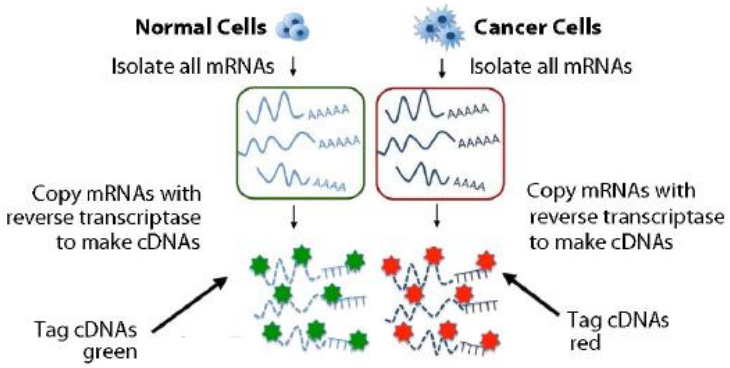


Figure 8.25 - Copying and labeling of transcriptome. Image by Taralyn Tan

In practice, the mRNAs are not used directly, but are copied into single-stranded DNA copies called cDNAs. The cDNAs are tagged with a fluorescent dye and added to the microarray under conditions that allow base pairing so that the cDNAs can find and base pair with complementary sequences on the matrix (Figure 8.26). The matrix is then washed to remove unhybridized cDNAs. The presence/absence/abundance of each mRNA is then readily determined by measuring the amount of dye at each box of the grid.

Figure 8.26 - Add labeled cDNAs to microarray plate. Image by Taralyn Tan

In Figure 8.27, a fluorescent cDNA has bound to the spot on the far right in the third row of the grid. This means that the sequence of the cDNA was complementary to the sequence of the gene sequence immobilized at that spot. Because the identity of the genes at each position on the grid is known, we then know that the sample contained mRNA that corresponded to that particular gene. In other words, that gene was being expressed in the cells from which the mRNAs were obtained.

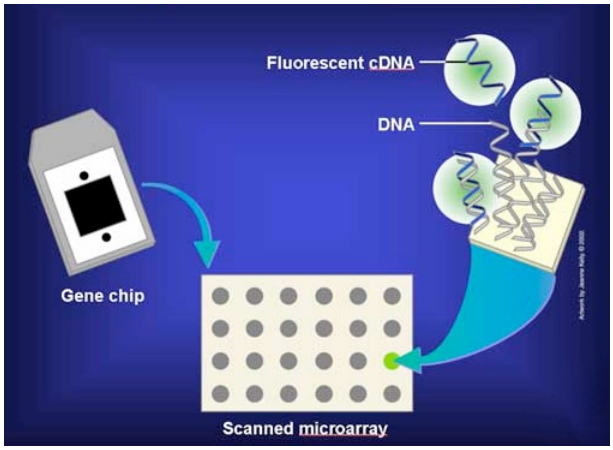


Figure 8.27 - Binding of a fluorescent cDNA copy of a specific mRNA to DNA immobilized on one spot in a microarray. Wikipedia

A more powerful analysis could be performed with two sets of mRNAs simultaneously. . One set of cDNAs could come from a cancerous tissue and the other from a non-cancerous tissue, for example. The cDNAs derived from each sample is marked with a different color (say green for normal and red for cancerous) (Figure 8.25). The cDNAs are mixed and then added to the matrix and complementary sequences are once again allowed to form duplexes (Figure 8.27).

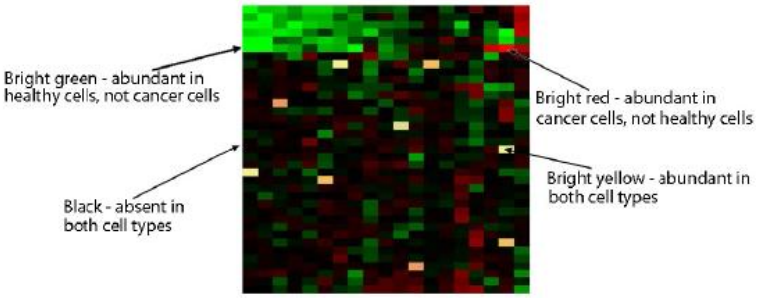


Figure 8.28 - Microarray analysis comparing gene expression in normal and cancer cells. Wikipedia

Unhybridized cDNAs are washed away and then the plate is analyzed. Red grid boxes correspond to an mRNA present in the cancerous tissue, but not in the non-cancerous tissue. Green grid boxes correspond to an mRNA present in the non-cancerous tissue, but not in the cancerous tissue. Yellow would correspond to mRNAs present in equal abundance in the two tissues (Figure 8.28). The intensity of each spot also gives information about the relative amounts of each mRNA in each tissue.

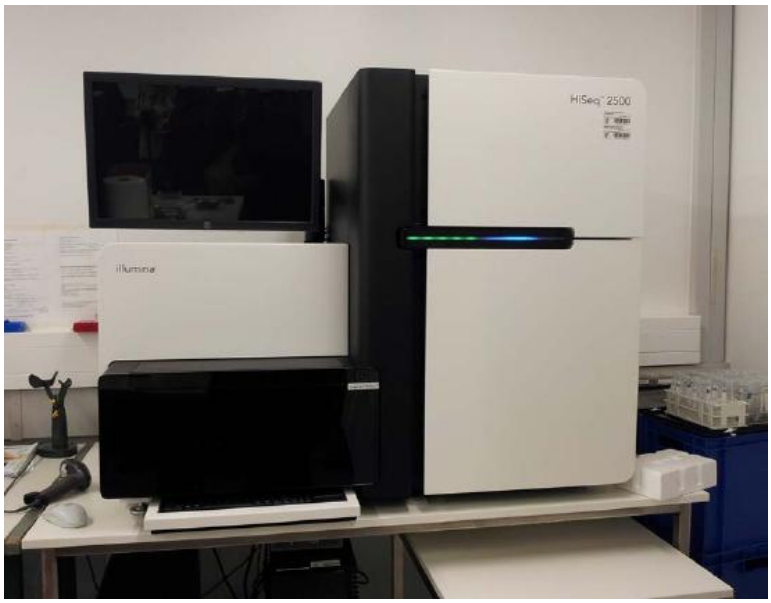


Figure 8.29 - Automated high throughput sequencer. Wikipedia

The same principle used for nucleic acid microarrays can be adapted for analyzing other molecules. For example, polypeptides could be bonded to the glass slide instead of DNA to create a protein chip. Protein chips are useful for studying the interactions of proteins with other molecules as well as for diagnostics.

RNA-Seq Technique

Like microarrays, a newer method called RNA-Seq, is a tool for simultaneously detecting and quantitating all of the transcripts in a given sample. This method relies on recently developed sequencing technologies called next-generation sequencing, or deep sequencing. These techniques allow for rapid, parallel sequencing of millions of DNA fragments and can, thus, be used not only for genomic DNA, but also to sequence all of the reverse-transcribed RNAs from a given sample.

To determine all the protein-coding genes that were being expressed in a particular set of cells under specific physiological conditions, all of the mRNA would first be extracted and reverse-transcribed into cDNA. This step is similar to the preparation of samples for microarrays. However, at this point, the cDNAs are fragmented into smaller pieces, and have small sequencing

adapters attached at either end. The fragments are then subjected to high-throughput sequencing, to obtain short sequences from all of the fragments. These data are aligned against the genome sequence and used to measure the level of expression of different genes. RNA-Seq offers some advantages over microarrays. With microarrays, an RNA can only be detected if the gene sequence corresponding to it is present on the grid. In RNA-Seq every RNA present in the sample is sequenced, so detection of RNAs is not limited by the probes on a chip. RNA-Seq is more sensitive than microarrays and offers a much larger range over which gene expression can be measured accurately.

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18.5.3: Basic Techniques in Protein Analysis

Learning Objectives

- Describe the techniques used in proteomics to analyze proteins

Basic Techniques in Protein Analysis

The ultimate goal of proteomics is to identify or compare the proteins expressed in a given genome under specific conditions, study the interactions between the proteins, and use the information to predict cell behavior or develop drug targets. Just as the genome is analyzed using the basic technique of DNA sequencing, proteomics requires techniques for protein analysis. The basic technique for protein analysis, analogous to DNA sequencing, is mass spectrometry.



Figure **18.5.3.1**: Mass Spectrometer: Matrix-Assisted Laser Desorbtion Ionisation – Time Of Flight (MALDI-TOF) Mass Spectrometer. Mass spectrometry can be used in protein analysis.

Mass Spectrometry

Mass spectrometry is used to identify and determine the characteristics of a molecule. It is a technique in which gas phase molecules are ionized and their mass-to-charge ratio is measured by observing acceleration differences of ions when an electric field is applied. Lighter ions will accelerate faster and be detected first. If the mass is measured with precision, then the composition of the molecule can be identified. In the case of proteins, the sequence can be identified. The challenge of techniques used for proteomic analyses is the difficulty in detecting small quantities of proteins, but advances in spectrometry have allowed researchers to analyze very small samples of protein. Variations in protein expression in diseased states, however, can be difficult to discern. Proteins are naturally-unstable molecules, which makes proteomic analysis much more difficult than genomic analysis.

X-ray crystallography and Nuclear Magnetic Resonance

X-ray crystallography enables scientists to determine the three-dimensional structure of a protein crystal at atomic resolution. Crystallographers aim high-powered X-rays at a tiny crystal containing trillions of identical molecules. The crystal scatters the X-rays onto an electronic detector that is the same type used to capture images in a digital camera. After each blast of X-rays, lasting from a few seconds to several hours, the researchers precisely rotate the crystal by entering its desired orientation into the computer that controls the X-ray apparatus. This enables the scientists to capture in three dimensions how the crystal scatters, or diffracts, X-rays. The intensity of each diffracted ray is fed into a computer, which uses a mathematical equation to calculate the position of every atom in the crystallized molecule. The result is a three-dimensional digital image of the molecule.

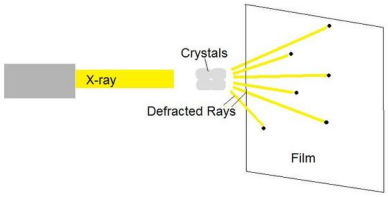


Figure 18.5.3.1: X-ray crystallography: X-rays that hit atomic nuclei are diffracted onto a detector.

Another protein imaging technique, nuclear magnetic resonance (NMR), uses the magnetic properties of atoms to determine the three-dimensional structure of proteins. NMR spectroscopy is unique in being able to reveal the atomic structure of macromolecules in solution, provided that highly-concentrated solution can be obtained. This technique depends on the fact that certain atomic nuclei are intrinsically magnetic. The chemical shift of nuclei depends on their local environment. The spins of neighboring nuclei interact with each other in ways that provide definitive structural information that can be used to determine complete three-dimensional structures of proteins.

Protein Microarrays and Two- Hybrid Screening

Protein microarrays have also been used to study interactions between proteins. These are large-scale adaptations of the basic two-hybrid screen. The premise behind the two-hybrid screen is that most eukaryotic transcription factors have modular activating and binding domains that can still activate transcription even when split into two separate fragments, as long as the fragments are brought within close proximity to each other. Generally, the transcription factor is split into a DNA-binding domain (BD) and an activation domain (AD). One protein of interest is genetically fused to the BD and another protein is fused to the AD. If the two proteins of interest bind each other, then the BD and AD will also come together and activate a reporter gene that signals interaction of the two hybrid proteins.

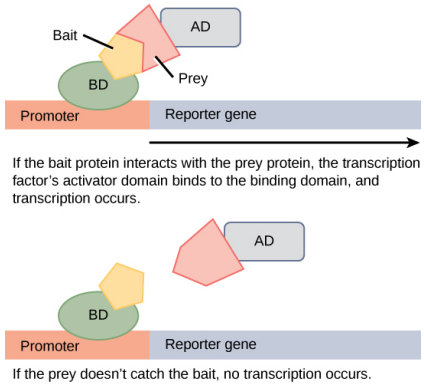


Figure 18.5.3.1: Two-hybrid screening: Two-hybrid screening is used to determine whether two proteins interact. In this method, a transcription factor is split into a DNA-binding domain (BD) and an activation domain (AD). The binding domain is able to bind the promoter in the absence of the activator domain, but it does not turn on transcription. A protein called the bait is attached to the BD, and a protein called the prey is attached to the AD. Transcription occurs only if the prey "catches" the bait.

Western Blot

The western blot, or protein immunoblot, is a technique that combines protein electrophoresis and antibodies to detect proteins in a sample. A western blot is fairly quick and simple compared to the above techniques and, thus, can serve as an assay to validate results from other experiments. The protein sample is first separated by gel electrophoresis, then transferred to a nitrocellulose or other type of membrane, and finally stained with a primary antibody that specifically binds the protein of interest. A fluorescent or radioactive-labeled secondary antibody binds to the primary antibody and provides a means of detection via either photography or x-ray film, respectively.

Key Points

- Mass Spectrometry is a technique that is useful for determining the size of a protein or protein complex.
- X-ray crystallography and NMR are techniques useful for determining the 3-D structure of a protein or protein complex.
- Protein microarrays are useful for determining protein-protein interactions.

Key Terms

- **microarray**: any of several devices containing a two-dimensional array of small quantities of biological material used for various types of assays
- **reporter gene**: a gene that researchers attach to a regulatory sequence of another gene of interest and whose product is easily identifiable in assays

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SECTION OVERVIEW

18.6: Applications of Genomics

Skills to Develop

- Explain pharmacogenomics
- Define polygenic

The introduction of DNA sequencing and whole genome sequencing projects, particularly the Human Genome project, has expanded the applicability of DNA sequence information. Genomics is now being used in a wide variety of fields, such as metagenomics, pharmacogenomics, and mitochondrial genomics. The most commonly known application of genomics is to understand and find cures for diseases.

Predicting Disease Risk at the Individual Level

Predicting the risk of disease involves screening currently healthy individuals by genome analysis at the individual level. Intervention with lifestyle changes and drugs can be recommended before disease onset. However, this approach is most applicable when the problem resides within a single gene defect. Such defects only account for approximately 5 percent of diseases in developed countries. Most of the common diseases, such as heart disease, are multi-factored or polygenic, which is a phenotypic characteristic that involves two or more genes, and also involve environmental factors such as diet. In April 2010, scientists at Stanford University published the genome analysis of a healthy individual (Stephen Quake, a scientist at Stanford University, who had his genome sequenced); the analysis predicted his propensity to acquire various diseases. A risk assessment was performed to analyze Quake's percentage of risk for 55 different medical conditions. A rare genetic mutation was found, which showed him to be at risk for sudden heart attack. He was also predicted to have a 23 percent risk of developing prostate cancer and a 1.4 percent risk of developing Alzheimer's. The scientists used databases and several publications to analyze the genomic data. Even though genomic sequencing is becoming more affordable and analytical tools are becoming more reliable, ethical issues surrounding genomic analysis at a population level remain to be addressed.

Art Connection

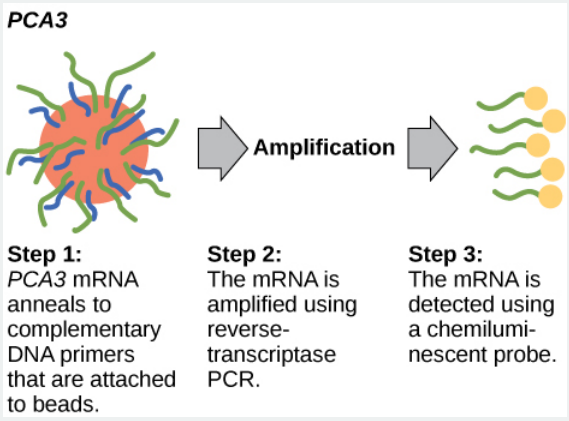


Figure 18.6.1: *PCA3* is a gene that is expressed in prostate epithelial cells and overexpressed in cancerous cells. A high concentration of *PCA3* in urine is indicative of prostate cancer. The *PCA3* test is considered to be a better indicator of cancer than the more well know PSA test, which measures the level of PSA (prostate-specific antigen) in the blood.

In 2011, the United States Preventative Services Task Force recommended against using the PSA test to screen healthy men for prostate cancer. Their recommendation is based on evidence that screening does not reduce the risk of death from prostate cancer. Prostate cancer often develops very slowly and does not cause problems, while the cancer treatment can have severe side effects. The *PCA3* test is considered to be more accurate, but screening may still result in men who would not have been harmed by the cancer itself suffering side effects from treatment. What do you think? Should all healthy men be screened for

prostate cancer using the *PCA3* or PSA test? Should people in general be screened to find out if they have a genetic risk for cancer or other diseases?

Pharmacogenomics and Toxicogenomics

Pharmacogenomics, also called toxicogenomics, involves evaluating the effectiveness and safety of drugs on the basis of information from an individual's genomic sequence. Genomic responses to drugs can be studied using experimental animals (such as laboratory rats or mice) or live cells in the laboratory before embarking on studies with humans. Studying changes in gene expression could provide information about the transcription profile in the presence of the drug, which can be used as an early indicator of the potential for toxic effects. For example, genes involved in cellular growth and controlled cell death, when disturbed, could lead to the growth of cancerous cells. Genome-wide studies can also help to find new genes involved in drug toxicity. Personal genome sequence information can be used to prescribe medications that will be most effective and least toxic on the basis of the individual patient's genotype. The gene signatures may not be completely accurate, but can be tested further before pathologic symptoms arise.

Microbial Genomics: Metagenomics

Traditionally, microbiology has been taught with the view that microorganisms are best studied under pure culture conditions, which involves isolating a single type of cell and culturing it in the laboratory. Because microorganisms can go through several generations in a matter of hours, their gene expression profiles adapt to the new laboratory environment very quickly. In addition, the vast majority of bacterial species resist being cultured in isolation. Most microorganisms do not live as isolated entities, but in microbial communities known as biofilms. For all of these reasons, pure culture is not always the best way to study microorganisms. Metagenomics is the study of the collective genomes of multiple species that grow and interact in an environmental niche. Metagenomics can be used to identify new species more rapidly and to analyze the effect of pollutants on the environment (Figure **18.6.2**).

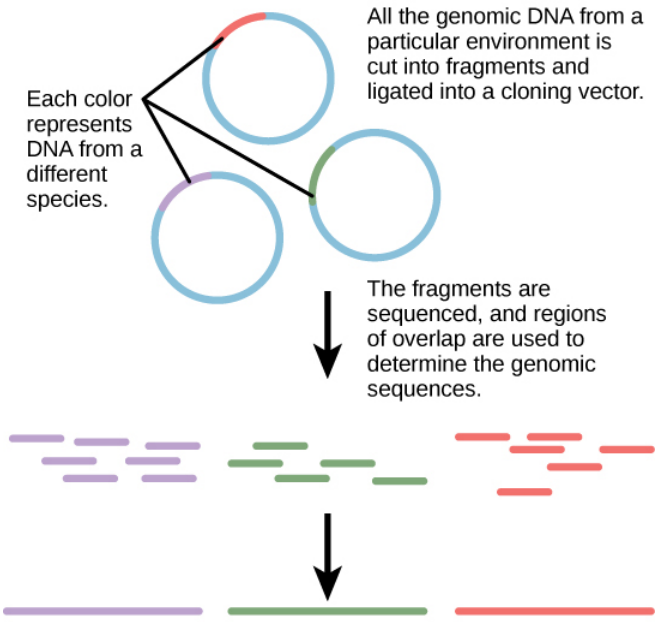


Figure **18.6.2**: Metagenomics involves isolating DNA from multiple species within an environmental niche.

Microbial Genomics: Creation of New Biofuels

Knowledge of the genomics of microorganisms is being used to find better ways to harness biofuels from algae and cyanobacteria. The primary sources of fuel today are coal, oil, wood, and other plant products, such as ethanol. Although plants are renewable resources, there is still a need to find more alternative renewable sources of energy to meet our population's energy demands. The microbial world is one of the largest resources for genes that encode new enzymes and produce new organic compounds, and it remains largely untapped. Microorganisms are used to create products, such as enzymes that are used in research, antibiotics, and

other anti-microbial mechanisms. Microbial genomics is helping to develop diagnostic tools, improved vaccines, new disease treatments, and advanced environmental cleanup techniques.

Mitochondrial Genomics

Mitochondria are intracellular organelles that contain their own DNA. Mitochondrial DNA mutates at a rapid rate and is often used to study evolutionary relationships. Another feature that makes studying the mitochondrial genome interesting is that the mitochondrial DNA in most multicellular organisms is passed on from the mother during the process of fertilization. For this reason, mitochondrial genomics is often used to trace genealogy.

Information and clues obtained from DNA samples found at crime scenes have been used as evidence in court cases, and genetic markers have been used in forensic analysis. Genomic analysis has also become useful in this field. In 2001, the first use of genomics in forensics was published. It was a collaborative attempt between academic research institutions and the FBI to solve the mysterious cases of anthrax communicated via the US Postal Service. Using microbial genomics, researchers determined that a specific strain of anthrax was used in all the mailings.

Genomics in Agriculture

Genomics can reduce the trials and failures involved in scientific research to a certain extent, which could improve the quality and quantity of crop yields in agriculture. Linking traits to genes or gene signatures helps to improve crop breeding to generate hybrids with the most desirable qualities. Scientists use genomic data to identify desirable traits, and then transfer those traits to a different organism. Scientists are discovering how genomics can improve the quality and quantity of agricultural production. For example, scientists could use desirable traits to create a useful product or enhance an existing product, such as making a drought-sensitive crop more tolerant of the dry season.

Summary

Imagination is the only barrier to the applicability of genomics. Genomics is being applied to most fields of biology; it is being used for personalized medicine, prediction of disease risks at an individual level, the study of drug interactions before the conduct of clinical trials, and the study of microorganisms in the environment as opposed to the laboratory. It is also being applied to developments such as the generation of new biofuels, genealogical assessment using mitochondria, advances in forensic science, and improvements in agriculture.

Art Connections

Figure **18.6.1**: In 2011, the United States Preventative Services Task Force recommended against using the PSA test to screen healthy men for prostate cancer. Their recommendation is based on evidence that screening does not reduce the risk of death from prostate cancer. Prostate cancer often develops very slowly and does not cause problems, while the cancer treatment can have severe side effects. The *PCA3* test is considered to be more accurate, but screening may still result in men who would not have been harmed by the cancer itself suffering side effects from treatment. What do you think? Should all healthy men be screened for prostate cancer using the *PCA3* or PSA test? Should people in general be screened to find out if they have a genetic risk for cancer or other diseases?

Answer

There are no right or wrong answers to these questions. While it is true that prostate cancer treatment itself can be harmful, many men would rather be aware that they have cancer so they can monitor the disease and begin treatment if it progresses. And while genetic screening may be useful, it is expensive and may cause needless worry. People with certain risk factors may never develop the disease, and preventative treatments may do more harm than good.

Glossary

metagenomics

study of the collective genomes of multiple species that grow and interact in an environmental niche

pharmacogenomics

study of drug interactions with the genome or proteome; also called toxicogenomics

polygenic
phenotypic characteristic caused by two or more genes

pure culture
growth of a single type of cell in the laboratory

18.6.1: Cancer Proteomics

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18.6.1: Cancer Proteomics

Learning Objectives

- Explain the ways in which cancer proteomics may lead to better treatments

Genomes and proteomes of patients suffering from specific diseases are being studied to understand the genetic basis of diseases. The most prominent set of diseases being studied with proteomic approaches is cancer. Proteomic approaches are being used to improve screening and early detection of cancer, which is achieved by identifying proteins whose expression is affected by the disease process.

An individual protein that indicates disease is called a biomarker, whereas a set of proteins with altered expression levels is called a protein signature. For a biomarker or protein signature to be useful as a candidate for early screening and detection of a cancer, it must be secreted in body fluids (e.g. sweat, blood, or urine) such that large-scale screenings can be performed in a non-invasive fashion. The current problem with using biomarkers for the early detection of cancer is the high rate of false-negative results. A false-negative is an incorrect test result that should have been positive. In other words, many cases of cancer go undetected, which makes biomarkers unreliable. Some examples of protein biomarkers used in cancer detection are CA-125 for ovarian cancer and PSA for prostate cancer. Protein signatures may be more reliable than biomarkers to detect cancer cells.

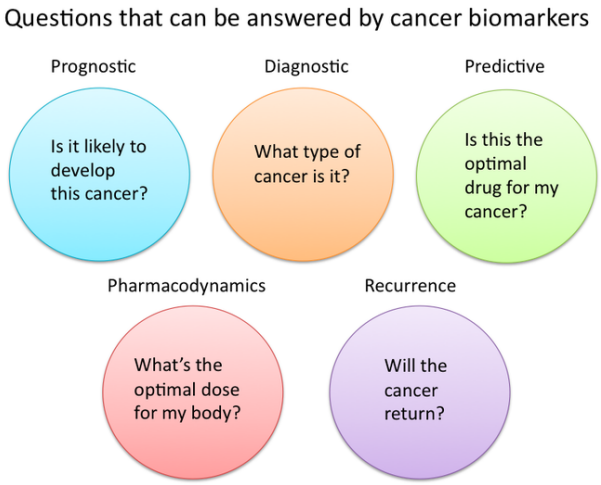


Figure **18.6.1.1**: Questions that can be answered by biomarkers: In cancer research and medicine, biomarkers are used in three primary ways: (A) Diagnostic – To help diagnose conditions, as in the case of identifying early stage cancers. (B) Prognostic – To forecast how aggressive a condition is, as in the case of determining a patient's ability to fare in the absence of treatment. (C) Predictive – To predict how well a patient will respond to treatment.

Proteomics is also being used to develop individualized treatment plans, which involves the prediction of whether or not an individual will respond to specific drugs and the side effects that the individual may experience. In addition, proteomics can be used to predict the possibility of disease recurrence. The National Cancer Institute has developed programs to improve the detection and treatment of cancer. The Clinical Proteomic Technologies for Cancer and the Early Detection Research Network are efforts to identify protein signatures specific to different types of cancers. The Biomedical Proteomics Program is designed to identify protein signatures and design effective therapies for cancer patients.

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Key Points

- Identifying those proteins whose expression is affected by disease processes can be used to improve screening and early detection of cancer.
- Different biomarkers and protein signatures are being used to analyze each type of cancer.
- A future goal of cancer proteomics is to have a personalized treatment plan for each individual.

Key Terms

- **biomarker**: a substance used as an indicator of a biological state, most commonly disease

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CHAPTER OVERVIEW

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19.1.1: Embryonic Development

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19.2.1: Cell Growth and Division

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19.7: Morphogenesis

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SECTION OVERVIEW

19.1: The Process of Development

19.1.1: Embryonic Development

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19.1.1: Embryonic Development

In animals, one can usually distinguish 4 stages of embryonic development.

- Cleavage
- Patterning
- Differentiation
- Growth

Cleavage

Mitosis and cytokinesis of the zygote, an unusually large cell, produces an increasing number of smaller cells, each with an exact copy of the genome present in the zygote. However, the genes of the zygote are not expressed at first. The early activities of cleavage are controlled by the mother's genome; that is, by mRNAs and proteins she deposited in the unfertilized egg. In humans, the switch-over occurs after 4–8 cells have been produced; in frogs not until thousands of cells have been produced. Cleavage ends with the formation of a **blastula**.

Patterning

During this phase, the cells produced by cleavage organize themselves in layers and masses, a process called **gastrulation**. The pattern of the future animal appears:

- front to rear (the **anterior-posterior** axis)
- back side and belly side (its **dorsal-ventral** axis)
- left and right sides.

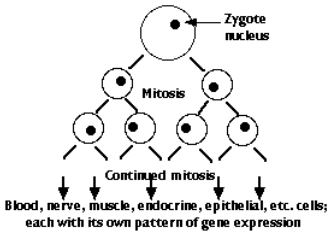


Figure 14.1.1 Zygote Mitosis

The genome of the zygote contains all the genes needed to make the hundreds of different types of cells that will make up the complete animal. There are two major categories of these genes:

- "housekeeping" genes = those that encode the RNAs and proteins needed by all kinds of cells. Examples:
  - genes for tRNAs, rRNAs
  - genes encoding the enzymes of glycolysis.
- tissue-specific genes = those that encode mRNAs and hence proteins that are used by one or a few specific kinds of cell. Examples:
  - genes for hemoglobin expressed in the precursors of red blood cells
  - the gene for insulin expressed in the beta cells of the islets of Langerhans

However, every cell descended from the zygote has been produced by mitosis and thus contains the complete genome of the organism (with a very few exceptions).

Two pieces of evidence:

- Dolly - Dolly is the sheep that was formed by inserting a nucleus from a single cell of an **adult** sheep into an enucleated sheep egg. She proves that the cell from the adult had lost none of the genes needed to build all the tissues of a sheep.
- Spemann's egg-tying experiments - Many years earlier, the German embryologist Hans Spemann demonstrated the same truth. He used strands of baby hair to tie loops around fertilized salamander eggs. Although the egg half with the nucleus began cleaving normally, the other side did not begin cleavage until a nucleus finally slipped through the knot. So long as the egg was tied so that both halves contained some of the gray crescent, the second half began normal cleavage and ultimately produced a

second tadpole (right). Even after 5 mitotic division of the zygote nucleus (the 32-cell stage), the entire genome was still available in each descendant nucleus.

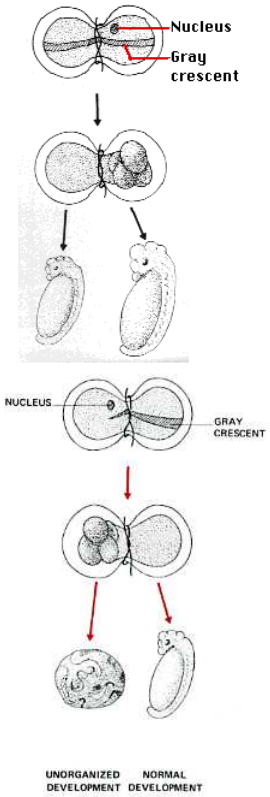


Figure 14.1.3 Frog embryo courtesy L. M. Beidler

1. A fertilized egg is much larger than the normal cells of an animal's body. Some (e.g., a hen's egg) are truly huge. The frog egg has a volume 1.6 millions times larger than a typical frog cell. The photo is of a 16-cell frog embryo. This mass of cells is no larger than the original egg. The eggs of mammals are smaller, but even they are larger than their descendant cells will be.
2. The cytoplasm of the fertilized egg is **not homogeneous**. It contains gradients of mRNAs and proteins. These are the products of the mother's genes and were deposited in the egg by her.
3. Cleavage of the fertilized egg partitions it into thousands of cells of normal size. Each contains a nucleus descended from the zygote nucleus.
4. But each nucleus finds itself partitioned off in cytoplasm containing a particular mix of mRNAs and proteins.
5. When the frog blastula has produced some 4,000 cells, transcription and translation of its nuclear genes begins (and the mother's mRNA molecules, that up to now have been the source of all protein synthesis, are destroyed).
6. The genes that are expressed by the nucleus in a given cell are regulated by the molecules, mostly protein transcription factors and microRNAs (miRNAs), found in the cytoplasm surrounding that nucleus.
7. Once a cell-specific pattern of gene expression is launched, that cell may release molecules that regulate the genes of nearby cells.
8. In this way, the foundation is laid for the building of an organism with hundreds of types of differentiated cells — each in its correct location and performing its correct functions.

Xenopus

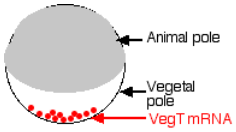


Figure 14.1.4 Vegetal Pole

- During egg formation, molecules of mRNA encoding the protein VegT are deposited at the vegetal pole of the cell.

- Cells that form there during cleavage translate the mRNA into the **VegT** protein.
- VegT is a transcription factor that turns on genes that produce members of the transforming growth factor-beta (TGF-β) family (e.g., **activin**).
- These proteins are needed for cells to start down the path to becoming **mesoderm**.
- Some of those cells will, in turn, become the **Spemann organizer**.
- Later, the Spemann organizer will secrete molecules that induce the ectodermal cells above them to develop into the tissues of the brain and spinal cord.

Demonstration

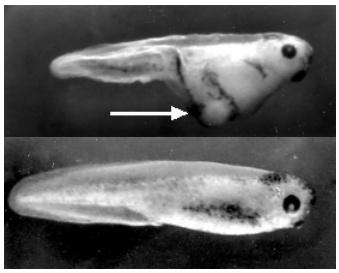


Figure 14.1.7 Double posterior larva

Inject the anterior of the fertilized egg with nanos mRNA. The result: another double-posterior larva.

Make female fruit flies that are transgenic for a recombinant gene containing:

- the gene for **nanos**
- coupled to the **3′ anterior-directing signal of the bicoid** gene.

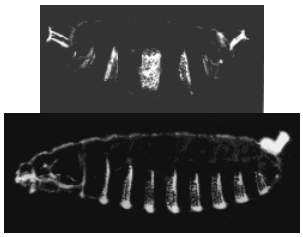


Figure 14.1.8 Larva images Elizabeth Gavis and Ruth Lehmann

A normal larva is shown on the right. The bright object at the right end of the normal larva and at both ends of the double posterior larva is the tip of the tail. These micrographs are courtesy of Elizabeth Gavis and Ruth Lehmann, in whose lab the third demonstration was performed.

The Mud Snail

The mud snail, **Ilyanassa obsoleta**, is a small gastropod that lives in mud flats along the Atlantic coast.

Like other **protostomes**, cleavage of the zygote produces daughter cells that are already committed to their fate. In other words, even as early as the two-cell stage, the cells are no longer totipotent. Unlike humans and other **deuterostomes**, then, identical twins cannot form.

In the 12 December 2002 issue of **Nature**, J. David Lambert and Lisa Nagy reported another mechanism by which two daughter cells become committed to different fates even though they have inherited the same genome.

They traced the distribution in the cells of early embryos of the **messenger RNAs** (mRNAs) encoding 3 proteins that are known to be important in the development of other animals such as Xenopus and Drosophila.

- *IoEve*, which is **I**lyanassa **o**bsoleta's version of ***even-skipped*** (***eve***) in Drosophila;
- ***IoDpp***, which is the snail's version of
  - ***decapentaplegic*** (***dpp***) in Drosophila and the genes encoding
  - **b**one **m**orphogenic **p**roteins (**BMP2** and **BMP4**) in vertebrates
- ***IoTld***, which encodes the snail's version of a protein called tolloid in Drosophila.

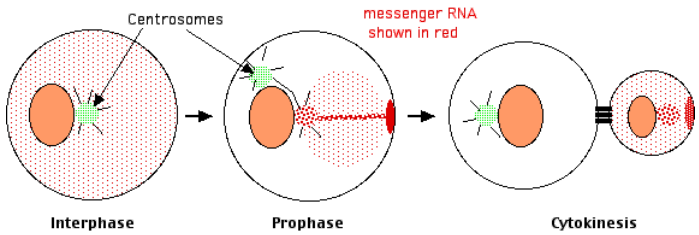


Figure 14.1.9 Duplication of centrosomes before mitosis

Lambert and Nagy found that

- in interphase the messenger RNAs were distributed diffusely throughout the cytosol, but
- as the cell got ready for cleavage, the mRNAs collected at **only one** of the now pair of centrosomes. They were collected there by traveling along the microtubules that radiate out from the centrosome.
- As cleavage continued, the mRNAs moved from the centrosome to a spot on the inner surface of the plasma membrane. They got there by traveling along actin filaments.
- At cytokinesis, this patch of accumulated mRNAs was incorporated exclusively into the smaller daughter cell.

Centrosome sorting (of proteins in this case) also plays a role in determining whether embryonic cells of ***Caenorhabditis elegans*** remain in the **germline** or become the **somatic** cells of the worm.

What comes next?

Development in Xenopus and Drosophila passes through three rather different (although often overlapping) phases:

- Establishing the main axes (anterior-posterior; dorsal-ventral; left-right). This is done by gradients of mRNAs and proteins encoded by the mother's genes and placed in the egg by her. It has been discussed here.
- Establishing the main body parts such as the notochord and central nervous system in vertebratesand the segments in DrosophilaThese are run by genes of the zygote itself.
- Filling in the details; that is, building the various organs of the animal.

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SECTION OVERVIEW

19.2: Cell Division

19.2.1: Cell Growth and Division

19.2.2: Frog Embryology

19.2.3: Cleavage

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19.2.1: Cell Growth and Division

Learning Objectives

- Describe the stages of the cell cycle
- Discuss how the cell cycle is regulated
- Describe the implications of losing control over the cell cycle
- Describe the stages of mitosis and cytokinesis, in order

So far in this chapter, you have read numerous times of the importance and prevalence of cell division. While there are a few cells in the body that do not undergo cell division (such as gametes, red blood cells, most neurons, and some muscle cells), most somatic cells divide regularly. A **somatic cell** is a general term for a body cell, and all human cells, except for the cells that produce eggs and sperm (which are referred to as germ cells), are somatic cells. Somatic cells contain **two** copies of each of their chromosomes (one copy received from each parent).

A **homologous** pair of chromosomes is the two copies of a single chromosome found in each somatic cell. The human is a **diploid** organism, having 23 homologous pairs of chromosomes in each of the somatic cells. The condition of having pairs of chromosomes is known as diploidy. Cells in the body replace themselves over the lifetime of a person. For example, the cells lining the gastrointestinal tract must be frequently replaced when constantly "worn off" by the movement of food through the gut. But what triggers a cell to divide, and how does it prepare for and complete cell division? The **cell cycle** is the sequence of events in the life of the cell from the moment it is created at the end of a previous cycle of cell division until it then divides itself, generating two new cells.

The Cell Cycle

One "turn" or cycle of the cell cycle consists of two general phases: interphase, followed by mitosis and cytokinesis. **Interphase** is the period of the cell cycle during which the cell is not dividing. The majority of cells are in interphase most of the time. **Mitosis** is the division of genetic material, during which the cell nucleus breaks down and two new, fully functional, nuclei are formed. **Cytokinesis** divides the cytoplasm into two distinctive cells.

Interphase

A cell grows and carries out all normal metabolic functions and processes in a period called G_1 (Figure 1). **G_1 phase** (gap 1 phase) is the first gap, or growth phase in the cell cycle. For cells that will divide again, G_1 is followed by replication of the DNA, during the S phase. The **S phase** (synthesis phase) is period during which a cell replicates its DNA.

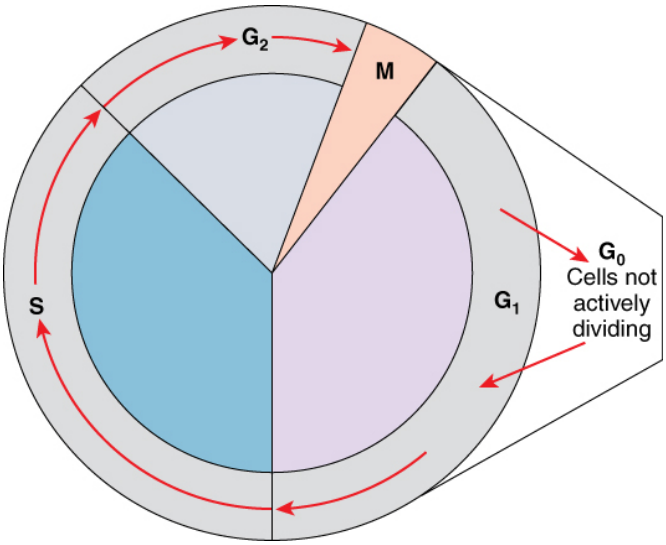


Figure 1. Cell Cycle. The two major phases of the cell cycle include mitosis (cell division), and interphase, when the cell grows and performs all of its normal functions. Interphase is further subdivided into G_1, S, and G_2 phases.

After the synthesis phase, the cell proceeds through the G_2 phase. The **G_2 phase** is a second gap phase, during which the cell continues to grow and makes the necessary preparations for mitosis. Between G_1, S, and G_2 phases, cells will vary the most in their duration of the G1 phase. It is here that a cell might spend a couple of hours, or many days. The S phase typically lasts between 8-10 hours and the G_2 phase approximately 5 hours. In contrast to these phases, the **G_0 phase** is a resting phase of the cell cycle. Cells that have temporarily stopped dividing and are resting (a common condition) and cells that have permanently ceased dividing (like nerve cells) are said to be in G_0.

The Structure of Chromosomes

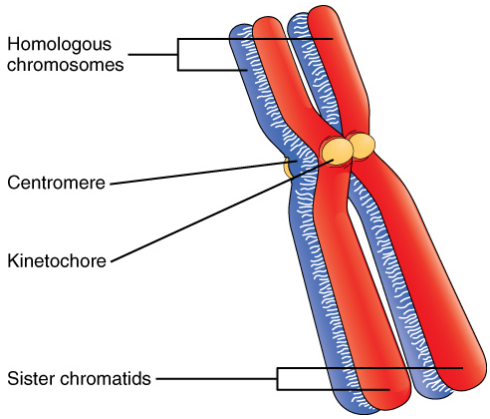


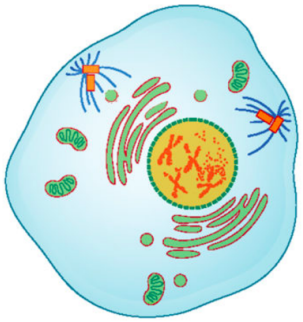
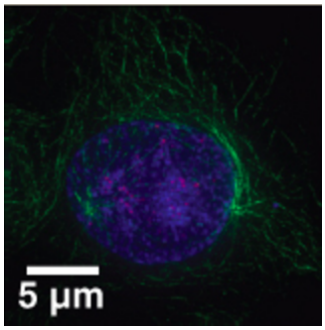
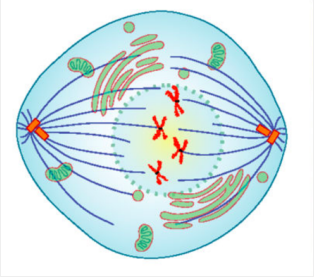
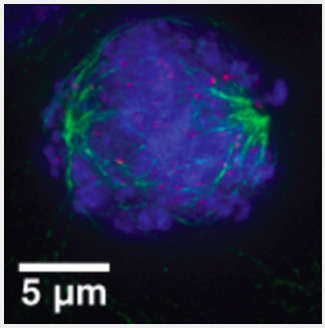
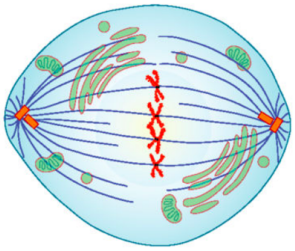
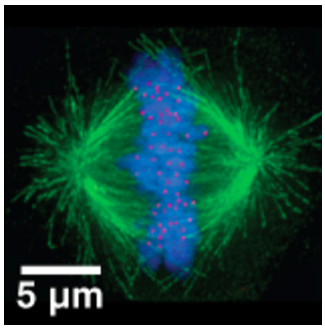
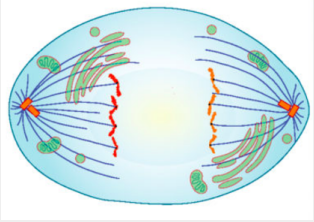
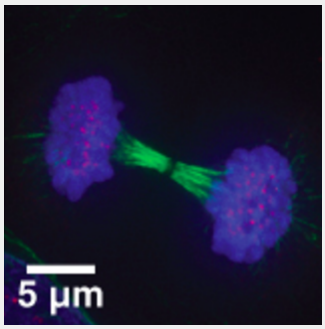
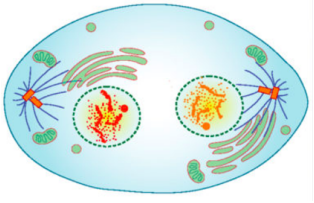
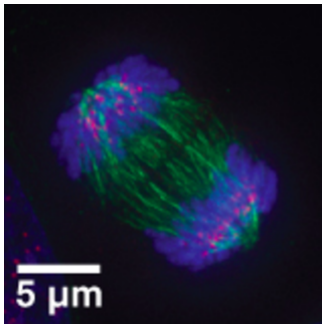
Figure 2. A Homologous Pair of Chromosomes with their Attached Sister Chromatids. The red and blue colors correspond to a homologous pair of chromosomes. Each member of the pair was separately inherited from one parent. Each chromosome in the homologous pair is also bound to an identical sister chromatid, which is produced by DNA replication, and results in the familiar "X" shape.

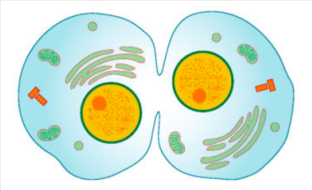
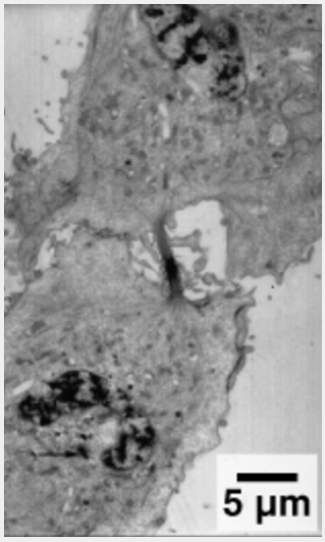
Billions of cells in the human body divide every day. During the synthesis phase (S, for DNA synthesis) of interphase, the amount of DNA within the cell precisely doubles. Therefore, after DNA replication but before cell division, each cell actually contains **two** copies of each chromosome. Each copy of the chromosome is referred to as a **sister chromatid** and is physically bound to the other copy. The **centromere** is the structure that attaches one sister chromatid to another. Because a human cell has 46 chromosomes, during this phase, there are 92 chromatids (46 × 2) in the cell. Make sure not to confuse the concept of a pair of chromatids (one chromosome and its exact copy attached during mitosis) and a homologous pair of chromosomes (two paired chromosomes which were inherited separately, one from each parent) (Figure 2).

Mitosis

The **mitotic phase** of the cell typically takes between 1 and 2 hours. During this phase, a cell undergoes two major processes. First, it completes mitosis, during which the contents of the nucleus are equitably pulled apart and distributed between its two halves. Cytokinesis then occurs, dividing the cytoplasm and cell body into two new cells. Mitosis is divided into four major stages that take place after interphase (Table 1) and in the following order: prophase, metaphase, anaphase, and telophase. The process is then followed by cytokinesis.

Table 1. Cell Division: Mitosis Followed by Cytokinesis

Phase	Illustration	Key Events	Micrograph
Prophase		Chromosomes condense and become visible Spindle fibers emerge from the centrosomes Nuclear envelope breaks down Centrosomes move toward opposite poles	
Prometaphase		Chromosomes continue to condense Kinetochores appear at the centromeres Mitotic spindle microtubules attach to kinetochores	
Metaphase		Chromosomes are lined up at the metaphase plate Each sister chromatid is attached to a spindle fiber originating from opposite poles	
Anaphase		Centromeres split in two Sister chromatids (now called chromosomes) are pulled toward opposite poles Certain spindle fibers begin to elongate the cell	
Telophase		Chromosomes arrive at opposite poles and begin to decondense Nuclear envelope surrounds each set of chromosomes The mitotic spindle breaks down Spindle fibers continue to push poles apart	

Cytokinesis		Animal cells: a cleavage furrow separates the daughter cells Plant cells: a cell plate, the precursor to a new cell wall, separates the daughter cells	

Prophase is the first phase of mitosis, during which the loosely packed chromatin coils and condenses into visible chromosomes. During prophase, each chromosome becomes visible with its identical partner attached, forming the familiar X-shape of sister chromatids. The nucleolus disappears early during this phase, and the nuclear envelope also disintegrates. A major occurrence during prophase concerns a very important structure that contains the origin site for microtubule growth. Recall the cellular structures called centrioles that serve as origin points from which microtubules extend. These tiny structures also play a very important role during mitosis. A **centrosome** is a pair of centrioles together. The cell contains two centrosomes side-by-side, which begin to move apart during prophase. As the centrosomes migrate to two different sides of the cell, microtubules begin to extend from each like long fingers from two hands extending toward each other. The **mitotic spindle** is the structure composed of the centrosomes and their emerging microtubules. Near the end of prophase there is an invasion of the nuclear area by microtubules from the mitotic spindle. The nuclear membrane has disintegrated, and the microtubules attach themselves to the centromeres that adjoin pairs of sister chromatids. The **kinetochore** is a protein structure on the centromere that is the point of attachment between the mitotic spindle and the sister chromatids. This stage is referred to as late prophase or “prometaphase” to indicate the transition between prophase and metaphase.

Metaphase is the second stage of mitosis. During this stage, the sister chromatids, with their attached microtubules, line up along a linear plane in the middle of the cell. A metaphase plate forms between the centrosomes that are now located at either end of the cell. The **metaphase plate** is the name for the plane through the center of the spindle on which the sister chromatids are positioned. The microtubules are now poised to pull apart the sister chromatids and bring one from each pair to each side of the cell.

Anaphase is the third stage of mitosis. Anaphase takes place over a few minutes, when the pairs of sister chromatids are separated from one another, forming individual chromosomes once again. These chromosomes are pulled to opposite ends of the cell by their kinetochores, as the microtubules shorten. Each end of the cell receives one partner from each pair of sister chromatids, ensuring that the two new daughter cells will contain identical genetic material.

Telophase is the final stage of mitosis. Telophase is characterized by the formation of two new daughter nuclei at either end of the dividing cell. These newly formed nuclei surround the genetic material, which uncoils such that the chromosomes return to loosely packed chromatin. Nucleoli also reappear within the new nuclei, and the mitotic spindle breaks apart, each new cell receiving its own complement of DNA, organelles, membranes, and centrioles. At this point, the cell is already beginning to split in half as cytokinesis begins.

Cytokinesis

The **cleavage furrow** is a contractile band made up of microfilaments that forms around the midline of the cell during cytokinesis. (Recall that microfilaments consist of actin.) This contractile band squeezes the two cells apart until they finally separate. Two new cells are now formed. One of these cells (the “stem cell”) enters its own cell cycle; able to grow and divide again at some future time. The other cell transforms into the functional cell of the tissue, typically replacing an “old” cell there. Imagine a cell that

completed mitosis but never underwent cytokinesis. In some cases, a cell may divide its genetic material and grow in size, but fail to undergo cytokinesis. This results in larger cells with more than one nucleus. Usually this is an unwanted aberration and can be a sign of cancerous cells.

Cell Cycle Control

A very elaborate and precise system of regulation controls direct the way cells proceed from one phase to the next in the cell cycle and begin mitosis. The control system involves molecules within the cell as well as external triggers. These internal and external control triggers provide “stop” and “advance” signals for the cell. Precise regulation of the cell cycle is critical for maintaining the health of an organism, and loss of cell cycle control can lead to cancer.

Mechanisms of Cell Cycle Control

As the cell proceeds through its cycle, each phase involves certain processes that must be completed before the cell should advance to the next phase. A **checkpoint** is a point in the cell cycle at which the cycle can be signaled to move forward or stopped. At each of these checkpoints, different varieties of molecules provide the stop or go signals, depending on certain conditions within the cell. A **cyclin** is one of the primary classes of cell cycle control molecules (Figure 3). A **cyclin-dependent kinase (CDK)** is one of a group of molecules that work together with cyclins to determine progression past cell checkpoints. By interacting with many additional molecules, these triggers push the cell cycle forward unless prevented from doing so by “stop” signals, if for some reason the cell is not ready. At the G_1 checkpoint, the cell must be ready for DNA synthesis to occur. At the G_2 checkpoint the cell must be fully prepared for mitosis. Even during mitosis, a crucial stop and go checkpoint in metaphase ensures that the cell is fully prepared to complete cell division. The metaphase checkpoint ensures that all sister chromatids are properly attached to their respective microtubules and lined up at the metaphase plate before the signal is given to separate them during anaphase.

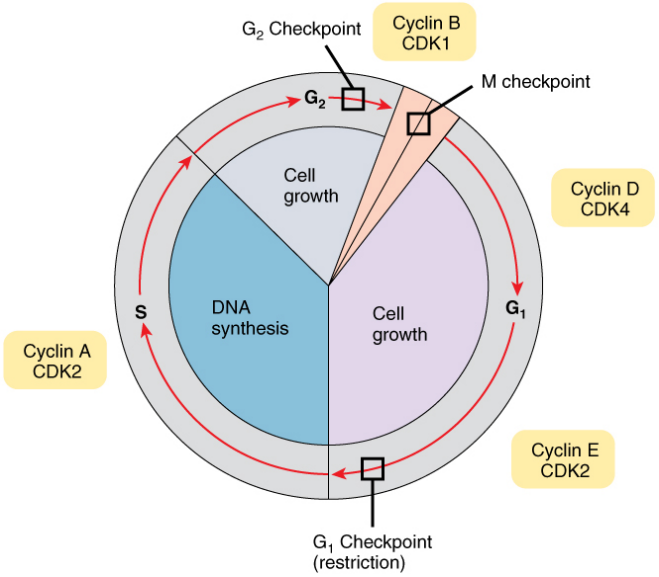


Figure 3. Control of the Cell Cycle. Cells proceed through the cell cycle under the control of a variety of molecules, such as cyclins and cyclin-dependent kinases. These control molecules determine whether or not the cell is prepared to move into the following stage.

The Cell Cycle Out of Control: Implications

Most people understand that cancer or tumors are caused by abnormal cells that multiply continuously. If the abnormal cells continue to divide unstopped, they can damage the tissues around them, spread to other parts of the body, and eventually result in death. In healthy cells, the tight regulation mechanisms of the cell cycle prevent this from happening, while failures of cell cycle control can cause unwanted and excessive cell division. Failures of control may be caused by inherited genetic abnormalities that compromise the function of certain “stop” and “go” signals. Environmental insult that damages DNA can also cause dysfunction in those signals. Often, a combination of both genetic predisposition and environmental factors lead to cancer. The process of a cell escaping its normal control system and becoming cancerous may actually happen throughout the body quite frequently. Fortunately, certain cells of the immune system are capable of recognizing cells that have become cancerous and destroying them. However, in

certain cases the cancerous cells remain undetected and continue to proliferate. If the resulting tumor does not pose a threat to surrounding tissues, it is said to be benign and can usually be easily removed. If capable of damage, the tumor is considered malignant and the patient is diagnosed with cancer.

? Try It

Cancer is an extremely complex condition, capable of arising from a wide variety of genetic and environmental causes. Typically, mutations or aberrations in a cell's DNA that compromise normal cell cycle control systems lead to cancerous tumors. Cell cycle control is an example of a homeostatic mechanism that maintains proper cell function and health. While progressing through the phases of the cell cycle, a large variety of intracellular molecules provide stop and go signals to regulate movement forward to the next phase. These signals are maintained in an intricate balance so that the cell only proceeds to the next phase when it is ready.

The homeostatic control of the cell cycle can be thought of like a car's cruise control. Cruise control will continually apply just the right amount of acceleration to maintain a desired speed, unless the driver hits the brakes, in which case the car will slow down. Similarly, the cell includes molecular messengers, such as cyclins, that push the cell forward in its cycle. In addition to cyclins, a class of proteins that are encoded by genes called proto-oncogenes provide important signals that regulate the cell cycle and move it forward. Examples of proto-oncogene products include cell-surface receptors for growth factors, or cell-signaling molecules, two classes of molecules that can promote DNA replication and cell division.

In contrast, a second class of genes known as tumor suppressor genes sends stop signals during a cell cycle. For example, certain protein products of tumor suppressor genes signal potential problems with the DNA and thus stop the cell from dividing, while other proteins signal the cell to die if it is damaged beyond repair. Some tumor suppressor proteins also signal a sufficient surrounding cellular density, which indicates that the cell need not presently divide. The latter function is uniquely important in preventing tumor growth: normal cells exhibit a phenomenon called "contact inhibition;" thus, extensive cellular contact with neighboring cells causes a signal that stops further cell division.

These two contrasting classes of genes, proto-oncogenes and tumor suppressor genes, are like the accelerator and brake pedal of the cell's own "cruise control system," respectively. Under normal conditions, these stop and go signals are maintained in a homeostatic balance. Generally speaking, there are two ways that the cell's cruise control can lose control: a malfunctioning (overactive) accelerator, or a malfunctioning (underactive) brake. When compromised through a mutation, or otherwise altered, proto-oncogenes can be converted to oncogenes, which produce oncoproteins that push a cell forward in its cycle and stimulate cell division even when it is undesirable to do so.

For example, a cell that should be programmed to self-destruct (a process called apoptosis) due to extensive DNA damage might instead be triggered to proliferate by an oncoprotein. On the other hand, a dysfunctional tumor suppressor gene may fail to provide the cell with a necessary stop signal, also resulting in unwanted cell division and proliferation. A delicate homeostatic balance between the many proto-oncogenes and tumor suppressor genes delicately controls the cell cycle and ensures that only healthy cells replicate. Therefore, a disruption of this homeostatic balance can cause aberrant cell division and cancerous growths.

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19.2.2: Frog Embryology

The Egg

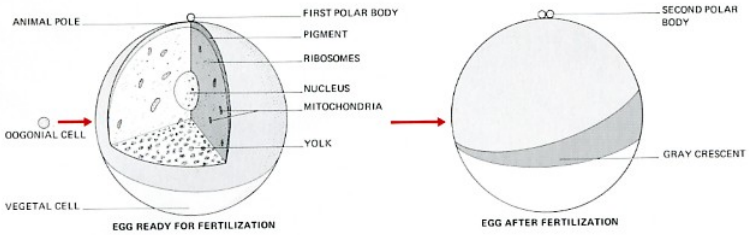


Figure 14.2.1 Frog Egg

The frog egg is a huge cell; its volume is over 1.6 million times larger than a normal frog cell. During embryonic development, the egg will be converted into a tadpole containing millions of cells but containing the same amount of organic matter.

- The upper hemisphere of the egg — the **animal pole** — is dark.
- The lower hemisphere — the **vegetal pole** — is light.
- When deposited in the water and ready for fertilization, the haploid egg is at metaphase of meiosis II.

Fertilization

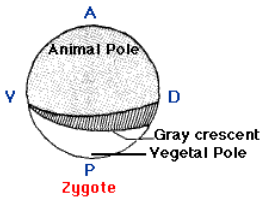


Figure 14.2.2 Frog Zygote

Entrance of the sperm initiates a sequence of events:

- Meiosis II is completed.
- The cytoplasm of the egg rotates about 30 degrees relative to the poles.
- In some amphibians (including Xenopus), this is revealed by the appearance of a light-colored band, the **gray crescent**.
- The gray crescent forms opposite the point where the sperm entered.
- It foretells the future pattern of the animal: its dorsal (**D**) and ventral (**V**) surfaces; its anterior (**A**) and posterior (**P**); its left and right sides.
- The haploid sperm and egg nuclei fuse to form the diploid zygote nucleus.

Cleavage

The zygote nucleus undergoes a series of mitoses, with the resulting daughter nuclei becoming partitioned off, by cytokinesis, in separate, and ever-smaller, cells. The **first cleavage** occurs shortly after the zygote nucleus forms. A furrow appears that runs longitudinally through the poles of the egg, passing through the point at which the sperm entered and bisecting the gray crescent. This divides the egg into two halves forming the **2-cell stage.** The **second cleavage** forms the **4-cell stage**. The cleavage furrow again runs through the poles but at right angles to the first furrow. The furrow in the **third cleavage** runs horizontally but in a plane closer to the animal than to the vegetal pole. It produces the **8-cell stage**.

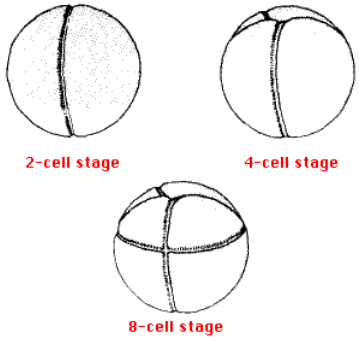


Figure 14.2.3 Various stages of cleavage in a frog zygote

The next few cleavages also proceed in synchrony, producing a 16-cell and then a 32-cell embryo. However, as cleavage continues, the cells in the animal pole begin dividing more rapidly than those in the vegetal pole and thus become smaller and more numerous. By the next day, continued cleavage has produced a hollow ball of thousands of cells called the **blastula**. A fluid-filled cavity, the **blastocoel**, forms within it.

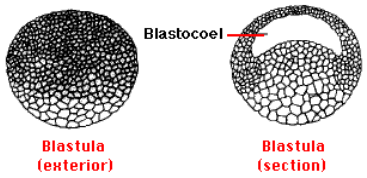


Figure 14.2.4 Frog Bastula

During this entire process there has been no growth of the embryo. In fact, because the cells of the blastula are so small, the blastula looks just like the original egg to the unaided eye. Not until the blastula contains some 4,000 cells is there any transcription of zygote genes. All of the activities up to now have been run by gene products (mRNA and proteins) deposited by the mother when she formed the egg.

Gastrulation

The start of gastrulation is marked by the pushing inward ("invagination") of cells in the region of the embryo once occupied by the middle of the gray crescent.

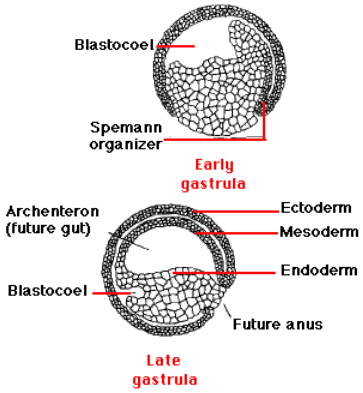


Figure 14.2.5 Frog gastrula

This produces an opening (the **blastopore**) that will be the future anus. a cluster of cells that develops into the **Spemann organizer** (named after one of the German embryologists who discovered its remarkable inductive properties).

As gastrulation continues, three distinct **"germ layers"** are formed:

- ectoderm
- mesoderm
- endoderm

Each of these will have special roles to play in building the complete animal. Some are listed in the table.

Germ-layer origin of various body tissues

Ectoderm	Mesoderm	Endoderm
skin	notochord	inner lining of gut, liver, pancreas
brain	muscles	inner lining of lungs
spinal cord	blood	inner lining of bladder
all other neurons	bone	thyroid and parathyroid glands
sense receptors	sex organs	thymus

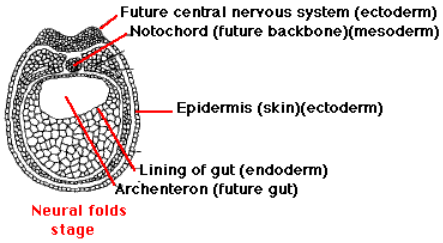


Figure 14.2.6 Frog neural folds

The Spemann organizer (mostly mesoderm) will develop into the **notochord**, which is the precursor of the backbone and induce the ectoderm lying above it to begin to form neural tissue instead of skin. This ectoderm grows up into two longitudinal folds, forming the **neural folds** stage. In time the lips of the folds fuse to form the **neural tube**. The neural tube eventually develops into the brain and spinal cord.

Differentiation

Although the various layers of cells in the frog gastrula have definite and different fates in store for them, these are not readily apparent in their structure. Only by probing for different patterns of gene expression (e.g., looking for tissue-specific proteins) can their differences be detected. In due course, however, the cells of the embryo take on the specialized structures and functions that they have in the tadpole, forming **neurons**, **blood cells**, **muscle cells**, **epithelial cells**, etc., etc.

Growth

At the time the tadpole hatches, it is a fully-formed organism. However, it has no more organic matter in it than the original frog egg had. Once able to feed, however, the tadpole can grow. It gains additional molecules with which it can increase the number of cells that make up its various tissues.

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19.2.3: Cleavage

Cleavage refers to the early cell divisions that occur as a fertilized egg begins to develop into an embryo.

Holoblastic Cleavage

In eggs that contain no (mammals) or only moderate amounts (frog) of yolk, cytokinesis divides the cells completely. The figure shows the results of the first two cleavages in the frog embryo.

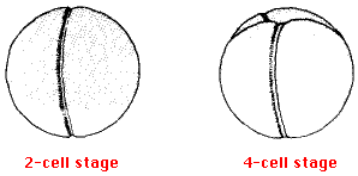


Figure 14.3.1: First two cleavages in a frog embryo

Meroblastic Cleavage

In eggs that contain a large amount of yolk, cytokinesis does not divide the egg completely.

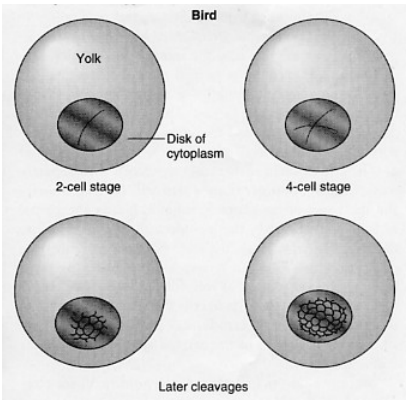


Figure 14.3.2: Bird cleavage

The hen's egg consists of just a tiny patch of cytoplasm resting on the surface of a large ball of yolk (the "white" of the egg is noncellular accessory protein). When the first cleavages occur in the hen's egg, the cleavage furrows do not continue down through the mass of yolk. Therefore, each of the cells produced in the earliest stages is bound on the top and on the sides by a plasma membrane, but the bottom of the cell is in direct contact with yolk.

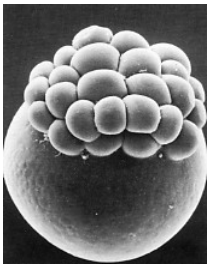


Figure 14.3.3: Zebrafish cleavage

This type of meroblastic cleavage is also found in the eggs of fish, reptiles, and 4 species of mammals — the monotremes. This photo, courtesy of H. W. Beames and Richard G. Kessel, shows the zebrafish (Danio) embryo at the 32-cell stage. Note that the cleavage furrows have not continued down through the yolk of the egg.

Insects use a different type of meroblastic cleavage.

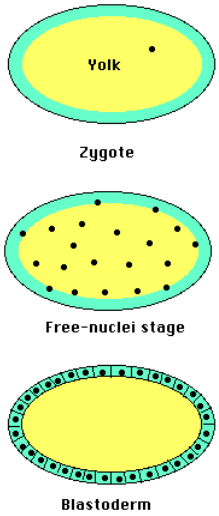


Figure 14.3.4: Insect cleavage

The yolk of the eggs of insects is concentrated in the center of the egg. The daughter nuclei produced by mitosis of the zygote nucleus remain suspended within the single egg compartment. After several thousand nuclei have been produced, they migrate to the cytoplasm-rich margin of the egg. Only then does a plasma membrane form around each one.

What does cleavage accomplish in the development of the organism? First, it provides a stockpile of cells out of which the embryo will be constructed. Second, cleavage establishes a normal relationship between the nucleus and the volume of cytoplasm it regulates (and which in turn regulates it). Even small eggs are enormous when compared with other kinds of cells. The volume of the frog egg is about 1.6 million times larger than that of a normal frog cell. But it, too, contains only a single nucleus. During cleavage, thousands of new nuclei are produced by mitosis all of which finally end up in a cell of normal dimensions. The frog blastula, with its thousands of cells is no larger than the original fertilized egg.

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SECTION OVERVIEW

19.3: Cell Differentiation

19.3.1: Stem Cells

19.3.2: Embryonic Stem Cells

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19.3.1: Stem Cells

Stem cells are cells that divide by mitosis to form either two stem cells, thus increasing the size of the stem cell "pool", or one daughter that goes on to differentiate, and one daughter that retains its stem-cell properties. How the choice is made is still unknown. However, several genes have been found whose activity prevents a daughter cell from differentiating.

Types of Stem Cells

Several adjectives are used to describe the developmental potential of stem cells; that is, the number of different kinds of differentiated cell that they can become.

1. **Totipotent cells.** In mammals, totipotent cells have the potential to become any type in the adult body and any cell of the extraembryonic membranes (e.g., placenta). The only totipotent cells are the **fertilized egg** and the first 4 or so cells produced by its cleavage (as shown by the ability of mammals to produce identical twins, triplets, etc.). In mammals, the expression totipotent **stem** cells is a misnomer — totipotent cells cannot make more of themselves.
2. **Pluripotent stem cells.** These are true stem cells, with the potential to make any differentiated cell in the body (but probably not those of the placenta which is derived from the trophoblast).

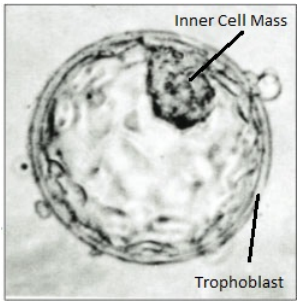


Figure **19.3.1.1**: Human blastocyst showing inner cell mass (top right) and trophoblast. (J. Conaghan).

Three types of pluripotent stem cells occur naturally:

- **Embryonic Stem (ES) Cells.** These can be isolated from the **inner cell mass** (ICM) of the blastocyst — the stage of embryonic development when implantation occurs. For humans, excess embryos produced during in vitro fertilization (IVF) procedures are used. Harvesting ES cells from human blastocysts is controversial because it destroys the embryo, which could have been implanted to produce another baby (but often was simply going to be discarded).
- **Embryonic Germ (EG) Cells.** These can be isolated from the precursor to the gonads in aborted fetuses.
- **Embryonic Carcinoma (EC) Cells.** These can be isolated from teratocarcinomas, a tumor that occasionally occurs in a gonad of a fetus. Unlike the other two, they are usually aneuploid.

All three of these types of pluripotent stem cells can only be isolated from embryonic or fetal tissue. They can be grown in culture, but only with special methods to prevent them from differentiating.

In mice and rats, embryonic stem cells can also:

- contribute to the formation of a healthy chimeric adult when injected into a blastocyst which is then implanted in a surrogate mother;
- enter the germline of these animals; that is, contribute to their pool of gametes;
- develop into teratomas when injected into immunodeficient (SCID) mice. These tumors produce a wide variety of cell types representing all three germ layers (ectoderm, mesoderm, and endoderm).

Using genetic manipulation in the laboratory, pluripotent stem cells can now be generated from differentiated cells. These **induced pluripotent stem cells** (iPSCs) are described below.

3. **Multipotent stem cells.** These are true stem cells but can only differentiate into a limited number of types. For example, the bone marrow contains multipotent stem cells that give rise to all the cells of the blood but not to other types of cells. Multipotent stem cells are found in adult animals; perhaps most organs in the body (e.g., brain, liver, lungs) contain them where

they can replace dead or damaged cells. These **adult stem cells** may also be the cells that — when one accumulates sufficient mutations — produce a clone of cancer cells.

Stem Cells for Human Therapy

The Dream

Many medical problems arise from damage to differentiated cells. Examples:

- Type 1 diabetes mellitus where the beta cells of the pancreas have been destroyed by an autoimmune attack
- **Parkinson's disease**; where dopamine-secreting cells of the brain have been destroyed
- Spinal cord injuries leading to paralysis of the skeletal muscles
- Ischemic stroke where a blood clot in the brain has caused neurons to die from oxygen starvation
- **Multiple sclerosis** with its loss of myelin sheaths around axons
- Blindness caused by damage to the cornea

The great developmental potential of stem cells has created intense research into enlisting them to aid in replacing the lost cells of such disorders. While progress has been slow, some procedures already show promise. Using multipotent "adult" stem cells.

- culturing human epithelial stem cells and using their differentiated progeny to replace a damaged cornea. This works best when the stem cells are from the patient (e.g. from the other eye). Corneal cells from another person (an allograft) are always at risk of rejection by the recipient's immune system.
- the successful repair of a damaged left bronchus using a section of a donated trachea that was first cleansed of all donor cells and then seeded with the recipient's epithelial cells and cartilage-forming cells grown from stem cells in her bone marrow. So far the patient is doing well and needs no drugs to suppress her immune system.

Using differentiated cells derived from embryonic stem (ES) cells. Phase I clinical trials are underway to assess the safety of

- injecting retinal cells derived from ES cells
  - into the eyes of young people with an inherited form of juvenile blindness;
  - into the eyes of adults with age-related macular degeneration.
- injecting glial cells derived from ES cells into patients paralyzed by spinal cord injuries.

The Immunological Problems

One major problem that must be solved before human stem cell therapy becomes a reality is the threat of rejection of the transplanted cells by the host's immune system (if the stem cells are allografts; that is, come from a genetically-different individual).

A Possible Solution

One way to avoid the problem of rejection is to use stem cells that are genetically identical to the host. This is already possible in the rare situations when the patient has healthy stem cells in an undamaged part of the body (like the stem cells being used to replace damaged corneas). But even where no "autologous" stems cells are available, there may be a solution: using **somatic-cell nuclear transfer** .

In this technique,

1. An egg has its own nucleus removed and replaced by
2. a nucleus taken from a somatic (e.g., skin) cell of the donor.
3. The now-diploid egg is allowed to develop in culture to the blastocyst stage when
4. embryonic stem cells can be harvested and grown up in culture.
5. When they have acquired the desired properties, they can be implanted in the donor with no fear of rejection.

Using this procedure it possible to not only grow blastocysts but even have these go on to develop into adult animals — **cloning** — with a nuclear genome identical to that of the donor of the nucleus. The first successful cloning by SCNT was with amphibians.

Later, mammals such as sheep (Dolly), cows, mice and others were successfully cloned. And in the 11 November 2007 issue of **Science**, researchers in Oregon reported success with steps 1–4 in rhesus monkeys (primates like us).

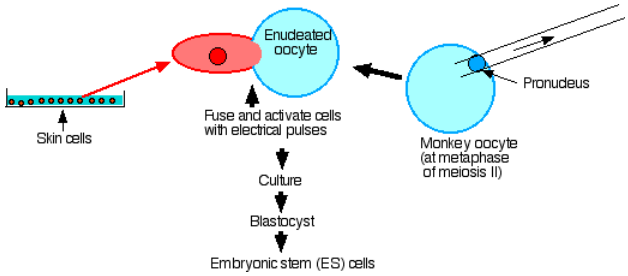


Figure 19.3.1.2: Somatic cell transfer in rhesus monkeys

Their procedure:

- Remove the spindle and thus all nuclear material from secondary oocytes at metaphase of meiosis II.
- Fuse each enucleated egg with a skin cell taken from a male monkey.
- Culture until the blastocyst stage is reached.
- Extract embryonic stem cells from the inner cell mass.
- Establish that they have the nuclear genome of the male (but mostly the mitochondrial genome of the female).
- Culture with factors to encourage differentiation: they grew cardiac muscle cells (which contracted), and even neuron-like cells.
- Inject into SCID mice and examine the tumors that formed. These contained cells of all three germ layers: ectoderm, mesoderm, and endoderm.
- However, even after more than 100 attempts, they have not been able to implant their monkey blastocysts in the uterus of a surrogate mother to produce a cloned monkey.

This should reassure people who view with alarm the report in May 2013 by the same workers that they have finally succeeded in producing embryonic stem cells (ESCs) using SCNT from differentiated human tissue. The workers assure us that they will not attempt to implant these blastocysts in a surrogate mother to produce a cloned human. And their failure with monkeys suggests that they would fail even if they did try.

While cloning humans still seems impossible, patient-specific ESCs

- could be used in cell-replacement therapy or, failing that,
- provide the material for laboratory study of the basis of — and perhaps treatment of — genetic diseases.

Whether they will be more efficient and more useful than induced pluripotent stem cells remains to be seen.

Questions that Remain to be Answered

- **Imprinted Genes.** Sperm and eggs each contain certain genes that carry an "imprint" identifying them later in the fertilized egg as being derived from the father or mother respectively. Creating an egg with a nucleus taken from an adult cell may not allow a proper pattern of imprinting to be established. When the diploid adult nucleus is inserted into the enucleated egg (at least those of sheep and mice), the new nucleus becomes "reprogrammed". What reprogramming actually means still must be learned, but perhaps it involves the proper methylation and demethylation of imprinted genes. For example, the inactive X chromosome in adult female cells must be reactivated in the egg, and this actually seems to happen.
- **Aneuploidy.** In primates (in contrast to sheep, cattle, and mice), the process of removing the resident nucleus causes molecules associated with the centrosome to be lost as well. Although injecting a donor nucleus allows mitosis to begin, spindle formation may be disrupted, and the resulting cells fail to get the correct complement of chromosomes (aneuploidy).
- **Somatic Mutations.** This procedure also raises the spectre of amplifying the effect(s) of somatic mutations. In other words, mutations that might be well-tolerated in a single somatic cell of the adult (used to provide the nucleus) might well turn out to be quite harmful when they become replicated in a clone of cells injected later into the patient.
- **Political Controversy.** The goal of this procedure (which is often called **therapeutic cloning** even though no new individual is produced) is to culture a blastocyst that can serve as a source of **ES cells**. But that same blastocyst could theoretically be implanted in a human uterus and develop into a baby that was genetically identical to the donor of the nucleus. In this way, a human would be cloned. And in fact, Dolly and other animals are now routinely cloned this way. The spectre of this is so

abhorrent to many that they would like to see the procedure banned despite its promise for helping humans. In fact, many are so strongly opposed to using human blastocysts — even when produced by nuclear transfer — that they would like to limit stem cell research to adult stem cells (even though these are only multipotent).

Possible Solutions to the Ethical Controversy

Induced pluripotent stem cells (iPSCs)

A promising alternative to the use of embryonic stem cells in human therapy are recently-developed methods of genetically reprogramming the nuclei of differentiated **adult** cells so that they regain the pluripotency of embryonic stem (ES) cells.

In June 2007, three laboratories reported that introducing extra copies of only 4 genes into adult mouse skin cells (fibroblasts) enables them to regain the properties of ES cells. When these cells, named **induced pluripotent stem cells** (iPSCs for short), were placed in mouse blastocysts, they participated in building all the tissues of the chimeric mice that resulted. (When placed in tetraploid (**4n**) blastocysts — unable by themselves to develop normally — embryos were formed that thus were clones of the skin cell donor.) The four genes: *c-Myc*, *Sox2*, *Oct3/4*, *Klf4*.

By 2009, several labs had succeeded in producing fertile adult mice from iPSCs derived from mouse embryonic fibroblasts. This shows that iPSCs are just a capable of driving complete development (pluripotency) as embryonic stem cells.

Reprogramming works in humans, too! Using the same four genes, the Yamanaka lab in Japan reported on 20 November 2007, that they now had reprogrammed human skin cells to become induced pluripotent stem cells (**iPSCs**). And the Thomson lab in Wisconsin accomplished the same thing using *SOX2*, *OCT4*, *NANOG*, and *LIN28*.

Further evidence of the remarkable role played by these few genes is the finding that during normal embryonic development of the zebrafish, the same or similar genes (SoxB1, Oct4, Nanog) are responsible for turning on the genes of the zygote. Earlier in development of the blastula, all the genes being expressed (including these) are the mother's — mRNAs and proteins that the mother deposited in the unfertilized egg. It makes sense that the same proteins that can reprogram a differentiated cell into a pluripotent state (iPSCs) are those that produce the pluripotent cells of the early embryo.

These achievements open the possibility of

- creating cells for laboratory study of the basis of genetic diseases.
  Examples: researchers have succeeded in deriving iPSCs from
  - patients with amyotrophic lateral sclerosis (ALS, "Lou Gehrig's disease"), and then causing them to differentiate into motor neurons (the cells affected in the disease) for study of their properties;
  - the skin cells of a patient with an inherited heart disease (long QT syndrome) and causing these to differentiate into beating heart cells for study in the laboratory.
  - The Jaenisch lab reported in the 6 March 2009 issue of **Cell** that they have succeeded in making iPSCs (they call them hiPSCs) from fibroblasts taken from patients with Parkinson's disease. The cells were then differentiated into dopamine-releasing cells — the cells lacking in this disease. What is particularly exciting is that they accomplished this after using the Cre-lox system to remove all the genes (e.g., *SOX2*, *OCT4*, *KLF4*) needed for reprogramming the fibroblasts to an embryonic-stem-cell-like condition.
  - Since that report, other laboratories — using other methods — have also created iPSCs from which all foreign DNA (vector and transgenes) has been removed. Not only should such cells be safer to use in therapy, but these results show that the stimulus to reprogram a differentiated cell into a pluripotent state need only be transitory.
- creating patient-specific cell transplants — avoiding the threat of immunological rejection — that could be used for human therapy.

  Therapy with iPSCs has already been demonstrated in mice. Three examples:

  1. The Jaenisch lab in Cambridge, MA reported (in **Science**, 21 December 2007) that they had successfully treated knock-in mice that make sickle-cell hemoglobin with the human β^S genes (and show many of the signs of sickle-cell disease in humans) by
  - harvesting some fully-differentiated fibroblasts from a sickle-cell mouse;
  - reprogramming these to become iPSCs by infecting them with *Oct4*, *Sox2*, *Klf4*, and *c-Myc*;

- then removing (using the Cre-lox system) the *c-Myc* to avoid the danger of this oncogene later causing cancer in the recipient mice;
- replacing the β^S genes in the iPSCs with normal human β^A genes;
- coaxing, with a cocktail of cytokines, these iPSCs to differentiate in vitro into hematopoietic (blood cell) precursors;
- injecting these into sickle-cell mice that had been irradiated to destroy their own bone marrow (as is done with human bone marrow transplants). (Although the recipient mice were different animals from the fibroblast donor, they were of the same inbred strain and thus genetically the same — like identical human twins. So the procedure fully qualifies as "**patient-specific**", i.e., with no danger of the injected cells being rejected by the recipient's immune system.)

The result: all the signs of sickle-cell disease (e.g., anemia) in the treated animals showed marked improvement.

2. In the 25 July 2013 issue of *Nature*, a team of Japanese scientists report that they were able to manufacture three-dimensional buds of human liver cells. Their process:

- create human iPSCs from human fibroblasts using the techniques described above;
- treat these with the substances needed for them to differentiate in liver cell precursors;
- culture these with a mixture of human endothelial cells and mesenchymal stem cells (to mimic the conditions that occur in normal embryonic development of the liver);
- implant the resulting solid masses (buds) of liver-like cells into immunodeficient mice.

The result: the implanted buds developed a blood supply and the mice began to secrete human albumin, human alpha-1-antitrypsin, and to to detoxify injected chemicals just as human livers do.

3. Workers in the Melton lab at Harvard University reported in the 9 October 2014 issue of **Cell** that they had succeeded in differentiating large numbers of human beta cells from human iPSCs (as well as from human ES cells). When transplanted into diabetic mice, these cells brought their elevated blood sugar levels back down.

Let us hope that what works in mice can someday be developed into a safe therapy that will work in humans. (In the case of Type 1 diabetes mellitus, however, even patient-derived beta cells will still be at risk of the same autoimmune rejection that caused the disease in the first place.)

Despite these successes, iPSCs may not be able to completely replace the need for embryonic stem cells and may even be dangerous to use in human therapy. Several groups have found that human iPSCs contain mutations as well as epigenetic patterns (e.g., methylation of their DNA) that are not found in embryonic stem cells. Some of the mutations are also commonly found in cancer cells.

Other approaches being explored

- ES cells can be derived from a **single cell** removed from an 8-cell **morula**. The success of preimplantation genetic diagnosis (PGD) in humans shows that removing a single cell from the morula does not destroy it — the remaining cells can develop into a blastocyst, implant, and develop into a healthy baby. Furthermore, the single cell removed for PGD can first be allowed to divide with one daughter used for PGD and the other a potential source of an ES cell line.

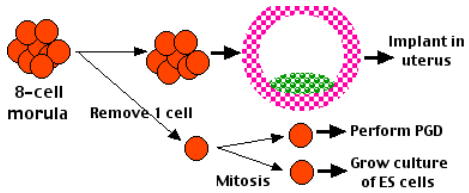


Figure **19.3.1.1**: Preimplantation using ES cell

- In altered nuclear transfer (**ANT**) — a modified version of SCNT (somatic-cell nuclear transfer) — a gene necessary for later implantation (*Cdx2* — encoding a homeobox transcription factor) is turned off (by RNA interference) in the donor nucleus before the nucleus is inserted into the egg. The blastocyst that develops
  - has a defective trophoblast that cannot implant in a uterus
  - but the cells of the inner cell mass are still capable of developing into cultures of ES cells. (The gene encoding the interfering RNA can then be removed using the Cre/*loxP* technique.)

- Jose Cibelli and his team at Advanced Cell Technology reported in the 1 February 2002 issue of **Science** that they had succeeded inIf this form of cloning by parthenogenesis works in humans [It does! — success with unfertilized human eggs was reported in June 2007.], it would have
  - stimulating monkey oocytes to begin dividing without completing meiosis II (therefore still **2n**)
  - growing these until the blastocyst stage, from which they were able to harvest
  - ES cells.
  - the **advantage** that no babies could be produced if the blastocyst should be implanted (two identical genomes cannot produce a viable mammal — probably because of incorrect imprinting);
  - the **disadvantage** that it will only help females (because only they can provide an oocyte!) (But men may have a procedure that works for them next.)
- On 24 March 2006, **Nature** published an online report that a group of German scientists had been able to derive pluripotent stem cells from the stem cells that make spermatogonia in the mouse. Both in vitro and when injected into mouse blastocysts, these cells differentiated in a variety of ways including representatives of all three germ layers. If this could work in humans, it would
  - provide a source of stem cells whose descendants would be "patient-specific"; that is, could be transplanted back into the donor (men only!) without fear of immune rejection.
  - avoid the controversy surrounding the need to destroy human blastocysts to provide embryonic stem cells.
- The 7 January 2007 issue of **Nature Biotechnology** reports the successful production of amniotic fluid-derived stem cells ("AFS"). These are present in the amniotic fluid removed during amniocentesis. With the proper culture conditions, they have been shown to be able to differentiate into a variety of cell types includingSo these cells are pluripotent. Although perhaps not as versatile as embryonic stem cells, they are more versatile than adult stem cells.
  - ectoderm (neural tissue)
  - mesoderm (e.g., bone, muscle)
  - endoderm (e.g., liver)

Applied to humans, none of the above procedures would involve the destruction of a potential human life.

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19.3.2: Embryonic Stem Cells

The other pages describe:

- the properties and potential therapeutic applications of embryonic (and other types of) stem cells
- how mouse embryonic stem cells can be used to make transgenic mice
- how the fusion of a differentiated cell from an adult sheep with an enucleated sheep egg can produce a **clone** of the cell donor ("Dolly")

The techniques used in the **early steps** of each process have been achieved with human cells.

Thirteen years ago a research team led by James Thomson of the University of Wisconsin reported (in the 6 November 1998 issue of **Science**) that they were able to grow human embryonic stem (**ES**) cells in culture.

At the time of implantation, the mammalian embryo is a **blastocyst**. It consists of the

- **trophoblast** — a hollow sphere of cells that will go on to implant in the uterus and develop into the placenta and umbilical cord.
- **inner cell mass** (**ICM**) that will develop into the baby as well as the extraembryonic amnion and yolk sac.

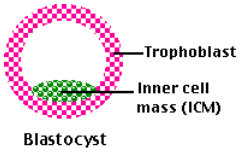


Figure 14.8.1 Blastocyst

The cells of the inner cell mass are considered **pluripotent**; that is, each is capable of producing descendants representing all of the hundreds of differentiated cell types in the newborn baby, including

- ectodermal cells like neurons and skin (epithelial cells)
- mesodermal cells like striated muscle, smooth muscle, cartilage, and bone
- endodermal cells like the liver and the lining of the intestine

The Process

- Remove the trophoblast cells from a human blastocyst (these were extras not needed for assisted reproductive technology).
- Separate the cells of the **inner cell mass** and culture them on a plate of "feeder" cells (mouse fibroblasts were used).
- Isolate single cells and grow them as clones.
- Test the clones.

The Results

- Each successful clone maintained a normal human karyotype (unlike most cultured human cells — HeLa cells, for example).
- These cells had high levels of the enzyme **telomerase**, which maintains normal chromosome length and is characteristic of cells with unlimited potential to divide ("immortal").
- When injected into **SCID mice**, these cells formed **teratomas**; tumors containing a mix of **differentiated** human cell types, including cells characteristic of
  - ectoderm
  - **mesoderm**
  - **endoderm**

Note

SCID = **severe combined immunodeficiency**.
SCID mice lack a functioning immune system (have neither T cells nor B cells) and so cannot reject foreign tissue. Some rare inherited diseases of humans are also called SCID. They produce a similar phenotype but involve different molecular defects.

Human embryonic stem cells have the potential to

- teach us about the process of human embryonic development, its genetic control, etc.
- provide a source of replacement cells to repair damaged human tissue. As the proper signals are discovered, it will be possible to cause these cells to differentiate along a **particular pathway**, e.g., to form insulin-secreting beta cells of the islets of Langerhans. Such cells might be able to replace lost or non-functioning cells in a human patient (e.g., with Type 1 diabetes mellitus).

However, there are problems that remain to be solved before this hope can be realized.

- Production of human ES cells requires the destruction of the blastocyst, and this is morally-repugnant to many people.
- Cell replacement therapy had better be "patient-specific"; that is, the donated cells should be genetically identical to the recipient. Otherwise, the replaced cells are at risk of being rejected by the host's immune system. [Link to a discussion of "therapeutic cloning" — a method to avoid this.
- ES cells are pluripotent and might differentiate in unwanted ways when introduced into the patient.

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SECTION OVERVIEW

19.4: Nuclear Reprogramming

19.4.1: The Organizer

19.4.2: Reproductive Cloning

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19.4.1: The Organizer

In the embryonic development of a zygote, gradients of mRNAs and proteins, deposited in the egg by the mother as she formed it, give rise to cells of diverse fates despite their identical genomes. But is the embryo fully patterned in the fertilized egg? It is difficult to imagine that the relatively simple gradients in the egg could account for all the complex migration and differentiation of cells during embryonic development. And, in fact, the answer is no. However, once these gradients have sent certain cells along a particular path of gene expression, the stage is set for those cells to begin influencing nearby cells to become increasingly diversified.

In other words, *cell-intrinsic signals* (established between a nucleus and the particular cytoplasmic environment that cleavage has placed it in) lay the foundation for *cell-cell interactions* to further guide the cells of the embryo to assume their proper position in the embryo and to differentiate into their final specialized form and function.

Cell-cell interactions could — and probably do — occur in several ways:

- diffusion of a signaling molecule out of one cell and into other cells in the vicinity;
- diffusion of a signaling molecule from one cell into an adjacent cell that then secretes the same molecule to diffuse to the next cell and so on (a "cell-relay" mechanism);
- extension of projections from the plasma membrane of one cell until they make **direct contact** with nearby cells. This enables proteins embedded in the plasma membrane to serve as signaling molecules.

The Spemann Organizer

In 1924, the Ph.D. student Hilde Mangold working in the laboratory of German embryologist Hans Spemann performed an experiment that demonstrated that the pattern of development of cells **is** influenced by the activities of other cells and stimulated a search, which continues to this day, for the signals at work. Spemann and Mangold knew that the cells that develop in the region of the gray crescent migrate into the embryo during gastrulation and form the notochord (the future backbone; made of **mesoderm**). She cut out a piece of tissue from the gray crescent region of one newt gastrula and transplanted it into the ventral side of a second newt gastrula. To make it easier to follow the fate of the transplant, she used the embryo of one variety of newt as the donor and a second variety as the recipient.

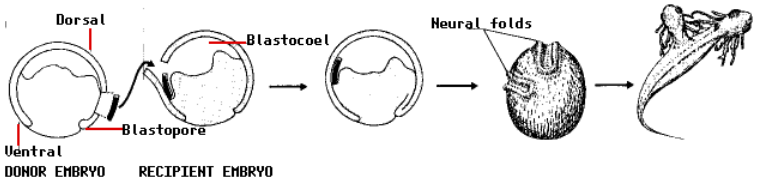


Figure **19.4.1.1**: Spemann Experiment

The remarkable results:

- the transplanted tissue developed into a second notochord
- **neural folds** developed above the extra notochord
- these went on to form a second central nervous system (portions of brain and spinal cord) and eventually
- a two-headed tadpole.

The most remarkable finding of all was that the neural folds were built from recipient cells, not donor cells. In other words, the transplant had altered the fate of the overlying cells (which normally would have ended up forming skin [epidermis] on the side of the animal) so that they produced a second head instead!

Spemann and Mangold used the term induction for the ability of one group of cells to influence the fate of another. And because of the remarkable inductive power of the gray crescent cells, they called this region the organizer. Ever since then, vigorous searches have been made to identify the molecules liberated by the organizer that induce overlying cells to become nerve tissue. One candidate after another has been put forward and then found not to be responsible. Part of the problem has been that not until just recently has it become clear that the organizer does NOT induce the central nervous system but instead it prevents signals originating from the ventral side of the blastula from inducing skin (epidermis) there.

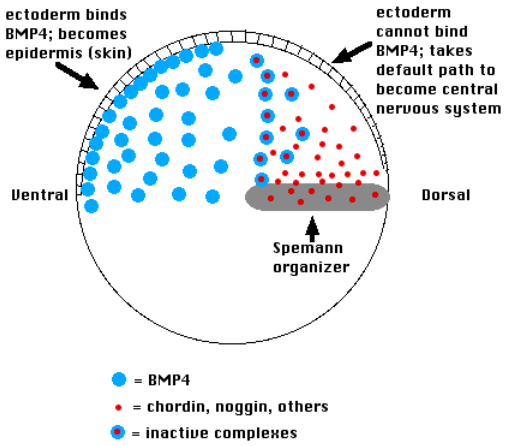


Figure 19.4.1.2: Spemann organizer

This is how it works:

- Cells on the **ventral** side of the blastula secrete a variety of proteins such as **b**one **m**orphogenetic **p**rotein-4 (**BMP-4**)
- These **induce** the **ectoderm** above to become **epidermis**.
- If their action is blocked, the ectodermal cells are allowed to follow their **default pathway**, which is to become nerve tissue of the brain and spinal cord.
- The Spemann **organizer blocks the action of BMP-4** by secreting molecules of the proteins **chordin** and **noggin**
- Both of these physically bind to BMP-4 molecules in the extracellular space and thus prevent BMP-4 from binding to receptors on the surface of the overlying ectoderm cells.
- This allows the ectodermal cells to follow their intrinsic path to forming neural folds and, eventually, the brain and spinal cord.

In the Spemann/Mangold experiment, transplanting an organizer to the ventral side provided a second source of chordin. This blocked BMP-4 binding to the overlying ectoderm and thus changed the fate of those cells to forming a second central nervous system rather than skin.

What Organizes the Organizer?

Protein synthesis by the cells of the organizer requires transcription of the relevant genes (e.g., *chordin*). Expression of organizer genes depends first on Wnt transcription factors. Their messenger RNAs were deposited by the mother in the vegetal pole of the egg. After fertilization and formation of the gray crescent, they migrated into the gray crescent region (destined to become the organizer) where they were translated into Wnt protein.

Its accumulation on the dorsal side of the embryo unleashes the activity of **Nodal** — a member of the Transforming Growth Factor-beta (TGF-β) family. Nodal induces these dorsal cells to begin expressing the proteins of Spemann's organizer.

A Tail Organizer

One of the distinguishing features of vertebrates is their tail, which extends out behind the anus. French researchers have reported (in the 24 July 2003 issue of **Nature**) their discovery of a tail "organizer", that is, a cluster of cells in the embryo that induces nearby cells to contribute to the formation of the tail. They worked with the zebrafish, *Danio rerio* (which also has a head organizer like that of newts). They removed tiny clusters of cells from the ventral part of the blastula (a region roughly opposite where the Spemann-like organizer forms) and transplanted this into a region of the host embryo that would normally form flank. The result: a second tail.

Using a fluorescent label, they were able to show that the extra tail was made not only from descendants of the transplanted cells but also from host cells that would normally have made flank. Three proteins were essential:

- a Wnt protein (establishes the anterior-posterior axis in all bilaterians)
- BMP (establishes the dorsal-ventral axis in all bilaterians)
- Nodal (establishes the left-right axis in all bilaterians)

Patterning the central nervous system in Drosophila

Remarkably, it turns out that proteins similar in structure to the bone morphogenetic proteins and also to chordin are found in Drosophila. The role of **BMP-4** is taken by a related protein encoded by the *decapentaplegic* gene (*dpp*) and the role of chordin is taken by a related protein called SOG encoded by the gene called *short gastrulation*.

In fact, these proteins and their mRNAs are completely interchangeable! An injection of the mRNAs for BMP-4 or chordin into the blastoderm of the Drosophila embryo can replace the function of DPP and SOG respectively, and conversely, injections of mRNA for DPP or SOG into the Xenopus embryo mimics the functions of BMP-4 and chordin respectively.

Table **19.4.1.1**: A selection of antagonistic pairs of proteins that guide the patterning of the embryo.

Xenopus		blocked by chordin
	and also by noggin	
Drosophila	Decapentaplegic (DPP)	blocked by short gastrulation (SOG)
		and also by a noggin homolog?

Dorsal vs Ventral Nerve Cords

Although their actions are similar, the distribution of these proteins in Drosophila differs from that in Xenopus (as well as in mammals and other vertebrates). In Drosophila, **DPP** is produced in the **dorsal** region of the embryo and **SOG** is produced in the **ventral** region.

However, their actions on overlying cells are the same as in Xenopus; that is, the SOG protein prevents the DPP protein from blocking the formation of the central nervous system. The result in Drosophila is that its central nervous system forms on the **ventral** side of the embryo, not on the dorsal! And, you may remember that one of the distinguishing traits of all arthropods (insects, crustaceans, arachnids) as well as many other invertebrates, such as the annelid worms, is a **ventral nerve cord**. Chordates, including all vertebrates, have a dorsal (spinal) nerve cord.

We're halfway done!

Xenopus development (and probably that of animals in general) passes through three rather different (although often overlapping) phases:

- establishing the main axes (dorsal-ventral; anterior-posterior; left-right). This is done by gradients of mRNAs and proteins encoded by the mother's genes and placed in the egg by her.
- establishing the main body parts such as
  - the notochord and central nervous system in vertebrates (discussed here and also described in Fro.g Embryology)
  - and the segments in Drosophila

  These are run by genes of the zygote itself.
- filling in the details; that is, building the various organs of the animal. (Our examples will include the wings, legs, and eyes of Drosophila.)

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19.4.2: Reproductive Cloning

Learning Objectives

- Differentiate reproductive cloning from cellular and molecular cloning

Reproductive Cloning

Reproductive cloning is a method used to make a clone or an identical copy of an entire multicellular organism. Most multicellular organisms undergo reproduction by sexual means, which involves genetic hybridization of two individuals (parents), making it impossible to generate an identical copy or clone of either parent. Recent advances in biotechnology have made it possible to artificially induce asexual reproduction of mammals in the laboratory.

Parthenogenesis, or “virgin birth,” occurs when an embryo grows and develops without the fertilization of the egg occurring; this is a form of asexual reproduction. An example of parthenogenesis occurs in species in which the female lays an egg. If the egg is fertilized, it is a diploid egg and the individual develops into a female; if the egg is not fertilized, it remains a haploid egg and develops into a male. The unfertilized egg is called a parthenogenic, or virgin, egg. Some insects and reptiles lay parthenogenic eggs that can develop into adults.

Sexual reproduction requires two cells; when the haploid egg and sperm cells fuse, a diploid zygote results. The zygote nucleus contains the genetic information to produce a new individual. However, early embryonic development requires the cytoplasmic material contained in the egg cell. This idea forms the basis for reproductive cloning. If the haploid nucleus of an egg cell is replaced with a diploid nucleus from the cell of any individual of the same species (called a donor), it will become a zygote that is genetically identical to the donor. Somatic cell nuclear transfer is the technique of transferring a diploid nucleus into an enucleated egg. It can be used for either therapeutic cloning or reproductive cloning.

The first cloned animal was Dolly, a sheep who was born in 1996. The success rate of reproductive cloning at the time was very low. Dolly lived for seven years and died of respiratory complications. There is speculation that because the cell DNA belongs to an older individual, the age of the DNA may affect the life expectancy of a cloned individual. Since Dolly, several animals (e.g. horses, bulls, and goats) have been successfully cloned, although these individuals often exhibit facial, limb, and cardiac abnormalities. There have been attempts at producing cloned human embryos as sources of embryonic stem cells. Sometimes referred to as cloning for therapeutic purposes, the technique produces stem cells that attempt to remedy detrimental diseases or defects (unlike reproductive cloning, which aims to reproduce an organism). Still, therapeutic cloning efforts have met with resistance because of bioethical considerations.

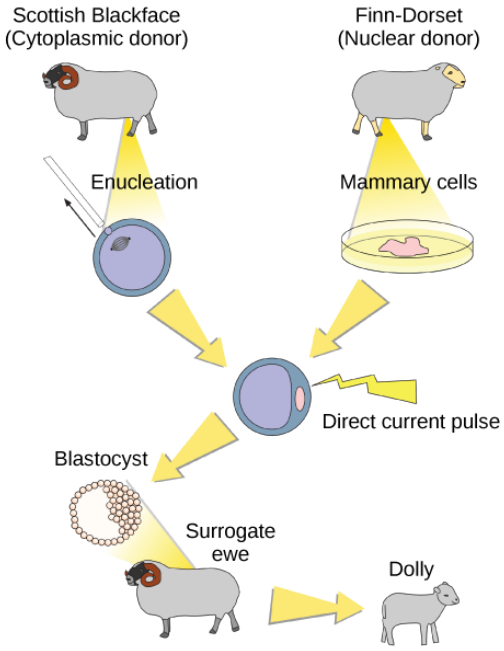


Figure 19.4.2.1: Reproductive Cloning of Dolly, the Sheep: Dolly the sheep was the first mammal to be cloned. To create Dolly, the nucleus was removed from a donor egg cell. The nucleus from a second sheep was then introduced into the cell, which was allowed to divide to the blastocyst stage before being implanted in a surrogate mother.

Key Points

- A form of asexual reproduction, parthenogenesis, occurs when an embryo grows and develops without the fertilization of the egg.
- In reproductive cloning, if the haploid nucleus of an egg cell is replaced with a diploid nucleus from the cell of an individual of the same species, it will become a zygote that is genetically identical to the donor.
- Reproductive cloning has become successful, but still has limitations as cloned individuals often exhibit facial, limb, and cardiac abnormalities.
- Therapeutic cloning, the cloning of human embryos as a source of embryonic stem cells, has been attempted in order to produce cells that can be used to treat detrimental diseases or defects.

Key Terms

- **clone**: a living organism produced asexually from a single ancestor, to which it is genetically identical
- **stem cell**: a primal undifferentiated cell from which a variety of other cells can develop through the process of cellular differentiation
- **parthenogenesis**: a form of asexual reproduction where growth and development of embryos occur without fertilization

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SECTION OVERVIEW

19.5: Pattern Formation

19.5.1: Establishing Body Axes

19.5.2: Segmentation

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19.5.1: Establishing Body Axes

Learning Objectives

- Summarize the mechanisms and cell types that establish the body axes

Vertebrate axis formation

During development, as the germ layers form, the ball of cells still retains its spherical shape. However, animal bodies have lateral-medial (left-right), dorsal-ventral (back-belly), and anterior-posterior (head-feet) axes. How are these established? In one of the most seminal experiments ever to be carried out in developmental biology, Spemann and Mangold took dorsal cells from one embryo and transplanted them into the belly region of another embryo. They found that the transplanted embryo now had two notochords: one at the dorsal site from the original cells and another at the transplanted site. This suggested that the dorsal cells were genetically programmed to form the notochord and define the axis. Since then, researchers have identified many genes that are responsible for axis formation. Mutations in these genes leads to the loss of symmetry required for organism development. Animal bodies have externally visible symmetry. However, the internal organs are not symmetric. For example, the heart is on the left side and the liver on the right. The formation of the central left-right axis is an important process during development. This internal asymmetry is established very early during development and involves many genes. Research is still ongoing to fully understand the developmental implications of these genes.

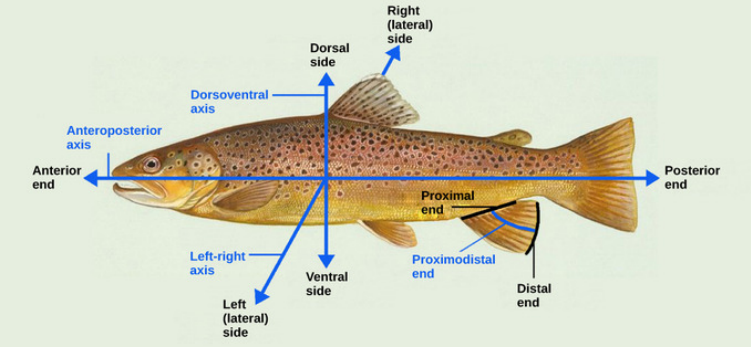


Figure **19.5.1.1**: Vertebrate Axis Formation: Animal bodies have three axes for symmetry:lateral-medial (left-right), dorsal-ventral (back-belly), and anterior-posterior (head-feet).

Neural tube

In the developing chordate (including vertebrates), the neural tube is the embryo's precursor to the central nervous system, which comprises the brain and spinal cord. The neural groove gradually deepens as the neural folds become elevated, and ultimately the folds meet and coalesce in the middle line and convert the groove into a closed tube, the neural tube or neural canal, the ectodermal wall of which forms the rudiment of the nervous system.

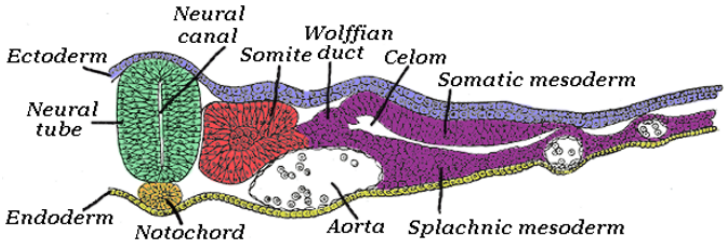


Figure **19.5.1.1**: Neural Tube: Transverse section of half of a chick embryo of forty-five hours' incubation. The dorsal (back) surface of the embryo is toward the top of this page, while the ventral (front) surface is toward the bottom. (Neural tube is in green.)

Primary and secondary neurulation

The neural tube develops in two ways: primary neurulation and secondary neurulation. Primary neurulation divides the ectoderm into three cell types: the internally located neural tube, the externally located epidermis, and the neural crest cells, which develop in

the region between the neural tube and epidermis but then migrate to new locations. Primary neurulation begins after the neural plate forms. The edges of the neural plate start to thicken and lift upward, forming the neural folds. The center of the neural plate remains grounded, allowing a U-shaped neural groove to form. This neural groove sets the boundary between the right and left sides of the embryo. The neural folds pinch in towards the midline of the embryo and fuse together to form the neural tube. In secondary neurulation, the cells of the neural plate form a cord-like structure that migrates inside the embryo and hollows to form the tube.

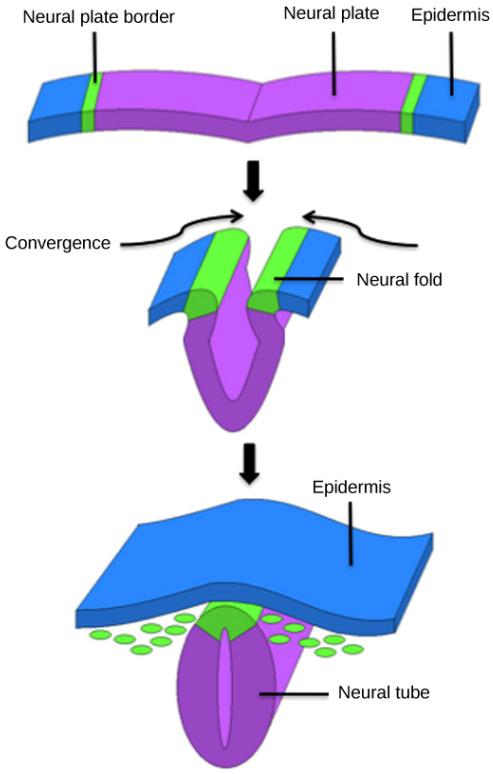


Figure 19.5.1.1: Neural Tube Formation: The central region of the ectoderm forms the neural tube, which gives rise to the brain and the spinal cord.

Each organism uses primary and secondary neurulation to varying degrees. Neurulation in fish proceeds only via the secondary form. In avian species the posterior regions of the tube develop using secondary neurulation and the anterior regions develop by primary neurulation. In mammals, secondary neurulation begins around the 35th somite. Mammalian neural tubes close in the head in the opposite order that they close in the trunk. In the head, neural crest cells migrate, the neural tube closes, and the overlying ectoderm closes. In the trunk, overlying ectoderm closes, the neural tube closes and neural crest cells migrate.

Neural tube subdivisions

Four neural tube subdivisions eventually develop into distinct regions of the central nervous system by the division of neuroepithelial cells: the prosencephalon, the mesencephalon, the rhombencephalon and the spinal cord. The prosencephalon further goes on to develop into the telencephalon (the forebrain or cerebrum) and the diencephalon (the optic vesicles and hypothalamus). The mesencephalon develops into the midbrain. The rhombencephalon develops into the metencephalon (the pons and cerebellum) and the myelencephalon (the medulla oblongata).

For a short time, the neural tube is open both cranially and caudally. These openings, called neuropores, close during the fourth week in the human. Improper closure of the neuropores can result in neural tube defects such as anencephaly or spina bifida. The dorsal part of the neural tube contains the alar plate, which is primarily associated with sensation. The ventral part of the neural tube contains the basal plate, which is primarily associated with motor (i.e., muscle) control.

Signaling molecules and other factors

The neural tube patterns along the dorsal-ventral axis establish defined compartments of neural progenitor cells that lead to distinct classes of neurons. This patterning occurs early in development and results from the activity of several secreted signaling molecules. Sonic hedgehog (Shh) is a key player in patterning the ventral axis, while Bone morphogenic proteins (Bmp) and Wnt family members play an important role in patterning the dorsal axis. Other factors shown to provide positional information to the neural progenitor cells include Fibroblast growth factors (FGF) and Retinoic Acid. Retinoic acid is required ventrally along with Shh to induce Pax6 and Olig2 during differentiation of motor neurons. Three main ventral cell types are established during early neural tube development: the floor plate cells, which form at the ventral midline during the neural fold stage; as well as the more dorsally located motor neurons and interneurons. These cell types are specified by the secretion of Shh from the notochord (located ventrally to the neural tube), and later from the floor plate cells. Shh acts as a morphogen, meaning that it acts in a concentration-dependent manner to specify cell types as it moves further from its source. The different combinations of expression of transcription factors along the dorsal-ventral axis of the neural tube are responsible for creating the identity of the neuronal progenitor cells.

Key Points

- The three axes of the animal body are established in development via the expression of specific sets of genes that regulate which cells will develop into specific structures.
- During development, the dorsal cells are genetically programmed to develop into the notochord and define the axis.
- The neural tube can develop in two ways: primary or secondary neurulation, which are used by organisms in varying degrees to establish the neural tube that will develop into the central nervous system (brain and spinal cord).
- Specific patterns along the neural tube that are established via secretion and production of specific signaling molecules (such as Wnt, Shh, BMP and retinoic acid) play a key role in patterning the dorsal and ventral axes.

Key Terms

- **neural tube**: hollow longitudinal dorsal tube formed in the folding and subsequent fusion of the opposite ectodermal folds in the embryo that gives rise to the brain and spinal cord
- **neurulation**: the process by which the beginnings of the vertebrate nervous system is formed in embryos
- **anencephaly**: a lethal birth defect in which most of the brain and parts of the skull are missing; absence of the encephalon
- **notochord**: a flexible rodlike structure that forms the main support of the body in the lowest chordates; a primitive spine

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19.5.2: Segmentation

Insects, like all arthropods, are segmented. The body of *Drosophila melanogaster* is built from 14 segments:

- 3 segments make up the **head** with its antennae and mouth parts.
- 3 segments make up the **thorax**. Each thoracic segment has a pair of legs (insects are the six-legged creatures). In Drosophila (and other flies), the middle thoracic segment carries a single pair of wings; the hind segment a pair of halteres.
- 8 **abdominal segments**.

What signals guide segment formation? The process begins with the gradients of messenger RNA (mRNA) that the mother deposited in her egg before it was fertilized. Shortly after fertilization, these are translated into their proteins with a gradient of **bicoid** diminishing from anterior to posterior and a gradient of **nanos** diminishing from posterior to anterior.

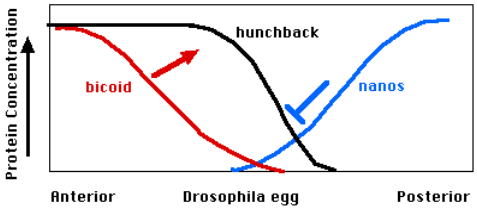


Figure 14.5.1 nanos graph

- **Bicoid** protein is a transcription factor. It binds to the **promoter** of a gene called ***hunchback*** (***hb***), turning it ON (red arrow).
- **Nanos** protein binds to hunchback mRNAs, inhibiting their translation (blue bar).
- These effects combine to produce a high level of hunchback protein at the anterior of the embryo; with a sharp cut-off toward the posterior.
- The hunchback protein is also a transcription factor (as we shall see).
- These concentration gradients regulate the turning on and off of other genes in sharply-defined regions of the embryo.
- These establish the various segments of the body.

Eve stripe 2

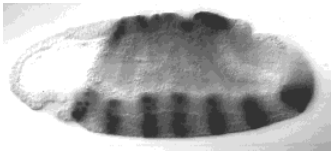


Figure 14.5.2 Gene even skipped

The gene ***even-skipped*** (***eve***) is expressed in 7 bands or stripes corresponding to 7 of Drosophila's 14 segments (skipping the even-numbered ones). The photo (courtesy of Peter A. Lawrence and Blackwell Scientific Publications) shows the 7 stripes of *eve* activation.

At first the gene is expressed in fairly broad zones, but in time its expression becomes restricted to ever-narrower stripes. The mechanism by which this occurs is known for the second stripe.

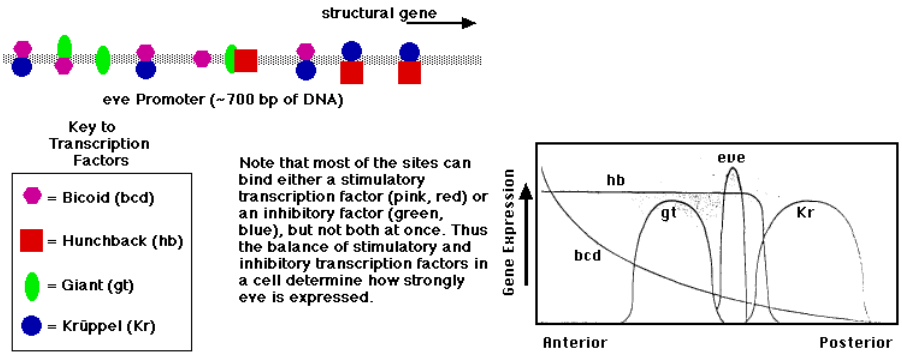


Figure 14.5.3 Eve promoter Figure 14.5.4 Eve stripe

The *eve* promoter has binding sites for the proteins encoded by ***bicoid*** (***bcd***), ***hunchback*** (***hb***), ***giant*** (***gt***) and ***Krüppel*** (***Kr***).

- Binding of **bicoid** and **hunchback** proteins **stimulates** transcription of *eve*.
- Binding of **giant** and **Krüppel represses** transcription.

Trapped in a valley between high levels of the giant and Krüppel proteins, expression of *eve* in the second stripe finally becomes limited to a band of cells only one cell thick. (A different set of promoter sites is used in the third eve stripe so expression is not repressed there.)In principle, then, such a system of interacting gradients of transcription factors could act as on-off switches, which in time partition the embryo into its future segments.

Drosophila development (and probably that of animals in general) passes through three rather different (although often overlapping) phases:

- establishing the main axes (dorsal-ventral; anterior-posterior; left-right). This is done by gradients of mRNAs and proteins encoded by the mother's genes and placed in the egg by her.
- establishing the main body parts such as the notochord and central nervous system in vertebrates.and the segments in Drosophila (discussed here). These are run by genes of the zygote itself.
- filling in the details; that is, building the various organs of the animal. (Our example will include the wings, legs, and eyes of Drosophila.)

Contributors

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SECTION OVERVIEW

19.6: Evolution of Pattern Formation

19.6.1: Homeobox Genes

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19.6.1: Homeobox Genes

Insect (Drosophila) and frog (Xenopus) development passes through three rather different (although often overlapping) phases: (1) establishing the main axes (dorsal-ventral; anterior-posterior; left-right). This is done by gradients of mRNAs and proteins encoded by the mother's genes and placed in the egg by her. (2) Establishing the main body parts such as the notochord and central nervous system in vertebrates and the segments in Drosophila These are run by genes of the zygote itself.

Now let us look for clues as to how the final working out of the embryo is done. We shall examine four examples:

1. the formation of **wings** (in Drosophila)
2. the formation of **legs** (also in Drosophila)
3. the formation of the **bones** (**radius** and **ulna**) of the front limb in mammals (mice)
4. the formation of **eyes** (probably in all animals)

Wings

The insect body plan consists of head, thorax, and abdomen. The thorax is built from three **segments**, **T1**, **T2**, and **T3**. Each carries a pair of legs; hence insects are six-legged creatures. In most of the insect orders, T2 and T3 each carry a pair of wings (the honeybee is an example). However, **flies** belong to the insect order **diptera**; they have only a single pair of wings (on T2). The third thoracic segment, T3, carries instead a pair of balancing organs called **halteres**.

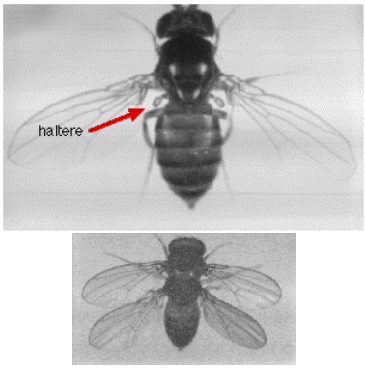


Figure 14.6.1 Flies with haltere Fig.14.6.2 Flies with haltere replaced by second pair of wings

In Drosophila, a gene called ***Ultrabithorax*** (***Ubx***) acts within the cells of T3 to suppress the formation of wings. By creating a double mutation in the *Ultrabithorax* gene (in its introns, as it turned out), Professor E. B. Lewis of Caltech was able to produce flies in which the halteres had been replaced by a **second pair of wings**. *Ultrabithorax* (*Ubx*) is an example of a "**selector gene**". Selector genes are genes that regulate (turning on or off) the expression of other genes. Thus selector genes act as "**master switches**" in development.

Wings and all their associated structures are complicated pieces of machinery. Nonetheless, mutations in a **single gene**, were able to cause the reprogramming of the building of T3 (and deprived the flies of their ability to fly). Selector genes encode **transcription factors**. *Ultrabithorax* encodes a transcription factor that is normally expressed at high levels in T3 (as well as in the first abdominal segment) of Drosophila.

These photographs were taken by, and kindly supplied by, Professor Lewis. He has spent his entire career studying selector genes in Drosophila. His life's work was honored when he shared the 1995 Nobel Prize for physiology or medicine.

Legs

Another selector gene, called ***Antennapedia*** (***Antp***), is normally turned "on" (expressed) in the thorax and turned "off" (repressed) in the cells of the head. However, mutations in ***Antp*** can cause it to turn on in the head and form a pair of legs where the antennae would normally be.

When you consider the many genes that must be involved in building a complex structure like an insect leg (or wing), it is remarkable that a single gene can switch them all on. It is also clear that once a selector gene turns "on" in certain cells of the

embryo, it remains "on" in all the cells derived from those cells. Those cells become irrevocably committed to carrying out the genetic program leading to the formation of a leg or wing.

Homeobox Genes

Most selector genes, including *Antp* and *Ubx*, are homeobox genes

Antp, *Ubx*, and a number of other selector genes have been cloned and sequenced. They all contain within their coding regions a sequence of some 180 nucleotides called a **homeobox**. The approximately 60 amino acids encoded by the homeobox are called a **homeodomain**. It mediates DNA binding by these proteins. Many proteins containing homeodomains have been shown to be transcription factors; probably they all are.

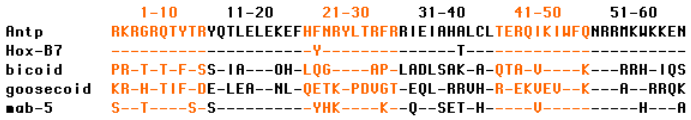


Figure 14.6.3: Homeodomains

The table shows the sequence of 60 amino acids in the homeodomain of the protein encoded by the Drosophila homeobox gene ***Antennapedia*** (***Antp***) compared with the homeodomain encoded by the mouse gene ***HoxB7***; by ***bicoid*** (***bcd***), another homeobox gene in Drosophila; by *goosecoid*, a homeobox gene in Xenopus; and by *mab-5*, a homeobox gene in the roundworm *Caenorhabditis elegans*. A dash indicates that the amino acid at that position is identical to the one in the *Antennapedia* homeobox domain. Note that the mouse homeobox in *HoxB7* differs from the *Antp* homeobox by only two amino acids (even though some 700 millions years have passed since these animals shared a common ancestor). *HoxB6*, used in the experiment described in the next section, differs from *Antp* in only 4 amino acids.

The Hox Cluster

Antp and *Ubx* are two of 8 homeobox genes that are linked in a cluster on one Drosophila chromosome. All of them encode transcription factors, each with a DNA-binding homeodomain and act in sequential zones of the embryo in the **same order** that they occur on the chromosome! The entire cluster is designated *HOM-C* with *lab*, *Pb*, *Dfd*, *Scr*, and *Antp* belonging to the *ANT-C* complex and *Ubx*, *Abd-A*, and *Abd-B* designated the *BX-C* complex, All animals that have been examined have at least one *Hox* cluster. Their genes show strong homology to the genes in *Drosophila*. Mice and humans have 4 *Hox* clusters (a total of 39 genes in humans) located on four different chromosomes.

- In mice: *HoxA*, *HoxB* (shown here), *HoxC*, *HoxD*
- In humans: *HOXA*, *HOXB*, *HOXC*, *HOXD*

As in Drosophila, they act along the developing embryo in the same sequence that they occupy on the chromosome. All the genes in the mammalian *Hox* clusters show some sequence homology to each other (especially in their homeobox) but very strong sequence homology to the equivalent genes in Drosophila. *HoxB7* differs from *Antp* at only two amino acids, *HoxB6* at four. In fact, when the **mouse *HoxB6*** gene is inserted in Drosophila, it can substitute for *Antennapedia* and produce legs in place of antennae just as mutant *Antp* genes do. This fascinating result indicates clearly that these selector genes have retained, through millions of years of evolution, their function of assigning particular positions in the embryo, but the structures actually built depend on a different set of genes specific for a particular species.

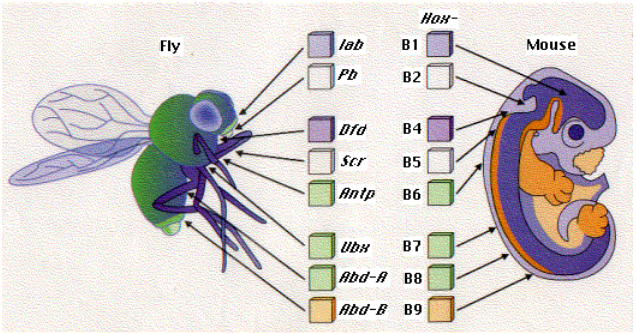


Figure 14.6.4 HOX

The Mammalian Skeleton

The foreleg of the mouse and the arm of humans contain a single upper bone, the humerus, and two lower bones, the radius and ulna. The building of the entire arm, including carpals and the phalanges of the fingers, is controlled by *Hox* cluster genes.

When mice were bred with homozygous mutations for **both *HoxA11* and *HoxD11***, they were born with neither radius nor ulna in the forelimbs. Here, then, is another example of the power of selector genes to initiate a whole program, perhaps involving hundreds of other genes, to form a structure as complex as a forelimb. Mice that are homozygous for mutant *HoxA10*, *C10*, and *D10* genes fail to form a lumbar and sacrum region in their vertebral column ("backbone"). Instead these vertebrae develop ribs like the thoracic vertebrae above them. However, if any one of these 6 *Hox* alleles is normal, the mice are much less severely affected. This shows the high degree of redundancy of these *Hox* genes.

Eyes

The compound eye of Drosophila is a marvel of precisely-organized structural elements. No one knows how many genes it takes to make the eye, but it must be a large number. Nevertheless, a single **selector gene**, ***eyeless*** (***ey***) (named, as is so often the case, for its mutant phenotype) can serve as a master switch turning on the entire cascade of genes needed to build the eye. Through genetic manipulation, it is possible to get the eyeless gene to be expressed in tissues where it is ordinarily not expressed. When ***eyeless*** is turned on in cells destined to form

- the insect's antennae, eyes form on the antennae
- wings, extra eyes form on the wings
- legs, eyes form on the legs.

Mice have a gene, ***small eyes*** (***Sey***; also known as ***Pax6***) that is similar in sequence to the Drosophila *eyeless* gene. As its name suggests, it, too, is involved in eye formation (even though the structure of the mouse eye is entirely different from the compound eye of Drosophila).

However, the sequences of the mouse ***small eyes*** gene and the Drosophila ***eyeless*** genes are so similar that the mouse gene can substitute for eyeless when introduced into Drosophila. So, like the genes of the *Hox* clusters, Drosophila ***eyeless*** and mouse ***small eyes*** have retained, through millions of years of independent evolution, their function of assigning particular positions in the embryo where certain structures should be built, but the structures actually built depend on a different set of genes specific for a particular species.

Humans also have a gene that is homologous to *small eyes* and *eyeless*: it is called ***aniridia***. Those rare humans who inherit a single mutant version of *aniridia* lack irises in their eyes.

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SECTION OVERVIEW

19.7: Morphogenesis

19.7.1: Apoptosis

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19.7.1: Apoptosis

Apoptosis is a process of programmed cell death that occurs in multicellular organisms. There are two ways in which cells die: (1) They are killed by injurious agents or (2) they are induced to commit suicide.

Death by injury

Cells that are damaged by injury, such as by mechanical damage or exposure to toxic chemicals undergo a characteristic series of changes. They (and their organelles like mitochondria) swell (because the ability of the plasma membrane to control the passage of ions and water is disrupted). The cell contents leak out, leading to inflammation of surrounding tissues.

Death by Suicide

Cells that are induced to commit suicide:

- shrink
- develop bubble-like blebs on their surface
- have the chromatin (DNA and protein) in their nucleus degraded
- have their mitochondria break down with the release of cytochrome c
- break into small, membrane-wrapped, fragments
- release (at least in mammalian cells) ATP and UTP
- These nucleotides bind to receptors on wandering phagocytic cells like macrophages and dendritic cells and attract them to the dying cells (a "**find-me**" signal")
- The phospholipid **phosphatidylserine**, which is normally hidden in the inner layer of the plasma membrane, is exposed on the surface
- This "**eat me**" signal is bound by other receptors on the phagocytes which then engulf the cell fragments
- The phagocytic cells secrete cytokines that **inhibit** inflammation (e.g., IL-10 and TGF-β)

The pattern of events in death by suicide is so orderly that the process is often called **programmed cell death** or **PCD**. The cellular machinery of programmed cell death turns out to be as intrinsic to the cell as, say, mitosis. Programmed cell death is also called *apoptosis*. (There is no consensus yet on how to pronounce it; some say *APE oh TOE sis*; some say *uh POP tuh sis*.)

Why should a cell commit suicide?

There are two different reasons.

1. Programmed cell death is as needed for proper development as mitosis is.

Examples:

- The resorption of the tadpole tail at the time of its metamorphosis into a frog occurs by apoptosis.
- The formation of the fingers and toes of the fetus requires the removal, by apoptosis, of the tissue between them.
- The sloughing off of the inner lining of the uterus (the endometrium) at the start of menstruation occurs by apoptosis.
- The formation of the proper connections (synapses) between neurons in the brain requires that surplus cells be eliminated by apoptosis.
- The elimination of T cells that might otherwise mount an autoimmune attack on the body occurs by apoptosis.
- During the pupal stage of insects that undergo complete metamorphosis, most of the cells of the larva die by apoptosis thus providing the nutrients for the development of the structures of the adult.

2. Programmed cell death is needed to destroy cells that represent a threat to the integrity of the organism.

Examples:

Cells infected with viruses

One of the methods by which **cytotoxic T lymphocytes** (CTLs) kill virus-infected cells is by inducing apoptosis and some viruses mount countermeasures to thwart it.

Cells of the immune system

As cell-mediated immune responses wane, the effector cells must be removed to prevent them from attacking body constituents. CTLs induce apoptosis in each other and even in themselves. Defects in the apoptotic machinery is associated with autoimmune diseases such as systemic lupus erythematosus and rheumatoid arthritis.

Cells with DNA damage

Damage to its genome can cause a cell

- to disrupt proper embryonic development leading to birth defects
- to become cancerous.

Cells respond to DNA damage by increasing their production of p53. p53 is a potent **inducer** of apoptosis. Is it any wonder that mutations in the *p53* gene, producing a defective protein, are so often found in cancer cells (that represent a lethal threat to the organism if permitted to live)?

Cancer cells

Radiation and chemicals used in cancer therapy induce apoptosis in some types of cancer cells.

What makes a cell decide to commit suicide?

The balance between the withdrawal of positive signals; that is, signals needed for continued survival, and the receipt of negative signals.

Withdrawal of positive signals

The continued survival of most cells requires that they receive continuous stimulation from other cells and, for many, continued adhesion to the surface on which they are growing. Some examples of positive signals: growth factors for neurons and Interleukin-2 (**IL-2**), an essential factor for the mitosis of lymphocytes

Receipt of negative signals

- increased levels of oxidants within the cell
- damage to DNA by these oxidants or other agents like ultraviolet light, X-rays and chemotherapeutic drugs
- accumulation of proteins that failed to fold properly into their proper tertiary structure
- molecules that bind to specific receptors on the cell surface and signal the cell to begin the apoptosis program. These **death activators** include:
  - **Tumor necrosis factor-alpha** (**TNF-α**) that binds to the **TNF receptor**
  - **Lymphotoxin** (also known as TNF-β) that also binds to the **TNF receptor**
  - **Fas ligand** (**FasL**), a molecule that binds to a cell-surface receptor named **Fas** (also called **CD95**)

The Mechanisms of Apoptosis

There are 3 different mechanisms by which a cell commits suicide by apoptosis.

1. Generated by signals arising within the cell
2. Triggered by **death activators** binding to receptors at the cell surface:
   - TNF-α
   - Lymphotoxin
   - Fas ligand (**FasL**)
3. Triggered by dangerous reactive oxygen species

Apoptosis triggered by internal signals

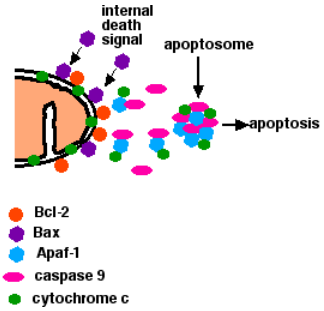


Figure 3.20.1 Apoptosis by internal trigger

- In a healthy cell, the outer membranes of its mitochondria display the protein **Bcl-2** on their surface. Bcl-2 **inhibits** apoptosis.
- Internal damage to the cell
  - causes a related protein, **Bax**, to migrate to the surface of the mitochondrion where it inhibits the protective effect of Bcl-2 and inserts itself into the outer mitochondrial membrane punching holes in it and causing
  - **cytochrome c** to leak out.
- The released cytochrome c binds to the protein **Apaf-1** ("apoptotic protease activating factor-1").
- Using the energy provided by ATP, these complexes aggregate to form **apoptosomes**. The apoptosomes bind to and activate **caspase-9**. Caspase-9 is one of a family of over a dozen caspases. They are all proteases. They get their name because they cleave proteins — mostly each other — at aspartic acid (Asp) residues.
- Caspase-9 cleaves and, in so doing, activates other caspases (caspase-3 and -7).
- The activation of these "executioner" caspases creates an expanding cascade of proteolytic activity (rather like that in blood clotting and complement activation) which leads to
  - digestion of structural proteins in the cytoplasm,
  - degradation of chromosomal DNA
  - phagocytosis of the cell

Apoptosis triggered by external signals

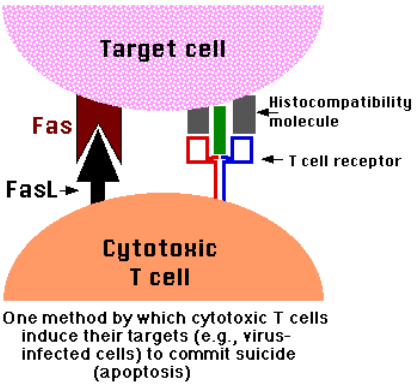


Figure 3.20.2 Apoptosis by external trigger

- **Fas** and the **TNF receptor** are integral membrane proteins with their receptor domains exposed at the surface of the cell
- Binding of the complementary **death activator** (**FasL** and **TNF** respectively) transmits a signal to the cytoplasm that leads to the activation of **caspase 8**
- Caspase 8 (like caspase 9) initiates a cascade of caspase activation leading to **phagocytosis** of the cell.
- **Example**: When cytotoxic T cells recognize (bind to) their target,
  - They produce more **FasL** at their surface.
  - This binds with the **Fas** on the surface of the target cell leading to its death by apoptosis.

  The early steps in apoptosis are reversible — at least in C. elegans. In some cases, final destruction of the cell is guaranteed only with its engulfment by a phagocyte.

Apoptosis-Inducing Factor (AIF)

Neurons, and perhaps other cells, have another way to self-destruct that — unlike the two paths described above — does not use caspases. Apoptosis-inducing factor (**AIF**) is a protein that is normally located in the intermembrane space of mitochondria. When the cell receives a signal telling it that it is time to die, AIF is released from the mitochondria (like the release of cytochrome c in the first pathway). It migrates into the nucleus and binds to DNA, which triggers the destruction of the DNA and cell death.

Apoptosis and Cancer

Some viruses associated with cancers use tricks to prevent apoptosis of the cells they have transformed.

- Several **human papilloma viruses** (**HPV**) have been implicated in causing cervical cancer. One of them produces a protein (E6) that binds and inactivates the apoptosis promoter **p53**.
- **Epstein-Barr Virus** (**EBV**), the cause of mononucleosis and associated with some lymphomas
  - produces a protein similar to Bcl-2
  - produces another protein that causes the cell to increase its own production of Bcl-2. Both these actions make the cell more resistant to apoptosis (thus enabling a cancer cell to continue to proliferate).

Even cancer cells produced without the participation of viruses may have tricks to avoid apoptosis.

- Some **B-cell leukemias** and lymphomas express high levels of **Bcl-2**, thus blocking apoptotic signals they may receive. The high levels result from a translocation of the *BCL-2* gene into an **enhancer** region for antibody production.
- **Melanoma** (the most dangerous type of skin cancer) cells avoid apoptosis by inhibiting the expression of the gene encoding **Apaf-1**.
- Some cancer cells, especially lung and colon cancer cells, secrete elevated levels of a soluble "decoy" molecule that binds to FasL, plugging it up so it cannot bind Fas. Thus, cytotoxic T cells (CTL) cannot kill the cancer cells by the mechanism shown above.
- Other cancer cells express high levels of **FasL**, and can kill any cytotoxic T cells (CTL) that try to kill them because CTL also express Fas (but are protected from their own FasL).

Apoptosis in the Immune System

The immune response to a foreign invader involves the proliferation of lymphocytes — T and/or B cells. When their job is done, they must be removed leaving only a small population of memory cells. This is done by apoptosis. Very rarely humans are encountered with genetic defects in apoptosis. The most common one is a mutation in the gene for Fas, but mutations in the gene for FasL or even one of the caspases are occasionally seen. In all cases, the genetic problem produces **autoimmune lymphoproliferative syndrome** or ALPS.

Features

- an accumulation of lymphocytes in the lymph nodes and spleen greatly enlarging them.
- the appearance of clones that are autoreactive; that is, attack "self" components producing such autoimmune disorders as
  - hemolytic anemia
  - thrombocytopenia
- the appearance of **lymphoma** — a cancerous clone of lymphocytes.

In most patients with ALPS, the mutation is present in the germline; that is, every cell in their body carries it. In a few cases, however, the mutation is somatic; that is, has occurred in a precursor cell in the bone marrow. These later patients are genetic mosaics — with some lymphocytes that undergo apoptosis normally and others that do not. The latter tend to out-compete the former and grow to become the major population in the lymph nodes and blood.

Apoptosis and Organ Transplants

For many years it has been known that certain parts of the body such as the anterior chamber of the eye and the testes are "immunologically privileged sites". Antigens within these sites fail to elicit an immune response. It turns out that cells in these sites differ from the other cells of the body in that they express high levels of **FasL** at all times. Thus antigen-reactive T cells, which express **Fas**, would be killed when they enter these sites. (This is the reverse of the mechanism described above.)

This finding raises the possibility of a new way of preventing graft rejection. If at least some of the cells on a transplanted kidney, liver, heart, etc. could be made to express high levels of FasL, that might protect the graft from attack by the T cells of the host's cell-mediated immune system. If so, then the present need for treatment with immunosuppressive drugs for the rest of the transplant recipient's life would be reduced or eliminated. So far, the results in animal experiments have been mixed. Allografts engineered to express FasL have shown increased survival for kidneys, but not for hearts or islets of Langerhans.

Apoptosis in Plants

Plants, too, can turn on a system of programmed cell death; for example, in an attempt to halt the spread of virus infection. The mechanism differs from that in animals although it, too, involves a protease that — like caspases — cleaves other proteins at Asp (and Asn) residues. Activation of this enzyme destroys the central vacuole, which is followed by disintegration of the rest of the cell.

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CHAPTER OVERVIEW

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20.1: Genetic Variation and Evolution



What helps ensure the survival of a species?

Genetic variation. It is this variation that is the essence of evolution. Without genetic differences among individuals, "survival of the fittest" would not be likely. Either all survive, or all perish.

Genetic Variation

Sexual reproduction results in infinite possibilities of genetic variation. In other words, sexual reproduction results in offspring that are genetically unique. They differ from both parents and also from each other. This occurs for a number of reasons.

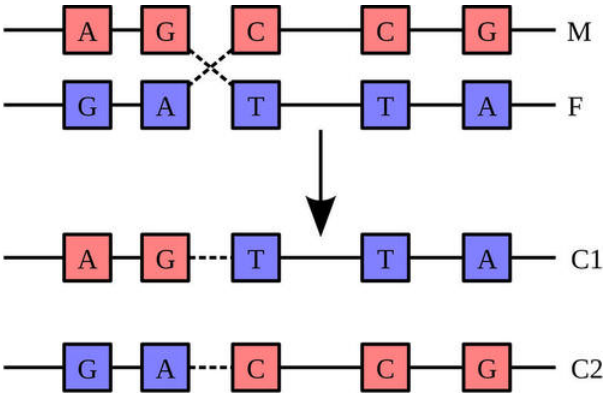
- When homologous chromosomes form pairs during prophase I of meiosis I, crossing-over can occur. **Crossing-over** is the exchange of genetic material between homologous chromosomes. It results in new combinations of genes on each chromosome.
- When cells divide during meiosis, homologous chromosomes are randomly distributed to daughter cells, and different chromosomes segregate independently of each other. This called is called **independent assortment**. It results in gametes that have unique combinations of chromosomes.
- In sexual reproduction, two gametes unite to produce an offspring. But which two of the millions of possible gametes will it be? This is likely to be a matter of chance. It is obviously another source of genetic variation in offspring. This is known as **random fertilization.**

All of these mechanisms working together result in an amazing amount of potential variation. Each human couple, for example, has the potential to produce more than 64 trillion genetically unique children. No wonder we are all different!

See *Sources of Variation* at http://learn.genetics.utah.edu/content/variation/sources/ for additional information.

Crossing-Over

Crossing-over occurs during prophase I, and it is the exchange of genetic material between non-sister chromatids of homologous chromosomes. Recall during prophase I, homologous chromosomes line up in pairs, gene-for-gene down their entire length, forming a configuration with four chromatids, known as a **tetrad**. At this point, the chromatids are very close to each other and some material from two chromatids switch chromosomes, that is, the material breaks off and reattaches at the same position on the homologous chromosome (**Figure** below). This exchange of genetic material can happen many times within the same pair of homologous chromosomes, creating unique combinations of genes. This process is also known as **recombination**.



Crossing-over. A maternal strand of DNA is shown in red. A paternal strand of DNA is shown in blue. Crossing over produces two chromosomes that have not previously existed. The process of recombination involves the breakage and rejoining of parental chromosomes (M, F). This results in the generation of novel chromosomes (C1, C2) that share DNA from both parents.

Independent Assortment and Random Fertilization

In humans, there are over 8 million configurations in which the chromosomes can line up during metaphase I of meiosis. It is the specific processes of meiosis, resulting in four unique haploid cells, that result in these many combinations. This independent assortment, in which the chromosome inherited from either the father or mother can sort into any gamete, produces the potential for tremendous genetic variation. Together with random fertilization, more possibilities for genetic variation exist between any two people than the number of individuals alive today. Sexual reproduction is the random fertilization of a gamete from the female using a gamete from the male. In humans, over 8 million (2^{23}) chromosome combinations exist in the production of gametes in both the male and female. A sperm cell, with over 8 million chromosome combinations, fertilizes an egg cell, which also has over 8 million chromosome combinations. That is over 64 trillion unique combinations, not counting the unique combinations produced by crossing-over. In other words, each human couple could produce a child with over 64 trillion unique chromosome combinations!

See *How Cells Divide: Mitosis vs. Meiosis* at http://www.pbs.org/wgbh/nova/miracle/divide.html for an animation comparing the two processes.

Summary

- Sexual reproduction has the potential to produce tremendous genetic variation in offspring.
- This variation is due to independent assortment and crossing-over during meiosis, and random union of gametes during fertilization.

Explore More

Use this resource to answer the questions that follow.

- **Genetic Variation** at http://www.eoearth.org/view/article/152942/.

1. What is meant by genetic variation?
2. Would natural selection occur without genetic variation? Explain your response.
3. What causes genetic variation?
4. How would genetic variation result in a change in phenotype?
5. What are the sources of genetic variation? Explain your response.

Review

1. What is crossing-over and when does it occur?
2. Describe how crossing-over, independent assortment, and random fertilization lead to genetic variation.
3. How many combinations of chromosomes are possible from sexual reproduction in humans?
4. Create a diagram to show how crossing-over occurs and how it creates new gene combinations on each chromosome.

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20.2: Changes in Allele Frequency

If two individuals mate that are heterozygous (e.g., **Bb**) for a trait, we find that

- 25% of their offspring are homozygous for the dominant allele (**BB**)
- 50% are heterozygous like their parents (**Bb**)
- 25% are homozygous for the recessive allele (**bb**) and thus, unlike their parents, express the recessive phenotype.

This is what Mendel found when he crossed monohybrids. It occurs because meiosis separates the two alleles of each heterozygous parent so that 50% of the gametes will carry one allele and 50% the other and when the gametes are brought together at random, each **B** (or **b**)-carrying egg will have a 1 in 2 probability of being fertilized by a sperm carrying **B** (or **b**). (Left table)

Results of random union of the two gametes produced by two individuals, each heterozygous for a given trait. As a result of meiosis, half the gametes produced by each parent with carry allele **B**; the other half allele **b**.			Results of random union of the gametes produced by an entire population with a gene pool containing 80% **B** and 20% **b**.		
	0.5 **B**	0.5 **b**		0.8 **B**	0.2 **b**
0.5 **B**	0.25 **BB**	0.25 **Bb**	0.8 **B**	0.64 **BB**	0.16 **Bb**
0.5 **b**	0.25 **Bb**	0.25 **bb**	0.2 **b**	0.16 **Bb**	0.04 **bb**

However, the frequency of two alleles in an **entire population** of organisms is unlikely to be exactly the same. Let us take as a hypothetical case, a population of hamsters in which 80% of all the gametes in the population carry a dominant allele for black coat (**B**) and 20% carry the recessive allele for gray coat (**b**).

Random union of these gametes (right table) will produce a generation:

- 64% homozygous for **BB** (0.8 x 0.8 = 0.64)
- 32% **Bb** heterozygotes (0.8 x 0.2 x 2 = 0.32)
- 4% homozygous (**bb**) for gray coat (0.2 x 0.2 = 0.04)

So 96% of this generation will have black coats; only 4% gray coats.

Will gray coated hamsters eventually disappear? No. Let's see why not.

- All the gametes formed by **BB** hamsters will contain allele **B** as will one-half the gametes formed by heterozygous (**Bb**) hamsters.
- So, 80% (0.64 + .5*0.32) of the pool of gametes formed by this generation with contain **B**.
- All the gametes of the gray (**bb**) hamsters (4%) will contain **b** but one-half of the gametes of the heterozygous hamsters will as well.
- So 20% (0.04 + .5*0.32) of the gametes will contain **b**.

So we have duplicated the initial situation exactly. The proportion of allele **b** in the population has remained the same. The heterozygous hamsters ensure that each generation will contain 4% gray hamsters. Now let us look at an algebraic analysis of the same problem using the expansion of the binomial $(\mathbf{p}+\mathbf{q})^2$.

$$(p+q)^2 = p^2 + 2pq + q^2 \tag{20.2.1}$$

The total number of genes in a population is its *gene pool*.

- Let p represent the frequency of one gene in the pool and q the frequency of its single allele.
- So, $p+q=1$
  - p^2 = the fraction of the population homozygous for p
  - q^2 = the fraction homozygous for q
  - $2pq$ = the fraction of heterozygotes
- In our example, **p** = 0.8, **q** = 0.2, and thus

$$(0.8+0.2)^2 = (0.8)^2 + 2(0.8)(0.2) + (0.2)^2 = 064 + 0.32 + 0.04 \quad (20.2.2)$$

The algebraic method enables us to work backward as well as forward. In fact, because we chose to make **B** fully dominant, the only way that the frequency of **B** and **b** in the gene pool could be known is by determining the frequency of the recessive phenotype (gray) and computing from it the value of **q**.

$\mathbf{q}^2$ = 0.04, so **q** = 0.2, the frequency of the **b** allele in the gene pool. Since **p** + **q** = 1, **p** = 0.8 and allele **B** makes up 80% of the gene pool. Because **B** is completely dominant over **b**, we cannot distinguish the **Bb** hamsters from the **BB** ones by their phenotype. But substituting in the middle term (**2pq**) of the expansion gives the percentage of heterozygous hamsters. **2pq** = (2)(0.8)(0.2) = 0.32

So, recessive genes do not tend to be lost from a population no matter how small their representation.

Hardy-Weinberg law

So long as certain conditions are met (discussed below), **gene frequencies** and **genotype ratios** in a randomly-breeding population remain constant from generation to generation. This is known as the Hardy-Weinberg law.

The Hardy-Weinberg law is named in honor of the two men who first realized the significance of the binomial expansion to population genetics and hence to evolution. Evolution involves changes in the gene pool. A population in Hardy-Weinberg equilibrium shows no change. What the law tells us is that populations are able to maintain a reservoir of variability so that if future conditions require it, the gene pool can change. If recessive alleles were continually tending to disappear, the population would soon become homozygous. Under Hardy-Weinberg conditions, genes that have no present selective value will nonetheless be retained.

When the Hardy-Weinberg Law Fails

To see what forces lead to evolutionary change, we must examine the circumstances in which the Hardy-Weinberg law may fail to apply. There are five:

1. mutation
2. gene flow
3. genetic drift
4. nonrandom mating
5. natural selection

Mutation

The frequency of gene **B** and its allele **b** will not remain in Hardy-Weinberg equilibrium if the rate of mutation of **B** -> **b** (or vice versa) changes. By itself, this type of mutation probably plays only a minor role in evolution; the rates are simply too low. However, gene (and whole genome) duplication - a form of mutation - probably has played a major role in evolution. In any case, evolution absolutely depends on mutations because this is the only way that new alleles are created. After being shuffled in various combinations with the rest of the gene pool, these provide the raw material on which natural selection can act.

Gene Flow

Many species are made up of local populations whose members tend to breed within the group. Each local population can develop a gene pool distinct from that of other local populations. However, members of one population may breed with occasional immigrants from an adjacent population of the same species. This can introduce new genes or alter existing gene frequencies in the residents.

In many plants and some animals, gene flow can occur not only between subpopulations of the same species but also between different (but still related) species. This is called **hybridization**. If the hybrids later breed with one of the parental types, new genes are passed into the gene pool of that parent population. This process is called **introgression**. It is simply gene flow between species rather than within them.

Comparison of the genomes of contemporary humans with the genome recovered from Neanderthal remains shows that from 1–3% of our genes were acquired by introgression following mating between members of the two populations tens of thousands of years

ago.

Whether within a species or between species, gene flow increases the variability of the gene pool.

Genetic Drift

As we have seen, interbreeding often is limited to the members of local populations. If the population is small, Hardy-Weinberg may be violated. Chance alone may eliminate certain members out of proportion to their numbers in the population. In such cases, the frequency of an allele may begin to drift toward higher or lower values. Ultimately, the allele may represent 100% of the gene pool or, just as likely, disappear from it.

Drift produces evolutionary change, but there is no guarantee that the new population will be more fit than the original one. Evolution by drift is aimless, not adaptive.

Nonrandom Mating

One of the cornerstones of the Hardy-Weinberg equilibrium is that mating in the population must be random. If individuals (usually females) are choosy in their selection of mates, the gene frequencies may become altered. Darwin called this **sexual selection**.

Nonrandom mating seems to be quite common. Breeding territories, courtship displays, "pecking orders" can all lead to it. In each case certain individuals do not get to make their proportionate contribution to the next generation.

Assortative mating

Humans seldom mate at random preferring phenotypes like themselves (e.g., size, age, ethnicity). This is called *assortative mating*. Marriage between close relatives is a special case of assortative mating. The closer the kinship, the more alleles shared and the greater the degree of **inbreeding**. Inbreeding can alter the gene pool. This is because it predisposes to **homozygosity**. Potentially harmful recessive alleles — invisible in the parents — become exposed to the forces of natural selection in the children.

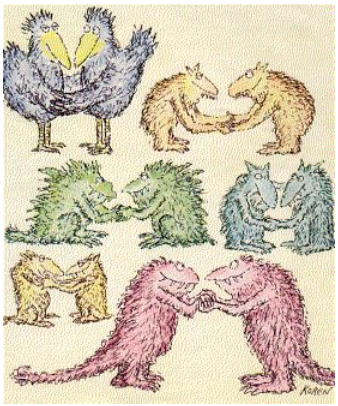


Figure 18.6.1: Assortative mating. (Drawing by Koren © 1977 The New Yorker Magazine, Inc.)

It turns out that many species - plants as well as animals - have mechanisms be which they avoid inbreeding. Examples:

- Link to discussion of self-incompatibility in plants.
- Male mice use olfactory cues to discriminate against close relatives when selecting mates. The preference is learned in infancy - an example of imprinting. The distinguishing odors are controlled by the MHC alleles of the mice and are detected by the vomeronasal organ (VNO).

Natural Selection

If individuals having certain genes are better able to produce mature offspring than those without them, the frequency of those genes will increase. This is simply expressing Darwin's natural selection in terms of alterations in the gene pool. (Darwin knew nothing of genes.) Natural selection results from *differential mortality* and/or *differential fecundity*.

Mortality Selection

Certain genotypes are less successful than others in surviving through to the end of their reproductive period. The evolutionary impact of mortality selection can be felt anytime from the formation of a new zygote to the end (if there is one) of the organism's

period of fertility. Mortality selection is simply another way of describing Darwin's criteria of fitness: **survival**.

Fecundity Selection

Certain phenotypes (thus genotypes) may make a disproportionate contribution to the gene pool of the next generation by producing a disproportionate number of young. Such fecundity selection is another way of describing another criterion of fitness described by Darwin: **family size**. In each of these examples of natural selection, certain phenotypes are better able than others to contribute their genes to the next generation. Thus, by Darwin's standards, they are more **fit**. The outcome is a gradual change in the gene frequencies in that population.

Calculating the Effect of Natural Selection on Gene Frequencies

The effect of natural selection on gene frequencies can be quantified. Let us assume a population containing

- 36% homozygous dominants (**AA**)
- 48% heterozygotes (**Aa**) and
- 16% homozygous recessives (**aa**)

The gene frequencies in this population are $p = 0.6$ and $q = 0.4$. The heterozygotes are just as successful at reproducing themselves as the homozygous dominants, but the homozygous recessives are only 80% as successful. That is, for every 100 **AA** (or **Aa**) individuals that reproduce successfully only 80 of the **aa** individuals succeed in doing so. The *fitness* (w) of the recessive phenotype is thus 80% or 0.8.

Their relative disadvantage can also be expressed as a *selection coefficient*, s, where

$$s = 1 - w \tag{20.2.3}$$

In this case,

$$s = 1 - 0.8 = 0.2. \tag{20.2.4}$$

The change in frequency of the dominant allele (Δp) after one generation is expressed by the equation

$$\Delta p = \frac{s p_0 q_0^2}{1 - s q_0^2} \tag{20.2.5}$$

where p_0 and q_0 are the initial frequencies of the dominant and recessive alleles respectively. Substituting, we get

$$\Delta p = \frac{(0.2)(0.6)(0.4)^2}{1 - (0.2)(0.4)^2} \tag{20.2.6}$$

$$= \frac{0.019}{0.968} \tag{20.2.7}$$

$$= 0.02 \tag{20.2.8}$$

So, in one generation, the frequency of allele **A** rises from its initial value of 0.6 to 0.62 and that of allele **a** declines from 0.4 to 0.38 ($q = 1 - p$).

The new equilibrium produces a population of

- 38.4% homozygous dominants (an increase of 2.4%) ($\mathbf{p^2}$ = 0.384)
- 47.1% heterozygotes (a decline of 0.9%)(**2pq** = 0.471) and
- 14.4% homozygous recessives (a decline of 1.6%)($\mathbf{q^2}$ = 0.144)

If the fitness of the homozygous recessives continues unchanged, the calculations can be reiterated for any number of generations. If you do so, you will find that although the frequency of the recessive genotype declines, the **rate** at which **a** is removed from the gene pool declines; that is, the process becomes less efficient at purging allele **a**. This is because when present in the heterozygote, **a** is protected from the effects of selection.

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20.3: Five Agents of Evolutionary Change

Skills to Develop

- Describe the different types of variation in a population
- Explain why only heritable variation can be acted upon by natural selection
- Describe genetic drift and the bottleneck effect
- Explain how each evolutionary force can influence the allele frequencies of a population

Individuals of a population often display different phenotypes, or express different alleles of a particular gene, referred to as polymorphisms. Populations with two or more variations of particular characteristics are called polymorphic. The distribution of phenotypes among individuals, known as the population variation, is influenced by a number of factors, including the population's genetic structure and the environment (Figure 20.3.1). Understanding the sources of a phenotypic variation in a population is important for determining how a population will evolve in response to different evolutionary pressures.



Figure 20.3.1: The distribution of phenotypes in this litter of kittens illustrates population variation. (credit: Pieter Lanser)

Genetic Variance

Natural selection and some of the other evolutionary forces can only act on heritable traits, namely an organism's genetic code. Because alleles are passed from parent to offspring, those that confer beneficial traits or behaviors may be selected for, while deleterious alleles may be selected against. Acquired traits, for the most part, are not heritable. For example, if an athlete works out in the gym every day, building up muscle strength, the athlete's offspring will not necessarily grow up to be a body builder. If there is a genetic basis for the ability to run fast, on the other hand, this may be passed to a child.

Heritability is the fraction of phenotype variation that can be attributed to genetic differences, or genetic variance, among individuals in a population. The greater the hereditability of a population's phenotypic variation, the more susceptible it is to the evolutionary forces that act on heritable variation.

The diversity of alleles and genotypes within a population is called genetic variance. When scientists are involved in the breeding of a species, such as with animals in zoos and nature preserves, they try to increase a population's genetic variance to preserve as much of the phenotypic diversity as they can. This also helps reduce the risks associated with inbreeding, the mating of closely related individuals, which can have the undesirable effect of bringing together deleterious recessive mutations that can cause abnormalities and susceptibility to disease. For example, a disease that is caused by a rare, recessive allele might exist in a population, but it will only manifest itself when an individual carries two copies of the allele. Because the allele is rare in a normal, healthy population with unrestricted habitat, the chance that two carriers will mate is low, and even then, only 25 percent of their offspring will inherit the disease allele from both parents. While it is likely to happen at some point, it will not happen frequently enough for natural selection to be able to swiftly eliminate the allele from the population, and as a result, the allele will be maintained at low levels in the gene pool. However, if a family of carriers begins to interbreed with each other, this will dramatically increase the likelihood of two carriers mating and eventually producing diseased offspring, a phenomenon known as inbreeding depression.

Changes in allele frequencies that are identified in a population can shed light on how it is evolving. In addition to natural selection, there are other evolutionary forces that could be in play: genetic drift, gene flow, mutation, nonrandom mating, and environmental variances.

Genetic Drift

The theory of natural selection stems from the observation that some individuals in a population are more likely to survive longer and have more offspring than others; thus, they will pass on more of their genes to the next generation. A big, powerful male gorilla, for example, is much more likely than a smaller, weaker one to become the population's silverback, the pack's leader who mates far more than the other males of the group. The pack leader will father more offspring, who share half of his genes, and are likely to also grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the population will, as a result, grow larger on average. That is, this would occur if this particular selection pressure, or driving selective force, were the only one acting on the population. In other examples, better camouflage or a stronger resistance to drought might pose a selection pressure.

Another way a population's allele and genotype frequencies can change is genetic drift (Figure **20.3.2**), which is simply the effect of chance. By chance, some individuals will have more offspring than others—not due to an advantage conferred by some genetically-encoded trait, but just because one male happened to be in the right place at the right time (when the receptive female walked by) or because the other one happened to be in the wrong place at the wrong time (when a fox was hunting).

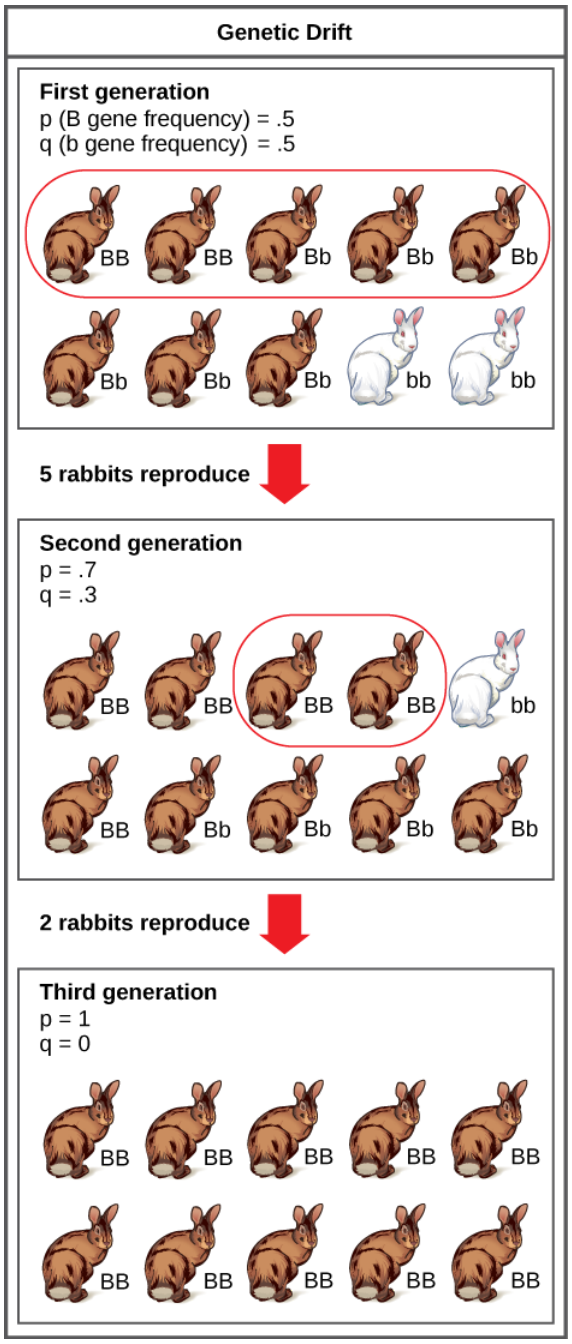


Figure **20.3.2**: Genetic drift in a population can lead to the elimination of an allele from a population by chance. In this example, rabbits with the brown coat color allele (*B*) are dominant over rabbits with the white coat color allele (*b*). In the first generation, the two alleles occur with equal frequency in the population, resulting in p and q values of 0.5. Only half of the individuals reproduce, resulting in a second generation with p and q values of .7 and .3, respectively. Only two individuals in the second generation reproduce, and by chance these individuals are homozygous dominant for brown coat color. As a result, in the third generation the recessive *b* allele is lost.

Exercise 20.3.1

Do you think genetic drift would happen more quickly on an island or on the mainland?

Answer

Genetic drift is likely to occur more rapidly on an island where smaller populations are expected to occur.

Small populations are more susceptible to the forces of genetic drift. Large populations, on the other hand, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before it leaves any offspring to the next generation, all of its genes—1/10 of the population's gene pool—will be suddenly lost. In a population of 100, that's only 1 percent of the overall gene pool; therefore, it is much less impactful on the population's genetic structure.

Genetic drift can also be magnified by natural events, such as a natural disaster that kills—at random—a large portion of the population. Known as the bottleneck effect, it results in a large portion of the genome suddenly being wiped out (Figure **20.3.3**). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.

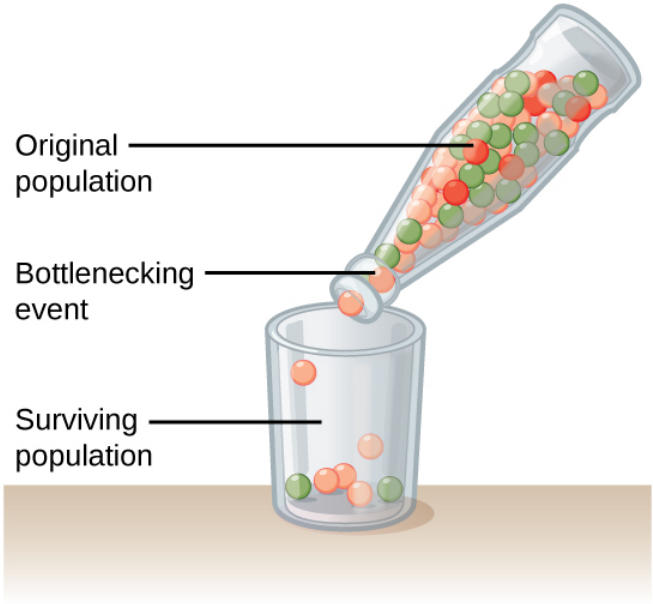


Figure **20.3.3**: A chance event or catastrophe can reduce the genetic variability within a population.

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location or if a population gets divided by a physical barrier of some kind. In this situation, those individuals are unlikely to be representative of the entire population, which results in the founder effect. The founder effect occurs when the genetic structure changes to match that of the new population's founding fathers and mothers. The founder effect is believed to have been a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners but rare in most other populations. This is likely due to the fact that a higher-than-normal proportion of the founding colonists carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause blood marrow and congenital abnormalities—even cancer.[1]

Link to Learning



Watch this short video to learn more about the founder and bottleneck effects.

Scientific Method Connection: Testing the Bottleneck Effect

Question: How do natural disasters affect the genetic structure of a population?

Background: When much of a population is suddenly wiped out by an earthquake or hurricane, the individuals that survive the event are usually a random sampling of the original group. As a result, the genetic makeup of the population can change dramatically. This phenomenon is known as the bottleneck effect.

Hypothesis: Repeated natural disasters will yield different population genetic structures; therefore, each time this experiment is run, the results will vary.

Test the hypothesis: Count out the original population using different colored beads. For example, red, blue, and yellow beads might represent red, blue, and yellow individuals. After recording the number of each individual in the original population, place them all in a bottle with a narrow neck that will only allow a few beads out at a time. Then, pour 1/3 of the bottle's contents into a bowl. This represents the surviving individuals after a natural disaster kills a majority of the population. Count the number of the different colored beads in the bowl, and record it. Then, place all of the beads back in the bottle and repeat the experiment four more times.

Analyze the data: Compare the five populations that resulted from the experiment. Do the populations all contain the same number of different colored beads, or do they vary? Remember, these populations all came from the same exact parent population.

Form a conclusion: Most likely, the five resulting populations will differ quite dramatically. This is because natural disasters are not selective—they kill and spare individuals at random. Now think about how this might affect a real population. What happens when a hurricane hits the Mississippi Gulf Coast? How do the seabirds that live on the beach fare?

Gene Flow

Another important evolutionary force is gene flow: the flow of alleles in and out of a population due to the migration of individuals or gametes (Figure **20.3.4**). While some populations are fairly stable, others experience more flux. Many plants, for example, send their pollen far and wide, by wind or by bird, to pollinate other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, can experience its fair share of immigration and emigration as developing males leave their mothers to seek out a new pride with genetically unrelated females. This variable flow of individuals in and out of the group not only changes the gene structure of the population, but it can also introduce new genetic variation to populations in different geological locations and habitats.

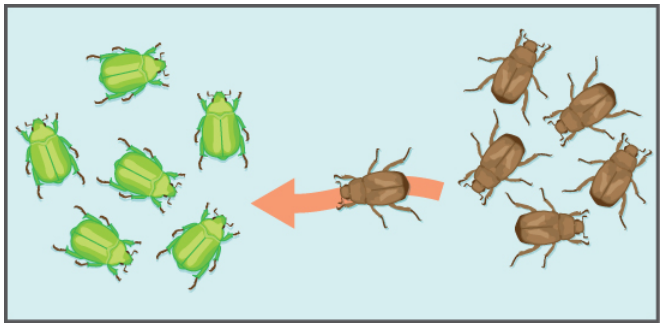


Figure 20.3.4: Gene flow can occur when an individual travels from one geographic location to another.

Mutation

Mutations are changes to an organism's DNA and are an important driver of diversity in populations. Species evolve because of the accumulation of mutations that occur over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance. Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection. Others are beneficial and will spread through the population. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. Some mutations do not do anything and can linger, unaffected by natural selection, in the genome. Some can have a dramatic effect on a gene and the resulting phenotype.

Nonrandom Mating

If individuals nonrandomly mate with their peers, the result can be a changing population. There are many reasons nonrandom mating occurs. One reason is simple mate choice; for example, female peahens may prefer peacocks with bigger, brighter tails. Traits that lead to more matings for an individual become selected for by natural selection. One common form of mate choice, called assortative mating, is an individual's preference to mate with partners who are phenotypically similar to themselves.

Another cause of nonrandom mating is physical location. This is especially true in large populations spread over large geographic distances where not all individuals will have equal access to one another. Some might be miles apart through woods or over rough terrain, while others might live immediately nearby.

Environmental Variance

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment (Figure 20.3.5). A beachgoer is likely to have darker skin than a city dweller, for example, due to regular exposure to the sun, an environmental factor. Some major characteristics, such as gender, are determined by the environment for some species. For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a different temperature range.



Figure 20.3.5: The sex of the American alligator (*Alligator mississippiensis*) is determined by the temperature at which the eggs are incubated. Eggs incubated at 30°C produce females, and eggs incubated at 33°C produce males. (credit: Steve Hillebrand, USFWS)

Geographic separation between populations can lead to differences in the phenotypic variation between those populations. Such geographical variation is seen between most populations and can be significant. One type of geographic variation, called a cline, can be seen as populations of a given species vary gradually across an ecological gradient. Species of warm-blooded animals, for example, tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a latitudinal cline. Alternatively, flowering plants tend to bloom at different times depending on where they are along the slope of a mountain, known as an altitudinal cline.

If there is gene flow between the populations, the individuals will likely show gradual differences in phenotype along the cline. Restricted gene flow, on the other hand, can lead to abrupt differences, even speciation.

Summary

Both genetic and environmental factors can cause phenotypic variation in a population. Different alleles can confer different phenotypes, and different environments can also cause individuals to look or act differently. Only those differences encoded in an individual's genes, however, can be passed to its offspring and, thus, be a target of natural selection. Natural selection works by selecting for alleles that confer beneficial traits or behaviors, while selecting against those for deleterious qualities. Genetic drift stems from the chance occurrence that some individuals in the germ line have more offspring than others. When individuals leave or join the population, allele frequencies can change as a result of gene flow. Mutations to an individual's DNA may introduce new variation into a population. Allele frequencies can also be altered when individuals do not randomly mate with others in the group.

Footnotes

1. 1 A. J. Tipping et al., "Molecular and Genealogical Evidence for a Founder Effect in Fanconi Anemia Families of the Afrikaner Population of South Africa," *PNAS* 98, no. 10 (2001): 5734-5739, doi: 10.1073/pnas.091402398.

Glossary

assortative mating
when individuals tend to mate with those who are phenotypically similar to themselves

bottleneck effect
magnification of genetic drift as a result of natural events or catastrophes

cline
gradual geographic variation across an ecological gradient

gene flow
flow of alleles in and out of a population due to the migration of individuals or gametes

genetic drift
effect of chance on a population's gene pool

genetic variance
diversity of alleles and genotypes in a population

geographical variation
differences in the phenotypic variation between populations that are separated geographically

heritability
fraction of population variation that can be attributed to its genetic variance

inbreeding
mating of closely related individuals

inbreeding depression

increase in abnormalities and disease in inbreeding populations

nonrandom mating

changes in a population's gene pool due to mate choice or other forces that cause individuals to mate with certain phenotypes more than others

population variation

distribution of phenotypes in a population

selective pressure

environmental factor that causes one phenotype to be better than another

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SECTION OVERVIEW

20.4: Quantifying Natural Selection

20.4.1: Hardy-Weinberg

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20.4.1: Hardy-Weinberg

Learning Objectives

- Explain how natural selection leads to adaptive evolution

An Introduction to Adaptive Evolution

Natural selection only acts on the population's heritable traits: selecting for beneficial alleles and, thus, increasing their frequency in the population, while selecting against deleterious alleles and, thereby, decreasing their frequency. This process is known as adaptive evolution. Natural selection does not act on individual alleles, however, but on entire organisms. An individual may carry a very beneficial genotype with a resulting phenotype that, for example, increases the ability to reproduce (fecundity), but if that same individual also carries an allele that results in a fatal childhood disease, that fecundity phenotype will not be passed on to the next generation because the individual will not live to reach reproductive age. Natural selection acts at the level of the individual; it selects for individuals with greater contributions to the gene pool of the next generation, known as an organism's evolutionary fitness (or Darwinian fitness).

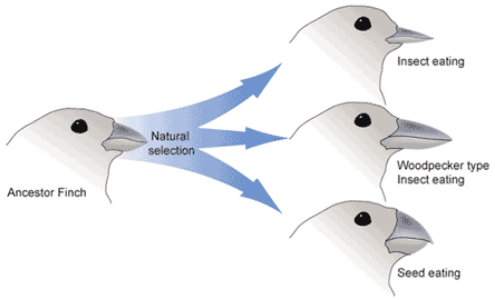


Figure **20.4.1.1**: Adaptive evolution in finches: Through natural selection, a population of finches evolved into three separate species by adapting to several difference selection pressures. Each of the three modern finches has a beak adapted to its life history and diet.

Fitness is often quantifiable and is measured by scientists in the field. However, it is not the absolute fitness of an individual that counts, but rather how it compares to the other organisms in the population. This concept, called relative fitness, allows researchers to determine which individuals are contributing additional offspring to the next generation and, thus, how the population might evolve.

There are several ways selection can affect population variation:

- stabilizing selection
- directional selection
- diversifying selection
- frequency-dependent selection
- sexual selection

As natural selection influences the allele frequencies in a population, individuals can either become more or less genetically similar and the phenotypes displayed can become more similar or more disparate. In the end, natural selection cannot produce perfect organisms from scratch, it can only generate populations that are better adapted to survive and successfully reproduce in their environments through the aforementioned selections.





Galápagos with David Attenborough: Two hundred years after Charles Darwin set foot on the shores of the Galápagos Islands, David Attenborough travels to this wild and mysterious archipelago. Amongst the flora and fauna of these enchanted volcanic islands, Darwin formulated his groundbreaking theories on evolution. Journey with Attenborough to explore how life on the islands has continued to evolve in biological isolation, and how the ever-changing volcanic landscape has given birth to species and sub-species that exist nowhere else in the world.

Key Points

- Natural selection increases or decreases biological traits within a population, thereby selecting for individuals with greater evolutionary fitness.
- An individual with a high evolutionary fitness will provide more beneficial contributions to the gene pool of the next generation.
- Relative fitness, which compares an organism's fitness to the others in the population, allows researchers to establish how a population may evolve by determining which individuals are contributing additional offspring to the next generation.
- Stabilizing selection, directional selection, diversifying selection, frequency -dependent selection, and sexual selection all contribute to the way natural selection can affect variation within a population.

Key Terms

- **natural selection**: a process in which individual organisms or phenotypes that possess favorable traits are more likely to survive and reproduce
- **fecundity**: number, rate, or capacity of offspring production
- **Darwinian fitness**: the average contribution to the gene pool of the next generation that is made by an average individual of the specified genotype or phenotype

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SECTION OVERVIEW

20.5: Reproductive Strategies

20.5.1: Sexual Selection

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20.5.1: Sexual Selection

Learning Objectives

- Discuss the effects of sexual dimorphism on the reproductive potential of an organism

Sexual Selection

The selection pressures on males and females to obtain matings is known as sexual selection. Sexual selection takes two major forms: intersexual selection (also known as 'mate choice' or 'female choice') in which males compete with each other to be chosen by females; and intrasexual selection (also known as 'male–male competition') in which members of the less limited sex (typically males) compete aggressively among themselves for access to the limiting sex. The limiting sex is the sex which has the higher parental investment, which therefore faces the most pressure to make a good mate decision.



Figure **20.5.1.1**: Sexual selection in elk: This male elk has large antlers to compete with rival males for available females (intrasexual competition).Tn addition, the many points on his antlers represent health and longevity, and therefore he may be more desirable to females (intersexual selection).

Sexual Dimorphism

Males and females of certain species are often quite different from one another in ways beyond the reproductive organs. Males are often larger, for example, and display many elaborate colors and adornments, such as the peacock's tail, while females tend to be smaller and duller in decoration. These differences are called sexual dimorphisms and arise from the variation in male reproductive success.

Females almost always mate, while mating is not guaranteed for males. The bigger, stronger, or more decorated males usually obtain the vast majority of the total matings, while other males receive none. This can occur because the males are better at fighting off other males, or because females will choose to mate with the bigger or more decorated males. In either case, this variation in reproductive success generates a strong selection pressure among males to obtain those matings, resulting in the evolution of bigger body size and elaborate ornaments in order to increase their chances of mating. Females, on the other hand, tend to get a handful of selected matings; therefore, they are more likely to select more desirable males.



Figure **20.5.1.1**: Sexual dimorphism: Morphological differences between males and females of the same species is known as sexual dimorphism.These differences can be observed in (a) peacocks and peahens, (b) Argiope appensa spiders (the female spider is the large one), and (c) wood ducks.

Sexual dimorphism varies widely among species; some species are even sex-role reversed. In such cases, females tend to have a greater variation in their reproductive success than males and are, correspondingly, selected for the bigger body size and elaborate traits usually characteristic of males.

The Handicap Principle

Sexual selection can be so strong that it selects for traits that are actually detrimental to the individual's survival, even though they maximize its reproductive success. For example, while the male peacock's tail is beautiful and the male with the largest, most colorful tail will more probably win the female, it is not a practical appendage. In addition to being more visible to predators, it makes the males slower in their attempted escapes. There is some evidence that this risk, in fact, is why females like the big tails in the first place. Because large tails carry risk, only the best males survive that risk and therefore the bigger the tail, the more fit the male. This idea is known as the handicap principle.



Figure **20.5.1.1**: A male bird of paradise: This male bird of paradise carries an extremely long tail as the result of sexual selection.The tail is flamboyant and detrimental to the bird's own survival, but it increases his reproductive success.This may be an example of the handicap principle.

The Good Genes Hypothesis

The good genes hypothesis states that males develop these impressive ornaments to show off their efficient metabolism or their ability to fight disease. Females then choose males with the most impressive traits because it signals their genetic superiority, which they will then pass on to their offspring. Though it might be argued that females should not be so selective because it will likely reduce their number of offspring, if better males father more fit offspring, it may be beneficial. Fewer, healthier offspring may increase the chances of survival more than many, weaker offspring.





BBC Planet Earth – Birds of Paradise mating dance: Extraordinary Courtship displays from these weird and wonderful creatures. From episode 1 “Pole to Pole”. This is an example of the extreme behaviors that arise from intense sexual selection pressure.

Key Points

- Sexual selection often results in the development of secondary sexual characteristics, which help to maximize a species ‘ reproductive success, but do not provide any survival benefits.
- The handicap principle states that only the best males survive the risks from traits that may actually be detrimental to a species; therefore, they are more fit as mating partners.
- In the good genes hypothesis, females will choose males that show off impressive traits to ensure they pass on genetic superiority to their offspring.
- Sexual dimorphisms, obvious morphological differences between the sexes of a species, arise when there is more variance in the reproductive success of either males or females.

Key Terms

- **sexual dimorphism**: a physical difference between male and female individuals of the same species
- **sexual selection**: a type of natural selection, where members of the sexes acquire distinct forms because members choose mates with particular features or because competition for mates with certain traits succeed
- **handicap principle**: a theory that suggests that animals of greater biological fitness signal this status through a behavior or morphology that effectively lowers their chances of survival

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SECTION OVERVIEW

20.6: Natural Selection's Role in Maintaining Variation

20.6.1: Natural Selection and Adaptive Evolution

20.6.2: Frequency-Dependent Selection

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20.6.1: Natural Selection and Adaptive Evolution

Learning Objectives

- Explain how natural selection leads to adaptive evolution

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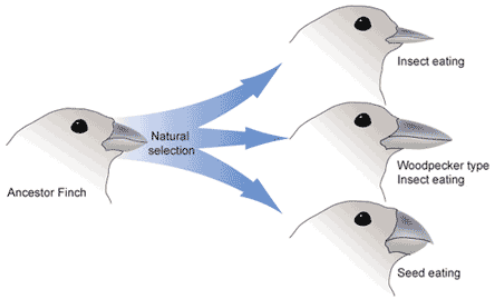


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20.6.2: Frequency-Dependent Selection

Learning Objectives

- Describe frequency-dependent selection

Frequency-dependent Selection

Another type of selection, called frequency-dependent selection, favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection).

Negative Frequency-dependent Selection

An interesting example of this type of selection is seen in a unique group of lizards of the Pacific Northwest. Male common side-blotched lizards come in three throat-color patterns: orange, blue, and yellow. Each of these forms has a different reproductive strategy: orange males are the strongest and can fight other males for access to their females; blue males are medium-sized and form strong pair bonds with their mates; and yellow males are the smallest and look a bit like female, allowing them to sneak copulations. Like a game of rock-paper-scissors, orange beats blue, blue beats yellow, and yellow beats orange in the competition for females. The big, strong orange males can fight off the blue males to mate with the blue's pair-bonded females; the blue males are successful at guarding their mates against yellow sneaker males; and the yellow males can sneak copulations from the potential mates of the large, polygynous orange males.



Figure **20.6.2.1**: Frequency-dependent selection in side-blotched lizards: A yellow-throated side-blotched lizard is smaller than either the blue-throated or orange-throated males and appears a bit like the females of the species, allowing it to sneak copulations. Frequency-dependent selection allows for both common and rare phenotypes of the population to appear in a frequency-aided cycle.

In this scenario, orange males will be favored by natural selection when the population is dominated by blue males, blue males will thrive when the population is mostly yellow males, and yellow males will be selected for when orange males are the most populous. As a result, populations of side-blotched lizards cycle in the distribution of these phenotypes. In one generation, orange might be predominant and then yellow males will begin to rise in frequency. Once yellow males make up a majority of the population, blue males will be selected for.Finally, when blue males become common, orange males will once again be favored.

An example of negative frequency-dependent selection can also be seen in the interaction between the human immune system and various infectious microbes such as pathogenic bacteria or viruses. As a particular human population is infected by a common strain of microbe, the majority of individuals in the population become immune to it. This then selects for rarer strains of the microbe which can still infect the population because of genome mutations; these strains have greater evolutionary fitness because they are less common.

Positive Frequency-dependent Selection

An example of positive frequency-dependent selection is the mimicry of the warning coloration of dangerous species of animals by other species that are harmless. The scarlet kingsnake, a harmless species, mimics the coloration of the eastern coral snake, a venomous species typically found in the same geographical region. Predators learn to avoid both species of snake due to the similar coloration, and as a result the scarlet kingsnake becomes more common, and its coloration phenotype becomes more variable due to relaxed selection. This phenotype is therefore more “fit” as the population of species that possess it (both dangerous and harmless) becomes more numerous. In geographic areas where the coral snake is less common, the pattern becomes less advantageous to the kingsnake, and much less variable in its expression, presumably because predators in these regions are not “educated” to avoid the pattern.



Figure **20.6.2.1**: Lampropeltis elapsoides, the scarlet kingsnake: The scarlet kingsnake mimics the coloration of the poisonous eastern coral snake. Positive frequency-dependent selection reinforces the common phenotype because predators avoid the distinct coloration.



Figure **20.6.2.1**: Micrurus fulvius, the eastern coral snake: The eastern coral snake is poisonous.

Negative frequency-dependent selection serves to increase the population’s genetic variance by selecting for rare phenotypes, whereas positive frequency-dependent selection usually decreases genetic variance by selecting for common phenotypes.

Key Points

- Negative frequency -dependent selection selects for rare phenotypes in a population and increases a population's genetic variance.
- Positive frequency-dependent selection selects for common phenotypes in a population and decreases genetic variance.
- In the example of male side-blotched lizards, populations of each color pattern increase or decrease at various stages depending on their frequency; this ensures that both common and rare phenotypes continue to be cyclically present.
- Infectious agents such as microbes can exhibit negative frequency-dependent selection; as a host population becomes immune to a common strain of the microbe, less common strains of the microbe are automatically favored.
- Variation in color pattern mimicry by the scarlet kingsnake is dependent on the prevalence of the eastern coral snake, the model for this mimicry, in a particular geographical region. The more prevalent the coral snake is in a region, the more common and variable the scarlet kingsnake's color pattern will be, making this an example of positive frequency-dependent selection.

Key Terms

- **frequency-dependent selection**: the term given to an evolutionary process where the fitness of a phenotype is dependent on its frequency relative to other phenotypes in a given population
- **polygynous**: having more than one female as mate

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SECTION OVERVIEW

20.7: Selection Acting on Traits Affected by Multiple Genes

20.7.1: Stabilizing, Directional, and Diversifying Selection

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20.7.1: Stabilizing, Directional, and Diversifying Selection

Learning Objectives

- Contrast stabilizing selection, directional selection, and diversifying selection.

Stabilizing Selection

If natural selection favors an average phenotype by selecting against extreme variation, the population will undergo stabilizing selection. For example, in a population of mice that live in the woods, natural selection will tend to favor individuals that best blend in with the forest floor and are less likely to be spotted by predators. Assuming the ground is a fairly consistent shade of brown, those mice whose fur is most-closely matched to that color will most probably survive and reproduce, passing on their genes for their brown coat. Mice that carry alleles that make them slightly lighter or slightly darker will stand out against the ground and will more probably die from predation. As a result of this stabilizing selection, the population's genetic variance will decrease.

image

Stabilizing selection: Stabilizing selection occurs when the population stabilizes on a particular trait value and genetic diversity decreases.

Directional Selection

When the environment changes, populations will often undergo directional selection, which selects for phenotypes at one end of the spectrum of existing variation.

A classic example of this type of selection is the evolution of the peppered moth in eighteenth- and nineteenth-century England. Prior to the Industrial Revolution, the moths were predominately light in color, which allowed them to blend in with the light-colored trees and lichens in their environment. As soot began spewing from factories, the trees darkened and the light-colored moths became easier for predatory birds to spot.

image

Directional selection: Directional selection occurs when a single phenotype is favored, causing the allele frequency to continuously shift in one direction.

Over time, the frequency of the melanic form of the moth increased because their darker coloration provided camouflage against the sooty tree; they had a higher survival rate in habitats affected by air pollution. Similarly, the hypothetical mouse population may evolve to take on a different coloration if their forest floor habitat changed. The result of this type of selection is a shift in the population's genetic variance toward the new, fit phenotype.



Figure **20.7.1.1**: The Evolution of the Peppered Moth: Typica and carbonaria morphs resting on the same tree.The light-colored typica (below the bark's scar) is nearly invisible on this pollution-free tree, camouflaging it from predators.

Diversifying (or Disruptive) Selection

Sometimes natural selection can select for two or more distinct phenotypes that each have their advantages. In these cases, the intermediate phenotypes are often less fit than their extreme counterparts. Known as diversifying or disruptive selection, this is seen in many populations of animals that have multiple male mating strategies, such as lobsters. Large, dominant alpha males obtain mates by brute force, while small males can sneak in for furtive copulations with the females in an alpha male's territory. In this case, both the alpha males and the "sneaking" males will be selected for, but medium-sized males, which cannot overtake the alpha males and are too big to sneak copulations, are selected against.

image

Diversifying (or disruptive) selection: Diversifying selection occurs when extreme values for a trait are favored over the intermediate values.This type of selection often drives speciation.

Diversifying selection can also occur when environmental changes favor individuals on either end of the phenotypic spectrum. Imagine a population of mice living at the beach where there is light-colored sand interspersed with patches of tall grass. In this scenario, light-colored mice that blend in with the sand would be favored, as well as dark-colored mice that can hide in the grass. Medium-colored mice, on the other hand, would not blend in with either the grass or the sand and, thus, would more probably be eaten by predators. The result of this type of selection is increased genetic variance as the population becomes more diverse.

Comparing Types of Natural Selection

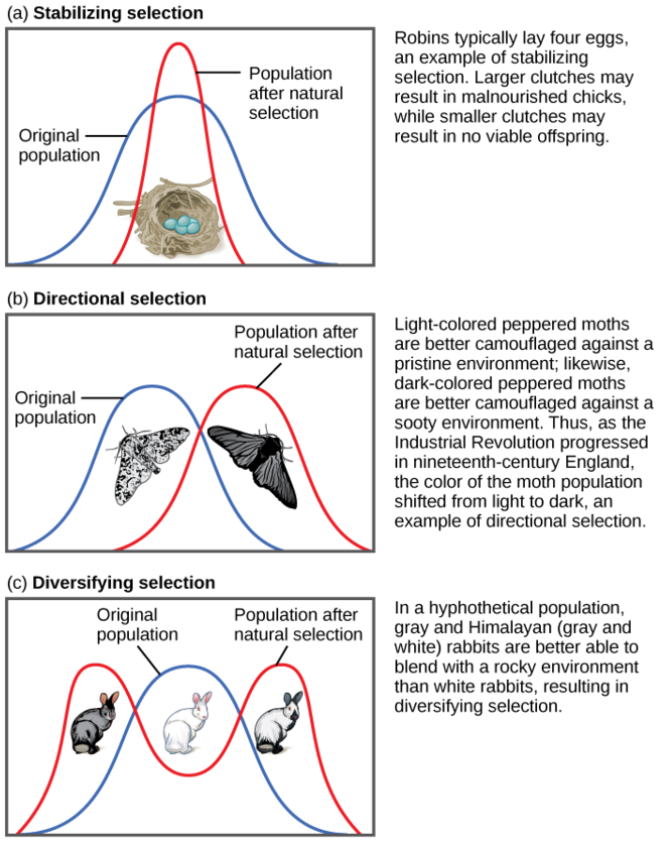


Figure 20.7.1.1: Types of natural selection: Different types of natural selection can impact the distribution of phenotypes within a population.In (a) stabilizing selection, an average phenotype is favored.In (b) directional selection, a change in the environment shifts the spectrum of phenotypes observed.In (c) diversifying selection, two or more extreme phenotypes are selected for, while the average phenotype is selected against.

Key Points

- Stabilizing selection results in a decrease of a population 's genetic variance when natural selection favors an average phenotype and selects against extreme variations.
- In directional selection, a population's genetic variance shifts toward a new phenotype when exposed to environmental changes.

- Diversifying or disruptive selection increases genetic variance when natural selection selects for two or more extreme phenotypes that each have specific advantages.
- In diversifying or disruptive selection, average or intermediate phenotypes are often less fit than either extreme phenotype and are unlikely to feature prominently in a population.

Key Terms

- **directional selection**: a mode of natural selection in which a single phenotype is favored, causing the allele frequency to continuously shift in one direction
- **disruptive selection**: (or diversifying selection) a mode of natural selection in which extreme values for a trait are favored over intermediate values
- **stabilizing selection**: a type of natural selection in which genetic diversity decreases as the population stabilizes on a particular trait value

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20.8: Experimental Studies of Natural Selection

Microbes are the system of choice for experimentally studying evolution because multiple generations can be followed in relatively short times, although some experiments have been running for decades. Two papers which you can read online about these experiments are

Microbial Experimental Evolution – a proving ground for evolutionary theory and a tool for discovery Michael J McDonald https://www.embopress.org/doi/pdf/10.15252/embr.201846992

Experimental studies of evolving populations now constitute one of the foundations of the theory of evolution. In particular, studies of microbial populations in the laboratory bring greater power and precision to experimental evolution studies, providing a means to carry out elaborate tests of theory and explore new ideas in evolutionary biology. A typical microbial evolution experiment starts with a culture, just like any other in a microbiology laboratory. Cells are inoculated into media and left to grow until the culture reaches a high population density. Instead of throwing out or using all of the resultant population, the experimental evolutionist transfers or dilutes the culture to allow continued growth and division. This cycle can be continued indefinitely, and as the generations accumulate, natural selection will drive the population to adapt to the laboratory environment. This simple process can be carried out in the laboratory using a range of experimental systems

What is adaptation by natural selection? Perspectives of an experimental microbiologist Richard E. Lenski, PLOS Genetics, https://doi.org/10.1371/journal.pgen.1006668

Ever since Darwin, the role of natural selection in shaping the morphological, physiological, and behavioral adaptations of animals and plants across generations has been central to understanding life and its diversity. New discoveries have shown with increasing precision how genetic, molecular, and biochemical processes produce and express those organismal features during an individual's lifetime. When it comes to microorganisms, however, understanding the role of natural selection in producing adaptive solutions has historically been, and sometimes continues to be, contentious. This tension is curious because microbes enable one to observe the power of adaptation by natural selection with exceptional rigor and clarity, as exemplified by the burgeoning field of experimental microbial evolution. I trace the development of this field, describe an experiment with *Escherichia coli* that has been running for almost 30 years, and highlight other experiments in which natural selection has led to interesting dynamics and adaptive changes in microbial populations.

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SECTION OVERVIEW

20.9: Interactions Among Evolutionary Forces

20.9.1: Genetic Variation

20.9.2: Genetic Drift

20.9.3: Gene Flow and Mutation

20.9.4: Nonrandom Mating and Environmental Variance

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20.9.1: Genetic Variation

Learning Objectives

- Assess the ways in which genetic variance affects the evolution of populations

Genetic Variation

Genetic variation is a measure of the genetic differences that exist within a population. The genetic variation of an entire species is often called genetic diversity. Genetic variations are the differences in DNA segments or genes between individuals and each variation of a gene is called an allele.For example, a population with many different alleles at a single chromosome locus has a high amount of genetic variation. Genetic variation is essential for natural selection because natural selection can only increase or decrease frequency of alleles that already exist in the population.

Genetic variation is caused by:

- mutation
- random mating between organisms
- random fertilization
- crossing over (or recombination) between chromatids of homologous chromosomes during meiosis

The last three of these factors reshuffle alleles within a population, giving offspring combinations which differ from their parents and from others.

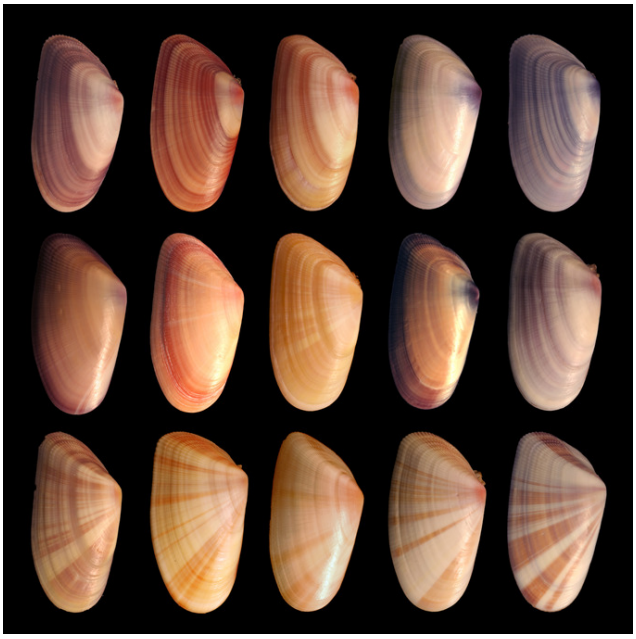


Figure **20.9.1.1**: Genetic variation in the shells of Donax variabilis: An enormous amount of phenotypic variation exists in the shells of Donax varabilis, otherwise known as the coquina mollusc. This phenotypic variation is due at least partly to genetic variation within the coquina population.

Evolution and Adaptation to the Environment

Variation allows some individuals within a population to adapt to the changing environment. Because natural selection acts directly only on phenotypes, more genetic variation within a population usually enables more phenotypic variation. Some new alleles increase an organism's ability to survive and reproduce, which then ensures the survival of the allele in the population. Other new alleles may be immediately detrimental (such as a malformed oxygen-carrying protein) and organisms carrying these new mutations will die out. Neutral alleles are neither selected for nor against and usually remain in the population. Genetic variation is advantageous because it enables some individuals and, therefore, a population, to survive despite a changing environment.



Figure **20.9.1.1**: Low genetic diversity in the wild cheetah population: Populations of wild cheetahs have very low genetic variation. Because wild cheetahs are threatened, their species has a very low genetic diversity. This low genetic diversity means they are often susceptible to disease and often pass on lethal recessive mutations; only about 5% of cheetahs survive to adulthood.

Geographic Variation

Some species display geographic variation as well as variation within a population. Geographic variation, or the distinctions in the genetic makeup of different populations, often occurs when populations are geographically separated by environmental barriers or when they are under selection pressures from a different environment. One example of geographic variation are clines: graded changes in a character down a geographic axis.

Sources of Genetic Variation

Gene duplication, mutation, or other processes can produce new genes and alleles and increase genetic variation. New genetic variation can be created within generations in a population, so a population with rapid reproduction rates will probably have high genetic variation. However, existing genes can be arranged in new ways from chromosomal crossing over and recombination in sexual reproduction. Overall, the main sources of genetic variation are the formation of new alleles, the altering of gene number or position, rapid reproduction, and sexual reproduction.

Key Points

- Genetic variation is an important force in evolution as it allows natural selection to increase or decrease frequency of alleles already in the population.
- Genetic variation can be caused by mutation (which can create entirely new alleles in a population), random mating, random fertilization, and recombination between homologous chromosomes during meiosis (which reshuffles alleles within an organism’s offspring).
- Genetic variation is advantageous to a population because it enables some individuals to adapt to the environment while maintaining the survival of the population.

Key Terms

- **genetic diversity**: the level of biodiversity, refers to the total number of genetic characteristics in the genetic makeup of a species

- **crossing over**: the exchange of genetic material between homologous chromosomes that results in recombinant chromosomes
- **phenotypic variation**: variation (due to underlying heritable genetic variation); a fundamental prerequisite for evolution by natural selection
- **genetic variation**: variation in alleles of genes that occurs both within and among populations

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20.9.2: Genetic Drift

Learning Objectives

- Distinguish between selection and genetic drift

Genetic Drift vs. Natural Selection

Genetic drift is the converse of natural selection. The theory of natural selection maintains that some individuals in a population have traits that enable to survive and produce more offspring, while other individuals have traits that are detrimental and may cause them to die before reproducing. Over successive generation, these selection pressures can change the gene pool and the traits within the population. For example, a big, powerful male gorilla will mate with more females than a small, weak male and therefore more of his genes will be passed on to the next generation. His offspring may continue to dominate the troop and pass on their genes as well. Over time, the selection pressure will cause the allele frequencies in the gorilla population to shift toward large, strong males.

Unlike natural selection, genetic drift describes the effect of chance on populations in the absence of positive or negative selection pressure. Through random sampling, or the survival or and reproduction of a random sample of individuals within a population, allele frequencies within a population may change. Rather than a male gorilla producing more offspring because he is stronger, he may be the only male available when a female is ready to mate. His genes are passed on to future generation because of chance, not because he was the biggest or the strongest. Genetic drift is the shift of alleles within a population due to chance events that cause random samples of the population to reproduce or not.

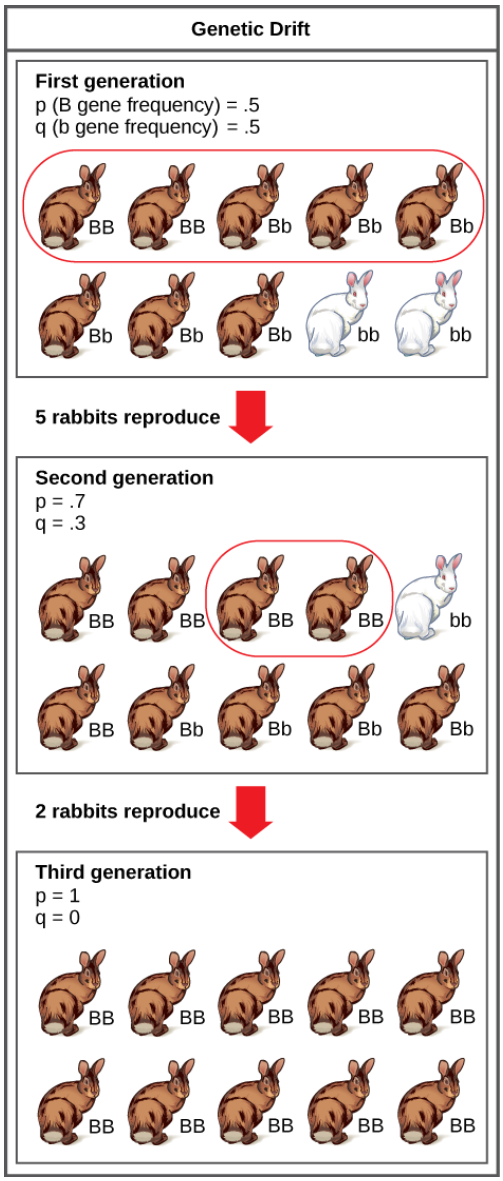


Figure 20.9.2.1: Effect of genetic drift: Genetic drift in a population can lead to the elimination of an allele from that population by chance. In this example, the brown coat color allele (B) is dominant over the white coat color allele (b). In the first generation, the two alleles occur with equal frequency in the population, resulting in p and q values of.5. Only half of the individuals reproduce, resulting in a second generation with p and q values of.7 and.3, respectively. Only two individuals in the second generation reproduce and, by chance, these individuals are homozygous dominant for brown coat color. As a result, in the third generation the recessive b allele is lost.

Small populations are more susceptible to the forces of genetic drift. Large populations, on the other hand, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before leaving any offspring to the next generation, all of its genes (1/10 of the population's gene pool) will be suddenly lost. In a population of 100, that individual represents only 1 percent of the overall gene pool; therefore, genetic drift has much less impact on the larger population's genetic structure.

The Bottleneck Effect

Genetic drift can also be magnified by natural events, such as a natural disaster that kills a large portion of the population at random. The bottleneck effect occurs when only a few individuals survive and reduces variation in the gene pool of a population. The genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.

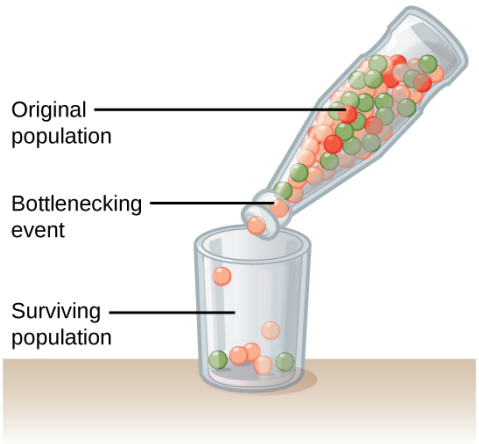


Figure 20.9.2.1: Effect of a bottleneck on a population: A chance event or catastrophe can reduce the genetic variability within a population.

The Founder Effect

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location or if a population gets divided by a physical barrier of some kind. In this situation, it is improbable that those individuals are representative of the entire population, which results in the founder effect. The founder effect occurs when the genetic structure changes to match that of the new population's founding fathers and mothers.

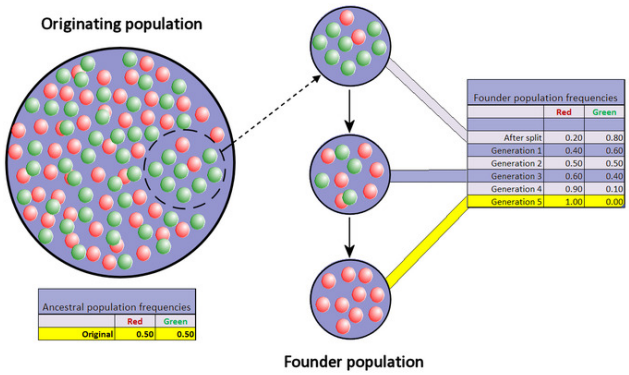


Figure 20.9.2.1: The Founder Effect: The founder effect occurs when a portion of the population (i.e. "founders") separates from the old population to start a new population with different allele frequencies.

The founder effect is believed to have been a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners, but rare in most other populations. This was probably due to the fact that a higher-than-normal proportion of the founding colonists carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause blood marrow and congenital abnormalities, even cancer.

Drift and fixation

The Hardy–Weinberg principle states that within sufficiently large populations, the allele frequencies remain constant from one generation to the next unless the equilibrium is disturbed by migration, genetic mutation, or selection.

Because the random sampling can remove, but not replace, an allele, and because random declines or increases in allele frequency influence expected allele distributions for the next generation, genetic drift drives a population towards genetic uniformity over time. When an allele reaches a frequency of 1 (100%) it is said to be "fixed" in the population and when an allele reaches a frequency of 0 (0%) it is lost. Once an allele becomes fixed, genetic drift for that allele comes to a halt, and the allele frequency cannot change unless a new allele is introduced in the population via mutation or gene flow. Thus even while genetic drift is a random, directionless process, it acts to eliminate genetic variation over time.

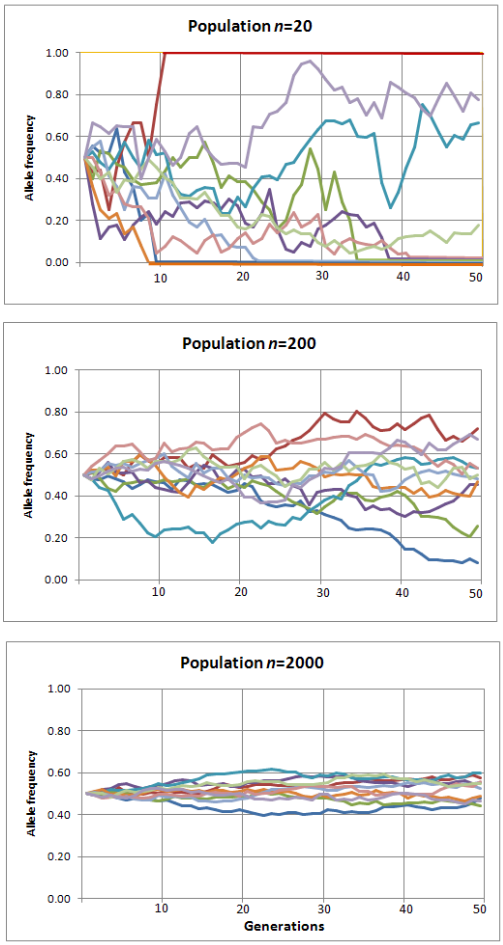


Figure 20.9.2.1: Genetic drift over time: Ten simulations of random genetic drift of a single given allele with an initial frequency distribution 0.5 measured over the course of 50 generations, repeated in three reproductively synchronous populations of different sizes. In these simulations, alleles drift to loss or fixation (frequency of 0.0 or 1.0) only in the smallest population.Effect of population size on genetic drift: Ten simulations each of random change in the frequency distribution of a single hypothetical allele over 50 generations for different sized populations; first population size n=20, second population n=200, and third population n=2000.

Key Points

- Genetic drift is the change in the frequency of an allele in a population due to random sampling and the random events that influence the survival and reproduction of those individuals.
- The bottleneck effect occurs when a natural disaster or similar event randomly kills a large portion (i.e. random sample) of the population, leaving survivors that have allele frequencies that were very different from the previous population.
- The founder effect occurs when a portion of the population (i.e. “founders”) separates from the old population to start a new population with different allele frequencies.
- Small populations are more susceptible genetic drift than large populations, whose larger numbers can buffer the population against chance events.

Key Terms

- **genetic drift**: an overall shift of allele distribution in an isolated population, due to random sampling
- **founder effect**: a decrease in genetic variation that occurs when an entire population descends from a small number of founders
- **random sampling**: a subset of individuals (a sample) chosen from a larger set (a population) by chance

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20.9.3: Gene Flow and Mutation

Learning Objectives

- Explain how gene flow and mutations can influence the allele frequencies of a population

Gene Flow

An important evolutionary force is gene flow: the flow of alleles in and out of a population due to the migration of individuals or gametes. While some populations are fairly stable, others experience more movement and fluctuation. Many plants, for example, send their pollen by wind, insects, or birds to pollinate other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, can receive new genetic variation as developing males leave their mothers to form new prides with genetically-unrelated females. This variable flow of individuals in and out of the group not only changes the gene structure of the population, but can also introduce new genetic variation to populations in different geological locations and habitats.

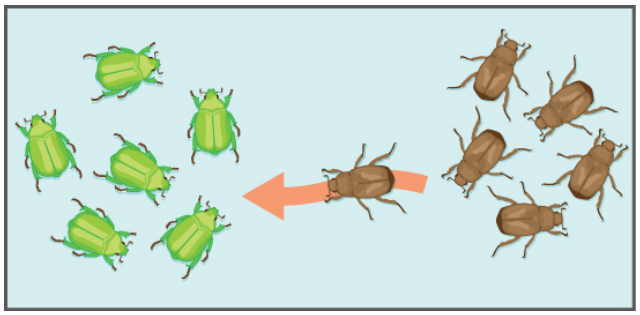


Figure **20.9.3.1**: Gene flow: Gene flow can occur when an individual travels from one geographic location to another.

Maintained gene flow between two populations can also lead to a combination of the two gene pools, reducing the genetic variation between the two groups. Gene flow strongly acts against speciation, by recombining the gene pools of the groups, and thus, repairing the developing differences in genetic variation that would have led to full speciation and creation of daughter species.

For example, if a species of grass grows on both sides of a highway, pollen is likely to be transported from one side to the other and vice versa. If this pollen is able to fertilize the plant where it ends up and produce viable offspring, then the alleles in the pollen have effectively linked the population on one side of the highway with the other.

Mutation

Mutations are changes to an organism's DNA and are an important driver of diversity in populations. Species evolve because of the accumulation of mutations that occur over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance. Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection. Others are beneficial and will spread through the population. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. Some mutations have no effect on an organism and can linger, unaffected by natural selection, in the genome while others can have a dramatic effect on a gene and the resulting phenotype.



Figure **20.9.3.1**: Mutation in a garden rose: A mutation has caused this garden moss rose to produce flowers of different colors. This mutation has introduce a new allele into the population that increases genetic variation and may be passed on to the next generation.

Key Points

- Plant populations experience gene flow by spreading their pollen long distances.
- Animals experience gene flow when individuals leave a family group or herd to join other populations.
- The flow of individuals in and out of a population introduces new alleles and increases genetic variation within that population.
- Mutations are changes to an organism's DNA that create diversity within a population by introducing new alleles.
- Some mutations are harmful and are quickly eliminated from the population by natural selection; harmful mutations prevent organisms from reaching sexual maturity and reproducing.
- Other mutations are beneficial and can increase in a population if they help organisms reach sexual maturity and reproduce.

Key Terms

- **gene flow**: the transfer of alleles or genes from one population to another
- **mutation**: any heritable change of the base-pair sequence of genetic material

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20.9.4: Nonrandom Mating and Environmental Variance

Learning Objectives

- Explain how environmental variance and nonrandom mating can change gene frequencies in a population

Nonrandom Mating

If individuals nonrandomly mate with other individuals in the population, i.e. they choose their mate, choices can drive evolution within a population. There are many reasons nonrandom mating occurs. One reason is simple mate choice or sexual selection; for example, female peahens may prefer peacocks with bigger, brighter tails. Traits that lead to more matings for an individual lead to more offspring and through natural selection, eventually lead to a higher frequency of that trait in the population. One common form of mate choice, called positive assortative mating, is an individual's preference to mate with partners that are phenotypically similar to themselves.



Figure **20.9.4.1**: Assortative mating in the American Robin: The American Robin may practice assortative mating on plumage color, a melanin based trait, and mate with other robins who have the most similar shade of color. However, there may also be some sexual selection for more vibrant plumage which indicates health and reproductive performance.

Another cause of nonrandom mating is physical location. This is especially true in large populations spread over large geographic distances where not all individuals will have equal access to one another. Some might be miles apart through woods or over rough terrain, while others might live immediately nearby.

Environmental Variance

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment. A beachgoer is likely to have darker skin than a city dweller, for example, due to regular exposure to the sun, an environmental factor. Some major characteristics, such as gender, are determined by the environment for some species. For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a different temperature range.



Figure 20.9.4.1: Temperature-dependent sex determination: The sex of the American alligator (Alligator mississippiensis) is determined by the temperature at which the eggs are incubated. Eggs incubated at 30 degrees C produce females, and eggs incubated at 33 degrees C produce males.

Geographic separation between populations can lead to differences in the phenotypic variation between those populations. Such geographical variation is seen between most populations and can be significant. One type of geographic variation, called a cline, can be seen as populations of a given species vary gradually across an ecological gradient.

image

Geographic variation in moose: This graph shows geographical variation in moose; body mass increase positively with latitude. Bergmann's Rule is an ecologic principle which states that as latitude increases the body mass of a particular species increases. The data are taken from a Swedish study investigating the size of moose as latitude increases as shows the positive relationship between the two, supporting Bergmann's Rule.

Species of warm-blooded animals, for example, tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a latitudinal cline. Alternatively, flowering plants tend to bloom at different times depending on where they are along the slope of a mountain, known as an altitudinal cline.

If there is gene flow between the populations, the individuals will likely show gradual differences in phenotype along the cline. Restricted gene flow, on the other hand, can lead to abrupt differences, even speciation.

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Key Points

- Nonrandom mating can occur when individuals prefer mates with particular superior physical characteristics or by the preference of individuals to mate with individuals similar to themselves.
- Nonrandom mating can also occur when mates are chosen based on physical accessibility; that is, the availability of some mates over others.
- Phenotypes of individuals can also be influenced by the environment in which they live, such as temperature, terrain, or other factors.
- A cline occurs when populations of a given species vary gradually across an ecological gradient.

Key Terms

- **cline**: a gradation in a character or phenotype within a species or other group
- **sexual selection**: a mode of natural selection in which some individuals out-reproduce others of a population because they are better at securing mates

- **assortative mating**: between males and females of a species, the mutual attraction or selection, for reproductive purposes, of individuals with similar characteristics

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20.10: The Limits of Selection

Learning Objectives

- Explain the limitations encountered in natural selection

No Perfect Organism

Natural selection is a driving force in evolution and can generate populations that are adapted to survive and successfully reproduce in their environments. However, natural selection cannot produce the perfect organism. Natural selection can only select on existing variation in the population; it cannot create anything from scratch. Therefore, the process of evolution is limited by a population's existing genetic variance, the physical proximity of alleles, non-beneficial intermediate morphs in a polymorphic population, and non-adaptive evolutionary forces.

Natural Selection Acts on Individuals, not Alleles

Natural selection is also limited because it acts on the phenotypes of individuals, not alleles. Some alleles may be more likely to be passed on with alleles that confer a beneficial phenotype because of their physical proximity on the chromosomes. Alleles that are carried together are in linkage disequilibrium. When a neutral allele is linked to beneficial allele, consequently meaning that it has a selective advantage, the allele frequency can increase in the population through genetic hitchhiking (also called genetic draft).

Any given individual may carry some beneficial alleles and some unfavorable alleles. Natural selection acts on the net effect of these alleles and corresponding fitness of the phenotype. As a result, good alleles can be lost if they are carried by individuals that also have several overwhelmingly bad alleles; similarly, bad alleles can be kept if they are carried by individuals that have enough good alleles to result in an overall fitness benefit.

Polymorphism

Furthermore, natural selection can be constrained by the relationships between different polymorphisms. One morph may confer a higher fitness than another, but may not increase in frequency because the intermediate morph is detrimental.



Figure **20.10.1**:

Polymorphism in the grove snail: Color and pattern morphs of the grove snail, Cepaea nemoralis.The polymorphism, when two or more different genotypes exist within a given species, in grove snails seems to have several causes, including predation by thrushes.

For example, consider a hypothetical population of mice that live in the desert. Some are light-colored and blend in with the sand, while others are dark and blend in with the patches of black rock. The dark-colored mice may be more fit than the light-colored mice, and according to the principles of natural selection the frequency of light-colored mice is expected to decrease over time. However, the intermediate phenotype of a medium-colored coat is very bad for the mice: these cannot blend in with either the sand or the rock and will more vulnerable to predators. As a result, the frequency of a dark-colored mice would not increase because the intermediate morphs are less fit than either light-colored or dark-colored mice. This a common example of disruptive selection.

Not all Evolution is Adaptive

Finally, it is important to understand that not all evolution is adaptive. While natural selection selects the fittest individuals and often results in a more fit population overall, other forces of evolution, including genetic drift and gene flow, often do the opposite by introducing deleterious alleles to the population's gene pool. Evolution has no purpose. It is not changing a population into a preconceived ideal. It is simply the sum of various forces and their influence on the genetic and phenotypic variance of a population.

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Key Points

- Natural selection is limited by a population ‘s existing genetic variation.
- Natural selection is limited through linkage disequilibrium, where alleles that are physically proximate on the chromosome are passed on together at greater frequencies.
- In a polymorphic population, two phenotypes may be maintained in the population despite the higher fitness of one morph if the intermediate phenotype is detrimental.
- Evolution is not purposefully adaptive; it is the result of various selection forces working together to influence genetic and phenotypical variances within a population.

Key Terms

- **linkage disequilibrium**: a non-random association of two or more alleles at two or more loci; normally caused by an interaction between genes
- **genetic hitchhiking**: changes in the frequency of an allele because of linkage with a positively or negatively selected allele at another locus
- **polymorphism**: the regular existence of two or more different genotypes within a given species or population

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CHAPTER OVERVIEW

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21.1: The Beaks of Darwin's Finches- Evidence of Natural Selection

The theory of evolution by natural selection describes a mechanism for species change over time. That species change had been suggested and debated well before Darwin. The view that species were static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks that expressed evolutionary ideas.

In the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc, Comte de Buffon and even by Charles Darwin's grandfather, Erasmus Darwin. During this time, it was also accepted that there were extinct species. At the same time, James Hutton, the Scottish naturalist, proposed that geological change occurred gradually by the accumulation of small changes from processes (over long periods of time) just like those happening today. This contrasted with the predominant view that the geology of the planet was a consequence of catastrophic events occurring during a relatively brief past. Hutton's view was later popularized by the geologist Charles Lyell in the nineteenth century. Lyell became a friend to Darwin and his ideas were very influential on Darwin's thinking. Lyell argued that the greater age of Earth gave more time for gradual change in species, and the process provided an analogy for gradual change in species.

In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a mechanism for evolutionary change that is now referred to as inheritance of acquired characteristics. In Lamarck's theory, modifications in an individual caused by its environment, or the use or disuse of a structure during its lifetime, could be inherited by its offspring and, thus, bring about change in a species. While this mechanism for evolutionary change as described by Lamarck was discredited, Lamarck's ideas were an important influence on evolutionary thought. The inscription on the statue of Lamarck that stands at the gates of the Jardin des Plantes in Paris describes him as the "founder of the doctrine of evolution."

Charles Darwin and Natural Selection

The actual mechanism for evolution was independently conceived of and described by two naturalists, Charles Darwin and Alfred Russell Wallace, in the mid-nineteenth century. Importantly, each spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world on *H.M.S. Beagle*, visiting South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, like Wallace's later journeys in the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands (west of Ecuador). On these islands, Darwin observed species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species that each had a unique beak shape (Figure **21.1.1**). He observed both that these finches closely resembled another finch species on the mainland of South America and that the group of species in the Galápagos formed a graded series of beak sizes and shapes, with very small differences between the most similar. Darwin imagined that the island species might be all species modified from one original mainland species. In 1860, he wrote, "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."[1]

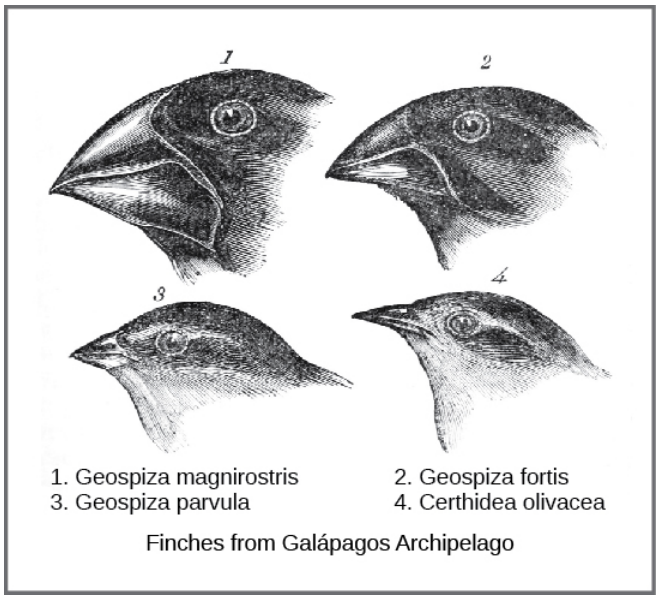


Figure 21.1.1: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources. This illustration shows the beak shapes for four species of ground finch: 1. Geospiza magnirostris (the large ground finch), 2. G. fortis (the medium ground finch), 3. G. parvula (the small tree finch), and 4. Certhidea olivacea (the green-warbler finch).

Wallace and Darwin both observed similar patterns in other organisms and independently conceived a mechanism to explain how and why such changes could take place. Darwin called this mechanism natural selection. Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, the characteristics of organisms are inherited, or passed from parent to offspring. Second, more offspring are produced than are able to survive; in other words, resources for survival and reproduction are limited. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is a competition for those resources in each generation. Both Darwin and Wallace's understanding of this principle came from reading an essay by the economist Thomas Malthus, who discussed this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Out of these three principles, Darwin and Wallace reasoned that offspring with inherited characteristics that allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called "descent with modification."

Papers by Darwin and Wallace (Figure **21.1.2**) presenting the idea of natural selection were read together in 1858 before the Linnaean Society in London. The following year Darwin's book, *On the Origin of Species*, was published, which outlined in considerable detail his arguments for evolution by natural selection.



(a) (b)

Figure 21.1.2: (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Demonstrations of evolution by natural selection can be time consuming. One of the best demonstrations has been in the very birds that helped to inspire the theory, the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of the operation of natural selection. The Grants found changes from one generation to the next in the beak shapes of the medium ground finches on the Galápagos island of Daphne Major. The medium ground finch feeds on seeds. The birds have inherited variation in the bill shape with some individuals having wide, deep bills and others having thinner bills. Large-billed birds feed more efficiently on large, hard seeds, whereas smaller billed birds feed more efficiently on small, soft seeds. During 1977, a drought period altered vegetation on the island. After this period, the number of seeds declined dramatically: the decline in small, soft seeds was greater than the decline in large, hard seeds. The large-billed birds were able to survive better than the small-billed birds the following year. The year following the drought when the Grants measured beak sizes in the much-reduced population, they found that the average bill size was larger (Figure **21.1.3**). This was clear evidence for natural selection (differences in survival) of bill size caused by the availability of seeds. The Grants had studied the inheritance of bill sizes and knew that the surviving large-billed birds would tend to produce offspring with larger bills, so the selection would lead to evolution of bill size. Subsequent studies by the Grants have demonstrated selection on and evolution of bill size in this species in response to changing conditions on the island. The evolution has occurred both to larger bills, as in this case, and to smaller bills when large seeds became rare.

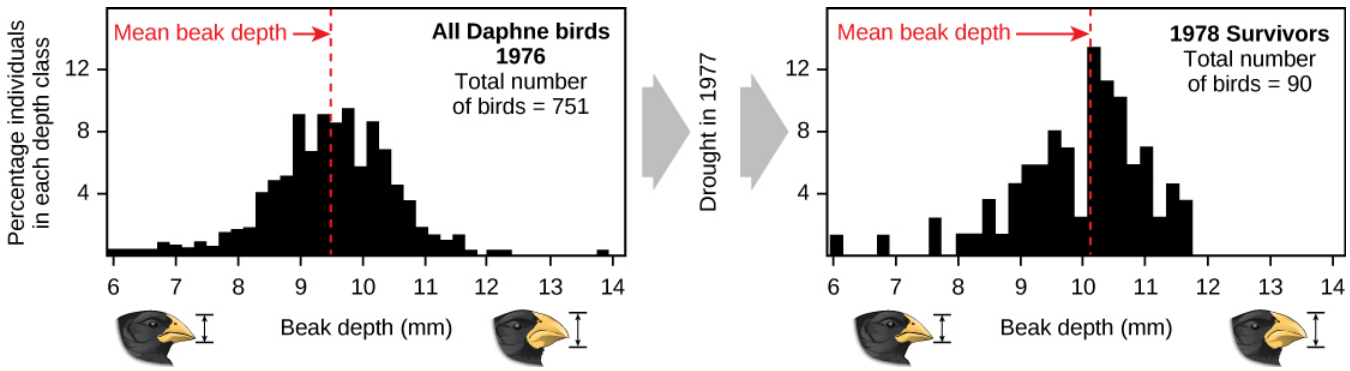


Figure 21.1.3: A drought on the Galápagos island of Daphne Major in 1977 reduced the number of small seeds available to finches, causing many of the small-beaked finches to die. This caused an increase in the finches' average beak size between 1976 and 1978.

Variation and Adaptation

Natural selection can only take place if there is variation, or differences, among individuals in a population. Importantly, these differences must have some genetic basis; otherwise, selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons, such as an individual being taller because of better nutrition rather than different genes.

Genetic diversity in a population comes from two main sources: mutation and sexual reproduction. Mutation, a change in DNA, is the ultimate source of new alleles or new genetic variation in any population. An individual that has a mutated gene might have a different trait than other individuals in the population. However, this is not always the case. A mutation can have one of three outcomes on the organisms' appearance (or phenotype):

- A mutation may affect the phenotype of the organism in a way that gives it reduced fitness—lower likelihood of survival, resulting in fewer offspring.
- A mutation may produce a phenotype with a beneficial effect on fitness.
- Many mutations, called neutral mutations, will have no effect on fitness.

Mutations may also have a whole range of effect sizes on the fitness of the organism that expresses them in their phenotype, from a small effect to a great effect. Sexual reproduction and crossing over in meiosis also lead to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce unique genotypes and, thus, phenotypes in each of the offspring.

A heritable trait that aids the survival and reproduction of an organism in its present environment is called an adaptation. An adaptation is a "match" of the organism to the environment. Adaptation to an environment comes about when a change in the range of genetic variation occurs over time that increases or maintains the match of the population with its environment. The variations in finch beaks shifted from generation to generation providing adaptation to food availability.

Whether or not a trait is favorable depends on the environment at the time. The same traits do not always have the same relative benefit or disadvantage because environmental conditions can change. For example, finches with large bills were benefited in one climate, while small bills were a disadvantage; in a different climate, the relationship reversed.

Patterns of Evolution

The evolution of species has resulted in enormous variation in form and function. When two species evolve in different directions from a common point, it is called divergent evolution. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants, which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments, and adaptation to different kinds of pollinators (Figure **21.1.4**).



(a) (b)

Figure 21.1.4: Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star and (b) purple coneflower vary in appearance, yet both share a similar basic morphology. (credit a, b: modification of work by Cory Zanker)

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. The wings of bats and insects, however, evolved from very different original structures. When similar structures arise through evolution independently in different

species it is called convergent evolution. The wings of bats and insects are called analogous structures; they are similar in function and appearance, but do not share an origin in a common ancestor. Instead they evolved independently in the two lineages. The wings of a hummingbird and an ostrich are homologous structures, meaning they share similarities (despite their differences resulting from evolutionary divergence). The wings of hummingbirds and ostriches did not evolve independently in the hummingbird lineage and the ostrich lineage—they descended from a common ancestor with wings.

The Modern Synthesis

The mechanisms of inheritance, genetics, were not understood at the time Darwin and Wallace were developing their idea of natural selection. This lack of understanding was a stumbling block to comprehending many aspects of evolution. In fact, blending inheritance was the predominant (and incorrect) genetic theory of the time, which made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the genetics work by Austrian monk Gregor Mendel, which was published in 1866, not long after publication of *On the Origin of Species*. Mendel's work was rediscovered in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. But over the next few decades genetics and evolution were integrated in what became known as the modern synthesis—the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s and is generally accepted today. In sum, the modern synthesis describes how evolutionary pressures, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects this gradual change of a population over time, called microevolution, with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called macroevolution.

Population Genetics

Recall that a gene for a particular character may have several variants, or alleles, that code for different traits associated with that character. For example, in the ABO blood type system in humans, three alleles determine the particular blood-type protein on the surface of red blood cells. Each individual in a population of diploid organisms can only carry two alleles for a particular gene, but more than two may be present in the individuals that make up the population. Mendel followed alleles as they were inherited from parent to offspring. In the early twentieth century, biologists began to study what happens to all the alleles in a population in a field of study known as population genetics.

Until now, we have defined evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetic terms, evolution is defined as a change in the frequency of an allele in a population. Using the ABO system as an example, the frequency of one of the alleles, I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan found a frequency of I^A to be 26.1 percent.[2] The I^B, I^0 alleles made up 13.4 percent and 60.5 percent of the alleles respectively, and all of the frequencies add up to 100 percent. A change in this frequency over time would constitute evolution in the population.

There are several ways the allele frequencies of a population can change. One of those ways is natural selection. If a given allele confers a phenotype that allows an individual to have more offspring that survive and reproduce, that allele, by virtue of being inherited by those offspring, will be in greater frequency in the next generation. Since allele frequencies always add up to 100 percent, an increase in the frequency of one allele always means a corresponding decrease in one or more of the other alleles. Highly beneficial alleles may, over a very few generations, become "fixed" in this way, meaning that every individual of the population will carry the allele. Similarly, detrimental alleles may be swiftly eliminated from the gene pool, the sum of all the alleles in a population. Part of the study of population genetics is tracking how selective forces change the allele frequencies in a population over time, which can give scientists clues regarding the selective forces that may be operating on a given population. The studies of changes in wing coloration in the peppered moth from mottled white to dark in response to soot-covered tree trunks and then back to mottled white when factories stopped producing so much soot is a classic example of studying evolution in natural populations (Figure **21.1.5**).

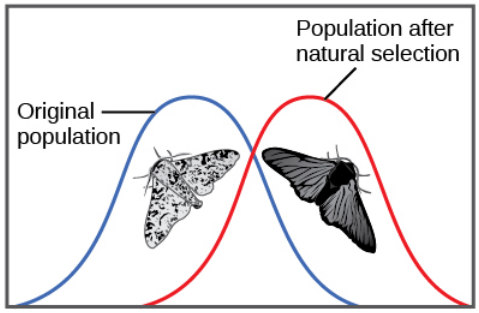


Figure 21.1.5: As the Industrial Revolution caused trees to darken from soot, darker colored peppered moths were better camouflaged than the lighter colored ones, which caused there to be more of the darker colored moths in the population.

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg independently provided an explanation for a somewhat counterintuitive concept. Hardy's original explanation was in response to a misunderstanding as to why a "dominant" allele, one that masks a recessive allele, should not increase in frequency in a population until it eliminated all the other alleles. The question resulted from a common confusion about what "dominant" means, but it forced Hardy, who was not even a biologist, to point out that if there are no factors that affect an allele frequency those frequencies will remain constant from one generation to the next. This principle is now known as the Hardy-Weinberg equilibrium. The theory states that a population's allele and genotype frequencies are inherently stable—unless some kind of evolutionary force is acting on the population, the population would carry the same alleles in the same proportions generation after generation. Individuals would, as a whole, look essentially the same and this would be unrelated to whether the alleles were dominant or recessive. The four most important evolutionary forces, which will disrupt the equilibrium, are natural selection, mutation, genetic drift, and migration into or out of a population. A fifth factor, nonrandom mating, will also disrupt the Hardy-Weinberg equilibrium but only by shifting genotype frequencies, not allele frequencies. In nonrandom mating, individuals are more likely to mate with like individuals (or unlike individuals) rather than at random. Since nonrandom mating does not change allele frequencies, it does not cause evolution directly. Natural selection has been described. Mutation creates one allele out of another one and changes an allele's frequency by a small, but continuous amount each generation. Each allele is generated by a low, constant mutation rate that will slowly increase the allele's frequency in a population if no other forces act on the allele. If natural selection acts against the allele, it will be removed from the population at a low rate leading to a frequency that results from a balance between selection and mutation. This is one reason that genetic diseases remain in the human population at very low frequencies. If the allele is favored by selection, it will increase in frequency. Genetic drift causes random changes in allele frequencies when populations are small. Genetic drift can often be important in evolution, as discussed in the next section. Finally, if two populations of a species have different allele frequencies, migration of individuals between them will cause frequency changes in both populations. As it happens, there is no population in which one or more of these processes are not operating, so populations are always evolving, and the Hardy-Weinberg equilibrium will never be exactly observed. However, the Hardy-Weinberg principle gives scientists a baseline expectation for allele frequencies in a non-evolving population to which they can compare evolving populations and thereby infer what evolutionary forces might be at play. The population is evolving if the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg principle.

Darwin identified a special case of natural selection that he called sexual selection. Sexual selection affects an individual's ability to mate and thus produce offspring, and it leads to the evolution of dramatic traits that often appear maladaptive in terms of survival but persist because they give their owners greater reproductive success. Sexual selection occurs in two ways: through male–male competition for mates and through female selection of mates. Male–male competition takes the form of conflicts between males, which are often ritualized, but may also pose significant threats to a male's survival. Sometimes the competition is for territory, with females more likely to mate with males with higher quality territories. Female choice occurs when females choose a male based on a particular trait, such as feather colors, the performance of a mating dance, or the building of an elaborate structure. In some cases male–male competition and female choice combine in the mating process. In each of these cases, the traits selected for, such as fighting ability or feather color and length, become enhanced in the males. In general, it is thought that sexual selection can proceed to a point at which natural selection against a character's further enhancement prevents its further evolution because it negatively impacts the male's ability to survive. For example, colorful feathers or an elaborate display make the male more obvious to predators.

Summary

Evolution by natural selection arises from three conditions: individuals within a species vary, some of those variations are heritable, and organisms have more offspring than resources can support. The consequence is that individuals with relatively advantageous variations will be more likely to survive and have higher reproductive rates than those individuals with different traits. The advantageous traits will be passed on to offspring in greater proportion. Thus, the trait will have higher representation in the next and subsequent generations leading to genetic change in the population.

The modern synthesis of evolutionary theory grew out of the reconciliation of Darwin's, Wallace's, and Mendel's thoughts on evolution and heredity. Population genetics is a theoretical framework for describing evolutionary change in populations through the change in allele frequencies. Population genetics defines evolution as a change in allele frequency over generations. In the absence of evolutionary forces allele frequencies will not change in a population; this is known as Hardy-Weinberg equilibrium principle. However, in all populations, mutation, natural selection, genetic drift, and migration act to change allele frequencies.

Footnotes

1. 1 Charles Darwin, *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle Round the World, under the Command of Capt. Fitz Roy, R.N*, 2nd. ed. (London: John Murray, 1860), http://www.archive.org/details/journalofresea00darw.
2. 2 Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, "Allele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population," *Journal of Medical Sciences* 7 (2007): 51-58, doi:10.3923/jms.2007.51.58

Glossary

adaptation
a heritable trait or behavior in an organism that aids in its survival in its present environment

analogous structure
a structure that is similar because of evolution in response to similar selection pressures resulting in convergent evolution, not similar because of descent from a common ancestor

convergent evolution
an evolution that results in similar forms on different species

divergent evolution
an evolution that results in different forms in two species with a common ancestor

gene pool
all of the alleles carried by all of the individuals in the population

genetic drift
the effect of chance on a population's gene pool

homologous structure
a structure that is similar because of descent from a common ancestor

inheritance of acquired characteristics
a phrase that describes the mechanism of evolution proposed by Lamarck in which traits acquired by individuals through use or disuse could be passed on to their offspring thus leading to evolutionary change in the population

macroevolution
a broader scale of evolutionary changes seen over paleontological time

microevolution
the changes in a population's genetic structure (i.e., allele frequency)

migration

the movement of individuals of a population to a new location; in population genetics it refers to the movement of individuals and their alleles from one population to another, potentially changing allele frequencies in both the old and the new population

modern synthesis

the overarching evolutionary paradigm that took shape by the 1940s and is generally accepted today

natural selection

the greater relative survival and reproduction of individuals in a population that have favorable heritable traits, leading to evolutionary change

population genetics

the study of how selective forces change the allele frequencies in a population over time

variation

the variety of alleles in a population

Contributors and Attributions

- Samantha Fowler (Clayton State University), Rebecca Roush (Sandhills Community College), James Wise (Hampton University). Original content by OpenStax (CC BY 4.0; Access for free at https://cnx.org/contents/b3c1e1d2-83...4-e119a8aafbdd).

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21.2: Speciation

One of the best definition os species is that of the evolutionary biologist Ernst Mayr: "A species is an actually or potentially interbreeding population that does not interbreed with other such populations when there is opportunity to do so." However, sometimes breeding may take place (as it can between a horse and a donkey) but if so, the offspring are not so fertile and/or well adapted as the parents (the mule produced is sterile).

Allopatric Speciation: the Role of Isolation in Speciation

The formation of two or more species often (some workers think always!) requires geographical isolation of subpopulations of the species. Only then can natural selection or perhaps genetic drift produce distinctive gene pools. It is no accident that the various **races** (or "**subspecies**") of animals almost never occupy the same territory. Their distribution is **allopatric** ("other country").

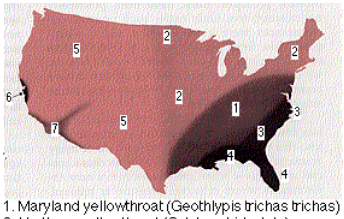


Figure 18.2.1 Yellowthroat

The seven distinct subspecies or races of the yellowthroat ***Geothlypis trichas*** (a warbler) in the continental U.S. would soon merge into a single homogeneous population if they occupied the same territory and bred with one another.

Darwin's Finches

As a young man of 26, Charles Darwin visited the Galapagos Islands off the coast of Ecuador. Among the animals he studied were what appeared to be 13 species* of finches found nowhere else on earth.

- Some have stout beaks for eating seeds of one size or another (#2, #3, #6).
- Others have beaks adapted for eating insects or nectar.
- One (#7) has a beak like a woodpecker's. It uses it to drill holes in wood, but lacking the long tongue of a true woodpecker, it uses a cactus spine held in its beak to dig the insect out.
- One (#12) looks more like a warbler than a finch, but its eggs, nest, and courtship behavior is like that of the other finches.

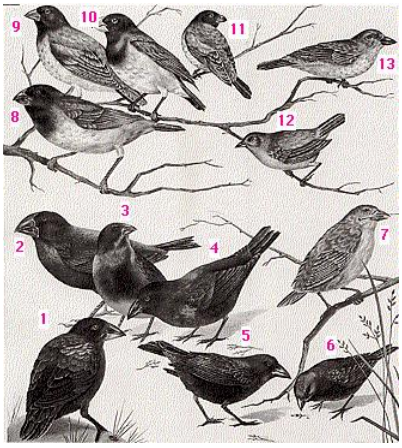


Figure 18.2.2 Darwin's finches

Darwin's finches. The finches numbered 1–7 are ground finches. They seek their food on the ground or in low shrubs. Those numbered 8–13 are tree finches. They live primarily on insects.

1. Large cactus finch (*Geospiza conirostris*)
2. Large ground finch (*Geospiza magnirostris*)
3. Medium ground finch (***Geospiza fortis***)
4. Cactus finch (*Geospiza scandens*)
5. Sharp-beaked ground finch (*Geospiza difficilis*)
6. Small ground finch (*Geospiza fuliginosa*)
7. Woodpecker finch (*Cactospiza pallida*)
8. Vegetarian tree finch (*Platyspiza crassirostris*)
9. Medium tree finch (***Camarhynchus pauper***)
10. Large tree finch (***Camarhynchus psittacula***)
11. Small tree finch (*Camarhynchus parvulus*)
12. Warbler finch (*Certhidia olivacea*)
13. Mangrove finch (*Cactospiza heliobates*)

(From BSCS, Biological Science: Molecules to Man, Houghton Mifflin Co., 1963)

* Genetic analysis provides evidence that:

- There are actually two species of warbler finch — *Certhidia olivacea* now called the green warbler finch and *Certhidia fusca*, the gray warbler finch.
- The various populations of *Geospiza difficilis* found on the different islands belong to one or another of three clades so genetically distinct that they deserve full species status.

Whether the number is 13 or 17, since Darwin's time, these birds have provided a case study of how a single species reaching the Galapagos from Central or South America could - over a few million years - give rise to the various species that live there today. Several factors have been identified that may contribute to speciation.

Ecological opportunity

When the ancestor of Darwin's finches reached the Galapagos, it found **no predators** (There were no mammals and few reptiles on the islands.) and **few, if any, competitors**. There were only a handful of other types of songbirds. In fact, if true warblers or woodpeckers had been present, their efficiency at exploiting their niches would surely have prevented the evolution of warblerlike and woodpeckerlike finches.

Geographical Isolation (allopatry)

The proximity of the various islands has permitted enough migration of Darwin's finches between them to enable distinct island populations to arise. But the distances between the islands is great enough to limit interbreeding between populations on different islands. This has made possible the formation of distinctive **subspecies** (= **races**) on the various islands.

The importance of geographical isolation is illuminated by a single, fourteenth, species of Darwin's finches that lives on **Cocos Island**, some 500 miles (800 km) to the northeast of the Galapagos. The first immigrants there must also have found relaxed selection pressures with few predators or competitors. How different the outcome, though. Where one immigrant species gave rise to at least 13 on the scattered Galapagos Islands, no such divergence has occurred on the single, isolated Cocos Island.

Evolutionary Change

In isolation, changes in the gene pool can occur through some combination of natural selection, genetic drift, and founder effect. These factors may produce distinct subpopulations on the different islands. So long as they remain separate (**allopatric**) we consider them **races** or **subspecies**. In fact, they might not be able to interbreed with other races but so long as we don't know, we assume that they could.

How much genetic change is needed to create a new species? Perhaps not as much as you might think. For example, changes at one or just a few gene loci might do the trick. For example, a single mutation altering flower color or petal shape could immediately prevent cross-pollination between the new and the parental types (a form of prezygotic isolating mechanism).

Reunion

The question of their status - subspecies or true species - is resolved if they ever do come to occupy the same territory again (become **sympatric**). If successful interbreeding occurs, the differences will gradually disappear, and a single population will be formed again. Speciation will not have occurred. If, on the other hand, two subspecies reunite but fail to resume breeding, speciation has occurred and they have become separate species.

An example: The medium tree finch ***Camarhynchus pauper*** is found only on **Floreana Island**. Its close relative, the large tree finch, ***Camarhynchus psittacula***, is found on all the central islands including Floreana. Were it not for its presence on Floreana, both forms would be considered subspecies of the same species. Because they do coexist and maintain their separate identity on Floreana, we know that speciation has occurred.

Isolating Mechanisms

What might keep two subpopulations from interbreeding when reunited geographically? There are several mechanisms.

Prezygotic Isolating Mechanisms act before fertilization occurs. Sexual selection - a failure to elicit mating behavior. On Floreana, *Camarhynchus psittacula* has a longer beak than *Camarhynchus pauper*, and the research teams led by Peter and Rosemary Grant have demonstrated that beak size is an important criterion by which Darwin's finches choose their mates. Two subpopulations may occupy different habitats in the same area and thus fail to meet at breeding time. In plants, a shift in the time of flowering can prevent pollination between the two subpopulations. Structural differences in the sex organs may become an isolating mechanism. The sperm may fail to reach or fuse with the egg.

Postzygotic Isolating Mechanisms act even if fertilization does occur. Even if a zygote is formed, genetic differences may have become so great that the resulting hybrids are less viable or less fertile than the parental types. The sterile mule produced by mating a horse with a donkey is an example. Sterility in the males produced by hybridization is more common than in females. In fact, it is the most common postzygotic isolating mechanism. When ***Drosophila melanogaster*** attempts to mate with its relative ***Drosophila simulans***, no viable males are even produced. Mutations in a single gene (encoding a component of the nuclear pore complex) are responsible.

Reinforcement

When two species that have separated in allopatry become reunited, their prezygotic and postzygotic isolating mechanisms may become more stringent than those between the same species existing apart from each other. This phenomenon is called **reinforcement**. It arises from natural selection working to favor individuals that avoid interspecific matings, which would produce less-fit hybrids, when the two species are first reunited.

Speciation by Hybridization

Hybridization between related angiosperms is sometimes followed by a doubling of the chromosome number. The resulting **polyploids** are now fully fertile with each other although unable to breed with either parental type - a new species has been created. This appears to have been a frequent mechanism of speciation in angiosperms. Even without forming a polyploid, interspecific hybridization can occasionally lead to a new species of angiosperm. Two species of sunflower, the "common sunflower", *Helianthus annuus*, and the "prairie sunflower", *H. petiolaris*, grow widely over the western half of the United States. They can interbreed, but only rarely are fertile offspring produced.

However, Rieseberg and colleagues have found evidence that successful hybridization between them has happened naturally in the past. They have shown that three other species of sunflower (each growing in a habitat too harsh for either parental type) are each the product of an ancient hybridization between *Helianthus annuus* and *H. petiolaris*. Although each of these species has the same **diploid** number of chromosomes as the parents (2**n** = 34), they each have a pattern of chromosome segments that have been derived, by **genetic recombination**, from both the parental genomes. They demonstrated this in several ways, notably by combining RFLP analysis with the polymerase chain reaction (PCR).

They even went on to produce (at a low frequency) *annuus* x *petiolaris* hybrids in the greenhouse that mimicked the phenotypes and genotypes of the natural hybrids. (These monumental studies were described in the 29 August 2003 issue of **Science**.)

Another example. In Pennsylvania, hybrids between a species of fruit fly (not Drosophila) that feeds on blueberries and another species (again, not Drosophila) that feeds on snowberries feed on honeysuckle where they neither encounter competition from their parental species nor have an opportunity to breed with them (no introgression). This study was published in the 28 July 2005 issue of **Nature**. So speciation can occur as a result of hybridization between two related species, if the hybrid

- receives a genome that enables it to breed with other such hybrids but not breed with either parental species,
- can escape to a habitat where it does not have to compete with either parent,
- is adapted to live under those new conditions.

Adaptive Radiation

The processes described in this page can occur over and over. In the case of Darwin's finches, they must have been repeated a number of times forming new species that gradually divided the available habitats between them. From the first arrival have come a variety of ground-feeding and tree-feeding finches as well as the warblerlike finch and the tool-using woodpeckerlike finch. The formation of a number of diverse species from a single ancestral one is called an **adaptive radiation**.

Speciateion in theHouse mice on the island of Madeira

A report in the 13 January 2000 issue of **Nature** describes a study of house mouse populations on the island of Madeira off the Northwest coast of Africa. These workers (Janice Britton-Davidian et al) examined the karyotypes of 143 house mice (***Mus musculus domesticus***) from various locations along the coast of this mountainous island.

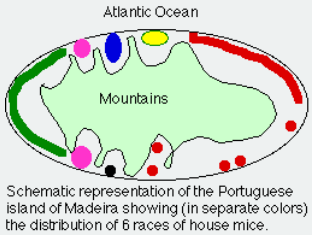


Figure 18.2.3 Madeira mice

Their findings:

- There are 6 distinct populations (shown by different colors)
- Each of these has a distinct karyotype, with a diploid number less than the "normal" (2**n** = 40).
- The reduction in chromosome number has occurred through **Robertsonian fusions**. Mouse chromosomes tend to be **acrocentric**; that is, the centromere connects one long and one very short arm. Acrocentric chromosomes are at risk of translocations that fuse the long arms of two different chromosomes with the loss of the short arms.
- The different populations are **allopatric**; isolated in different valleys leading down to the sea.
- The distinct and uniform karyotype found in each population probably arose from genetic drift rather than natural selection.
- The 6 different populations are technically described as **races** because there is no opportunity for them to attempt interbreeding.
- However, they surely meet the definition of true species. While hybrids would form easily (no prezygotic isolating mechanisms), these would probably be infertile as proper synapsis and segregation of such different chromosomes would be difficult when the hybrids attempted to form gametes by meiosis.

Sympatric Speciation

Sympatric speciation refers to the formation of two or more descendant species from a single ancestral species all occupying the same geographic location. Some evolutionary biologists don't believe that it ever occurs. They feel that interbreeding would soon eliminate any genetic differences that might appear. But there is some compelling (albeit indirect) evidence that sympatric speciation can occur.

Speciation in three-spined sticklebacks

The three-spined sticklebacks, freshwater fishes that have been studied by Dolph Schluter (who received his Ph.D. for his work on Darwin's finches with Peter Grant) and his current colleagues in British Columbia, provide an intriguing example that is best explained by sympatric speciation.

They have found:

- Two different species of three-spined sticklebacks in each of five different lakes.
  - a large benthic species with a large mouth that feeds on large prey in the littoral zone
  - a smaller limnetic species with a smaller mouth that feeds on the small plankton in open water.
- DNA analysis indicates that each lake was colonized independently, presumably by a marine ancestor, after the last ice age.
- DNA analysis also shows that the two species in each lake are more closely related to each other than they are to any of the species in the other lakes.
- Nevertheless, the two species in each lake are reproductively isolated; neither mates with the other.
- However, aquarium tests showed that
  - The benthic species from one lake will spawn with the benthic species from the other lakes and likewise the limnetic species from the different lakes will spawn with each other.
  - These benthic and limnetic species even display their mating preferences when presented with sticklebacks from Japanese lakes; that is, a Canadian benthic prefers a Japanese benthic over its close limnetic cousin from its own lake.
- Their conclusion: in each lake, what began as a single population faced such competition for limited resources that
  - **disruptive selection** — competition favoring fishes at either extreme of body size and mouth size over those nearer the mean — coupled with
  - **assortative mating** — each size preferred mates like it

  favored a divergence into two subpopulations exploiting different food in different parts of the lake.
- The fact that this pattern of speciation occurred the same way on three separate occasions suggests strongly that **ecological factors** in a sympatric population can cause speciation.

Sympatric speciation driven by ecological factors may also account for the extraordinary diversity of crustaceans living in the depths of Siberia's Lake Baikal.

How many genes are needed to start down the path to sympatric speciation?

Perhaps not very many. The European corn borer, *Ostrinia nubilalis*, (which despite its common name is a major pest in the U.S. as well) exists as two distinct races designated **Z** and **E**. Both can be found in the same area; that is, they are sympatric. But in the field, they practice assortative mating - only breeding with mates of their own race.

The females of both races synthesize and release a pheromone that is a sex attractant for the males. Both races use the same substance but different isomers of it. Which isomer is produced is under the control of a single enzyme-encoding gene locus. The ability of the males to respond to one isomer or the other is controlled by 2 loci.

The Problem of Clines

There is another possible way for new species to arise in the absence of geographical barriers. If a population ranges over a large area and if the individuals in that population can disperse over only a small portion of this range, then gene flow across these great distances would be reduced. The occurrence of gradual phenotypic (and genotypic) differences in a population across a large geographical area is called a **cline**. Successful interbreeding occurs freely at every point along the cline, but individuals at the ends of the cline may not be able to interbreed. This can be tested in the laboratory.

And, on occasions, it is tested in nature. If a cline bends around so that the ends meet, and the populations reunited at the junction cannot interbreed, then the definition of separate species has been met. Such species are called **ring species** and this type of speciation is called **parapatric speciation**.

Two examples:

1. The Caribbean slipper spurge *Euphorbia tithymaloides*.
Genetic analysis shows that this wildflower originated in Central America where Mexico and Guatemala share a common boundary. From there it spread in two directions

- northeast through the Yucatan peninsula and then island-hopped through Jamaica, the Dominican Republic, Puerto Rico and into the Virgin Islands;
- south through Central America, on through Venezuela, and then north through Barbados and the other islands of the Lesser Antilles finally also reaching the Virgin Islands.

Reunited in the Virgin Islands, the two populations have diverged sufficiently that they retain their distinctive genotypic and phenotypic traits. Ongoing studies will determine to what degree they may be reproductively isolated.

2. The large-blotched salamander *Ensatina eschscholtzii*.

This animal is found in California where it occurs in a number of different subspecies or races. A single subspecies is found in Northern California, and it is thought to be the founder of all the others. Over time that original population spread southward in two directions:

- down the Sierra Nevada mountains east of the great central San Joaquin Valley and
- down the coast range of mountains west of the valley.

South of the valley, the eastern group has moved west and now meets the western group, closing the ring. Here the two populations fail to interbreed successfully, maintaining their distinct identities. But each subspecies interbreeds in an unbroken chain up the two paths their ancestors took.

Ring species present a difficult problem in assigning species designations. It is easy to say that the populations at the ends of the cline represent separate species, but where did one give rise to the other? At every point along the cline, interbreeding goes on successfully.

The same problem faces paleontologists examining the gradual phenotypic changes seen in an unbroken line of ever-younger fossils from what one presumes to be a single line of descent. If one could resurrect the ancestral species (A) and the descendant species (B) and they could not interbreed, then they meet the definition of separate species. But there was no moment in time when one could say that A became B. So the clines of today are a model in **space** of Darwin's descent with modification occurring over **time**.

Although clines present a problem for classifiers, they are a beautiful demonstration of Darwin's conviction that the accumulation of small inherited differences can lead to the formation of new species.

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21.3: Artificial Selection- Human-Initiated Change

The development of a new crop variety is an example of **agricultural biotechnology**, a range of tools that include both traditional breeding techniques and more modern lab-based methods. Traditional methods date back thousands of years, whereas biotechnology uses the tools of genetic engineering developed over the last few decades.

Selective Breeding (Artificial Selection)

Nearly all the fruits and vegetables found in your local market would not occur naturally. In fact, they exist only because of human intervention that began thousands of years ago. Humans created the vast majority of crop species by using traditional breeding practices on naturally-occurring, wild plants. These practices rely upon **selective breeding** (artificial selection), human-facilitated reproduction of individuals with desirable traits. For example, high yield varieties were produced through selective breeding. Traditional breeding practices, although low-tech and simple to perform, have the practical outcome of modifying an organism's genetic information, thus producing new traits.

Selective breeding is limited, however, by the life cycle of the plant and the genetic variants that are naturally present. For example, even the fastest flowering corn variety has a generation time of 60 days (the time required for a seed to germinate, produce a mature plant, get pollinated, and ultimately produce more seeds) in perfect conditions. Each generation provides an opportunity to selectively breed individual plants and generate seeds that are slightly closer to the desired outcome (for example, producing bigger, juicier kernels). Furthermore, if no individuals happen to possess gene variants that result in bigger, juicier kernels, it is not possible to artificially select this trait. Finally, traditional breeding shuffles all of the genes between the two individuals being bred, which can number into the tens of thousands (maize, for example, has 32,000 genes). When mixing such a large number of genes, the results can be unpredictable.

An interesting example is maize (corn). Biologists have discovered that maize was developed from a wild plant called teosinte. Through traditional breeding practices, humans living thousands of years ago in what is now Southern Mexico began selecting for desirable traits until they were able to transform the plant into what is now known as maize (figure **21.3.*a***). In doing so, they permanently (and unknowingly) altered its genetic instructions.

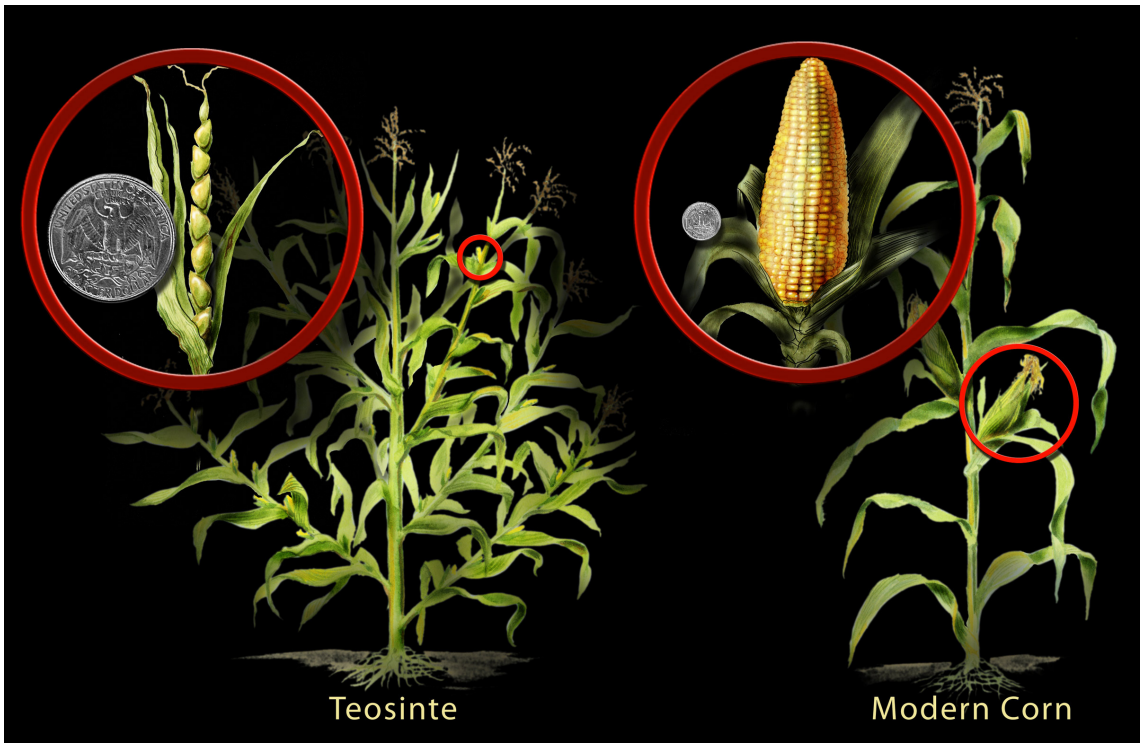


Figure **21.3.*a***: A wild grass called teosinte was genetically modified through selective breeding to produce what is now known as maize (corn). This process of transformation started thousands of years ago by indigenous people of what is now Mexico. Image by Nicolle Rager Fuller/National Science Foundation (public domain).

This history of genetic modification is common to nearly all crop species. For example, cabbage, broccoli, Brussel sprouts, cauliflower, and kale were all developed from a single species of wild mustard plant (figure **21.3.*b***). Wild nightshade was the source of tomatoes, eggplant, tobacco, and potatoes, the latter developed by humans 7,000 – 10,000 years ago in South America.



Figure **21.3.*b***: *Brassica oleracea* is a plant in the mustard family and is known as wild cabbage. From it were developed many familiar crops, such as cauliflower, broccoli, Brussel sprouts, and of course, cabbage. Image by Kulac (CC-BY-SA).

Genetic Engineering

Genetic engineering is the process of directly altering an organism's DNA to produce the desired crops more rapidly than selective breeding. Because genes can be obtained from other species or even synthesized in the lab, scientists are not limited by existing genetic variation within a crop species (or closely related species with which they can be crossed). This broadens the possible traits that can be added to crops. Modern genetic engineering is more precise than selective breeding in the sense that biologists can modify just a single gene. Also, genetic engineering can introduce a gene between two distantly-related species, such as inserting a bacterial gene into a plant (figure **21.3.*c***).

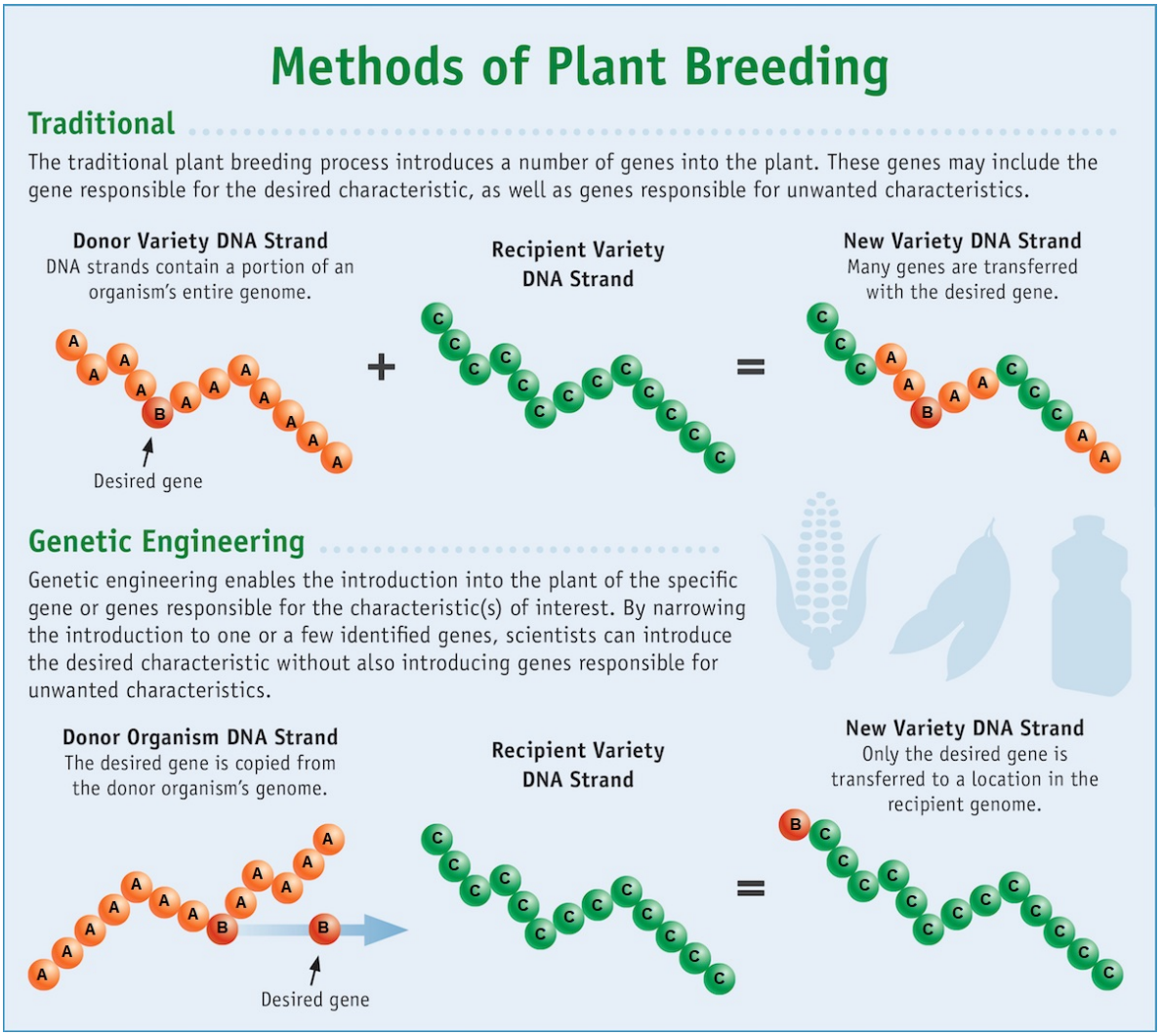


Figure **21.3.*c***: Both selective (traditional) breeding and modern genetic engineering produce genetic modifications. Genetic engineering allows for fewer and more precise genetic modifications. The traditional plant breeding process introduces a number of genes into the plant. These genes may include the gene responsible for the desired characteristic, as well as genes responsible for unwanted characteristics. In traditional breeding, the donor variety DNA strand (A) and recipient variety DNA strand (C) are combined to produce the new variety DNA strand. The donor DNA strand contains a portion of an organism's entire genome, including the desired gene (B). In the new variety DNA strand, many genes are transferred with the desired gene. Genetic engineering enables the introduction into the plant of the specific gene or genes responsible for the characteristics of interest. By narrowing the introduction to one of a few identified genes, scientists can introduce the desired characteristic without also introducing genes responsible for unwanted characteristics. In genetic engineering, the desired gene (B) is copied from the donor organism's genome (A). The desired gene from the donor organism DNA strand and the recipient variety DNA strand (C) are combined to produce the new variety DNA strand. Only the desired gene is transferred to a location in the recipient genome. Modified from Michael J. Ermarth/FDA (public domain).

Genetically modified organisms (**GMOs**) are those that have had their DNA altered through genetic engineering. Genetically modified crops are sometimes called genetically engineered (GE) crops. **Transgenic organisms** are a type of genetically modified organism that contains genes from a different species. Because they contain unique combinations of genes and are not restricted to the laboratory, transgenic plants and other GMOs are closely monitored by government agencies to ensure that they are fit for human consumption and do not endanger other plant and animal life. Because these foreign genes (transgenes) can spread to other species in the environment, particularly in the pollen and seeds of plants, extensive testing is required to ensure ecological stability.

How to Genetically Modify Plant Cells

DNA can be inserted into plant cells through various techniques. For example, a **gene gun** propels DNA bound to gold particles into plant cells. (DNA is negatively charge and clings to positively charged gold.) A more traditional approach employs the plant pathogen ***Agrobacterium tumefaciens*** (figure **21.3.*d***). Ordinarily, this bacterium causes crown gall disease in plants by inserting

a circular piece of DNA, called the **Ti plasmid**, into plant cells. This DNA incorporates into plant chromosomes, giving them genes to produce the gall (figure **21.3.*e***), which provides a home for the bacterial pathogen.

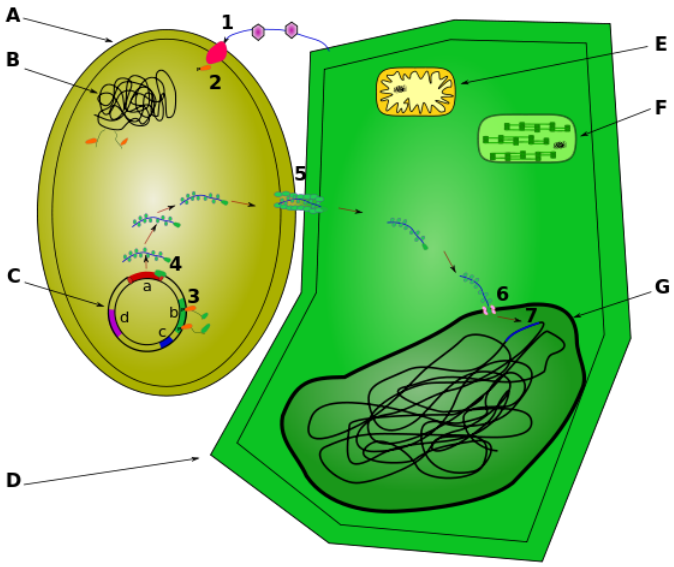


Figure **21.3.*d***: An *Agrobacterium tumefaciens* cell (A) inserts the Ti plasmid (C), which contains T-DNA (a) into a plant cell (D). The T-DNA eventually enters the plant nucleus (G), where the plant DNA is stored. Image by Chandres (CC-BY-SA).



Figure **21.3.*e***: A crown gall caused by *Agrobacterium tumefaciens*. This bacterium inserts DNA into plant cells, which causes them to produce the crown gall. This process can be adjusted by scientists to insert genes that code for desirable traits into crop species. Image by Scott Nelson (public domain).

Scientists alters the process by which *Agrobacterium* infects and genetically alter plant cells to produce genetically modified plants with agriculturally beneficial traits as follows (figure **21.3.*f***):

1. T-DNA, which codes for the crown gall is removed from the Ti plasmid, and genes for desired traits are added.
2. The modified plasmid is then added back to *Agrobacterium.*
3. *Agrobacterium* infects undifferentiated plant cells (stem cells that can develop into any part of the plant; figure **21.3.*g***).

4. The modified plant cells are given hormones to produce the entire plant.

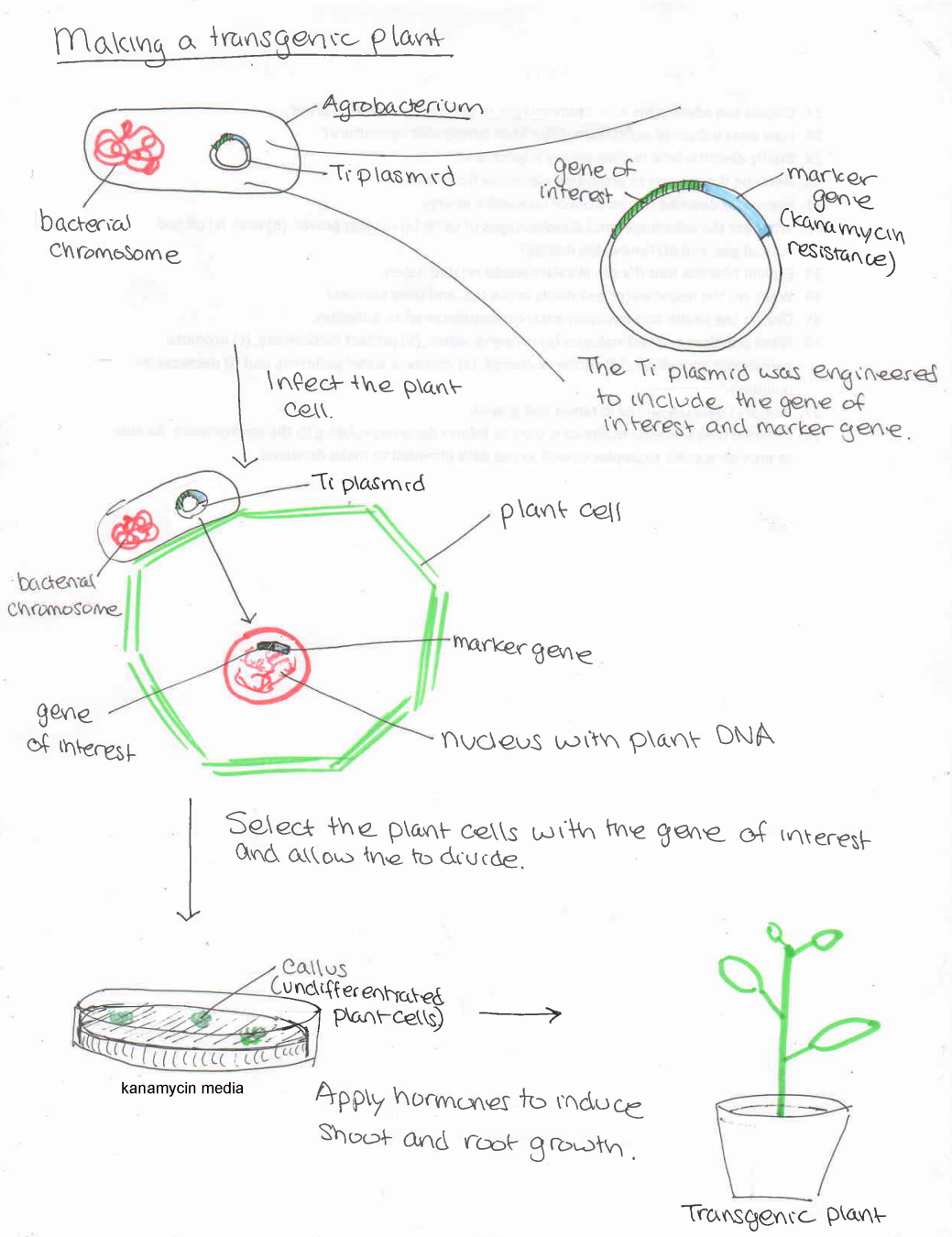


Figure **21.3.*f***: The process of producing a transgenic plant using *Agrobacterium*. The Ti plasmid was engineered to include the gene of interest and marker gene, which will later indicate which cells are transgenic. A rectangle represents *Agrobacterium*. It contains regular bacterial DNA and the Ti plasmid, represented by a circle. The T-DNA (which provides instructors for producing a crown gall) is removed, and a transgene (gene of interest) and maker gene are inserted instead. The gene of interest is colored green, and the marker gene (for resistance to the antibiotic kanamycin) is colored blue. Next, plant cells are infected with *Agrobacterium*. The bacterial cell inserts the Ti plasmid into a polyhedral plant cell. The transgene is transferred to the plant cell nucleus, which contains regular plant DNA. Next, the plant cells with the gene of interest are selected and allowed them to divide. This is done by culturing the plant cells on kanamycin media in a petri dish. Calluses, clusters of undifferentiated plant cells, are produced. Finally, hormones are applied to induce shoot and root growth. An arrow points from the petri dish to a potted transgenic plant. Image by Melissa Ha (CC-BY).

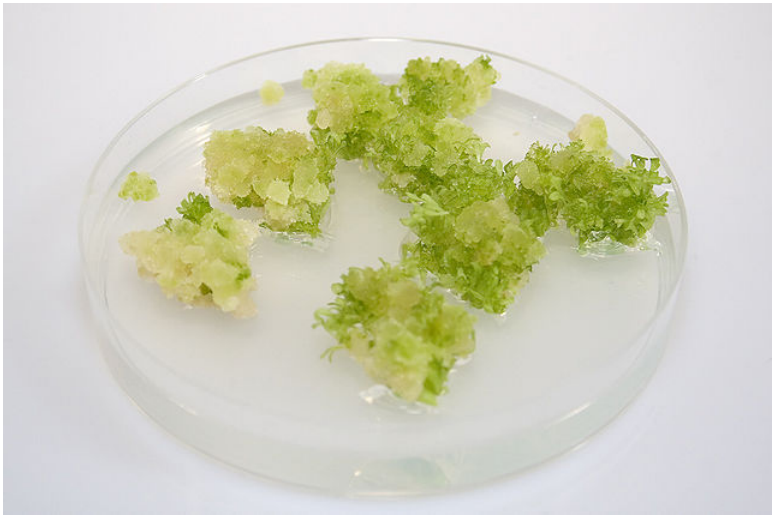


Figure **21.3.*g***: Individual plant cells are first genetically engineered with *Agrobacterium*. They then grow into **calluses** (blobs of undifferentiated plant cells) and are given hormones to induce root and shoot development. Because all the cells in the plant that eventually grows descended from a single genetically engineered cell, the entire plant is transgenic. Image by Igge (CC-BY-SA).

Examples of Genetically Modified Crops

Many genetically modified crops have been approved in the U.S. and produce our foods. The first genetically modified organism approved by the U.S. Food and Drug Administration (FDA) in 1994 was **Flavr Savr™ tomatoes**, which have a longer shelf life (delayed rotting) because a gene responsible for breaking down cells in inhibited. Flavr Savr tomatoes are genetically modified (because their DNA has been altered) but not trasgenic (because they do not contain genes from another species). The Flavr Savr tomato did not successfully stay in the market because of problems maintaining and shipping the crop. **Golden rice** produces β-carotene, a precursor to vitamin A (figure **21.3.*h***; β-carotene is also in high concentrations in carrots, sweet potatoes, and cantaloupe, giving them their orange color.) **Roundup Ready®** corn, cotton, and soybeans are resistant to this common herbicide, making it easier to uniformly spray it in a field to kill the weeds without harming the crops (figure **21.3.*i***).



Figure **21.3.*h***: Golden rice has an orange-yellow color because it contains up to 35 µg β-carotene (a precursor to vitamin A) per gram of rice, which could prevent millions of cases of blindness worldwide. Image by International Rice Research Institute (CC-BY).



Figure **21.3.*i***: Roundup is a common herbicide. Roundup Ready® plants are genetically modified to resist roundup, meaning the herbicide does not kill them. This allows farmers to uniformly spray Roundup, killing weeds without harming the crops. Image by Mike Mozart (CC-BY).

Crops have also been engineered to produce insecticides. *Bacillus thuringiensis* (Bt) is a bacterium that produces protein crystals that are toxic to many insect species that feed on plants. Insects that have eaten Bt toxin stop feeding on the plants within a few hours. After the toxin is activated in the intestines of the insects, death occurs within a couple of days. The gene to produce **Bt toxin** has been added to many crops including corn (figure **21.3.*j***), potatoes, and cotton, providing plants with defense against insects.

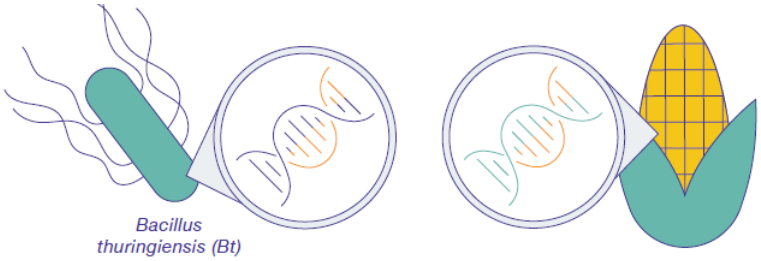


Figure **21.3.*j***: Genetic engineering to produce Bt corn. The gene from *Bacillus thuringiensis* that produces Bt toxin is removed and inserted into the corn plant. The Bt corn now produces the insecticide (Bt toxin) and can defend itself against pests. Image by FDA (public domain).

Genetically modified foods are widespread in the United States. For example, 94% of soy crops were genetically modified for herbicide resistance in 2020. Likewise, 8% of cotton and 10% of corn crops were modified for herbicide resistance in addition to the 83% of cotton and 79% of corn crops that were genetically modified in multiple ways.

Genetically modified animals have recently entered the market as well. **AquaAdvantage® salmon** are modified to grow more rapidly and were approved in November of 2015. However, as of March 2021, they have still not been sold due to legal challenges. In 2020, the FDA approved **GalSafe™ pigs** for medicine and food production. These pigs lack a molecule on the outside of their cells that cause allergies in some people.

Advantages of Genetically Modified Crops

Advances in biotechnology may provide consumers with foods that are nutritionally-enriched, longer-lasting, or that contain lower levels of certain naturally occurring toxins present in some food plants. For example, researchers are using biotechnology to try to reduce saturated fats in cooking oils and reduce allergens in foods. Whether these benefits will reach the people who need them most remains to be seen. While cultivating golden rice could address vitamin A deficiency in millions of people, it has not

historically been accessible to these people because it is patented and expensive. Similarly, genetically modified seeds could increase the income of impoverished farmers if they were available at low or no cost, but this is not always the case.

Rainbow and SunUp papayas are a success story of how genetically modified crops can benefit small farmers and the economy in general. In the early 1990s, an emerging disease was destroying Hawaii's production of papaya and threatening to decimate the $11-million industry (figure **21.3.*k***). Fortunately, a man named Dennis Gonsalves (figure **21.3.*l***), who was raised on a sugar plantation and then became a plant physiologist at Cornell University, would develop papaya plants genetically engineered to resist the deadly virus. By the end of the decade, the Hawaiian papaya industry and the livelihoods of many farmers were saved thanks to the free distribution of Dr. Gonsalves's seeds.

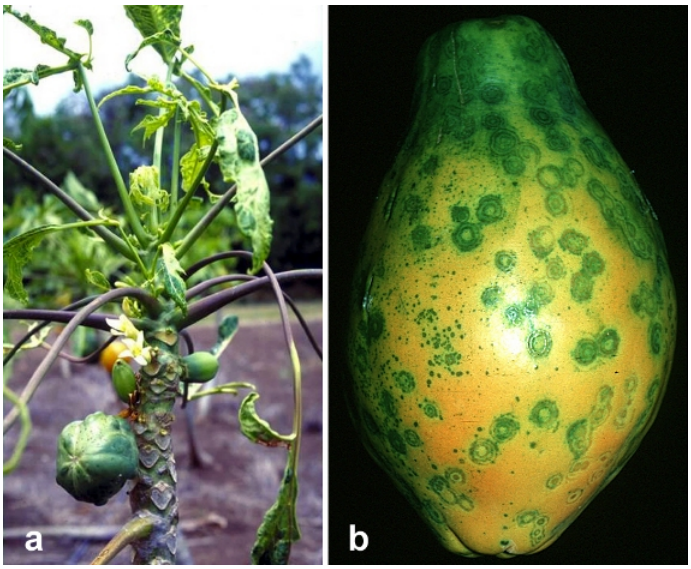


Figure **21.3.*k***: The symptoms of papaya ringspot virus are shown on the tree (a) and fruit (b). Image by APS (public domain).



Figure **21.3.*l***: Dennis Gonsalves genetically engineered papayas to resist the ringspot virus. Image by ARS USDA (public domain).

The effect of genetically modified crops on the environment depends on the specific genetic modification and which agricultural practices it promotes. For example, Bt crops produce their own insecticides such that external application of these chemicals is unnecessary, reducing the negative impacts of industrial agriculture. Ongoing research is exploring whether crops can be engineered to fix nitrogen in the atmosphere (as some bacteria do) rather than relying on ammonium, nitrites, and nitrates in the soil. If these crops were successfully engineered, they could reduce synthetic fertilizer application and minimize nutrient runoff that leads to eutrophication.

Genetically modified crops may have the potential to conserve natural resources, enable animals to more effectively use nutrients present in feed, and help meet the increasing world food and land demands. In practice, however, countries that use genetically modified crops compared to those that do not only enjoy a slight (or nonexistent) increase in yield.

Disadvantages of Genetically Modified Crops

Social Concerns

Intellectual property rights are one of the important factors in the current debate on genetically modified crops. Genetically modified crops can be patented by agribusinesses, which can lead to them controlling and potentially exploiting agricultural markets. Some accuse companies, such as Monsanto, of allegedly controlling seed production and pricing, much to the detriment of farmers (figure **21.3.*m***).



Figure **21.3.*m***: Protesters in Washington D.C. oppose genetically modified organisms and Monsanto specifically. Image cropped from Sarah Stierch (CC-BY).

Environmental Concerns

Genetically modified crops present several environmental concerns. Monoculture farming already reduces biodiversity, and cultivating genetically modified crops, for which individual plants are quite similar genetically, exacerbates this. The use of Roundup Ready® crops naturally encourages widespread herbicide use, which could unintentionally kill nearby native plants. This practice would also increase herbicide residues on produce. While Bt crops are beneficial in the sense that they do not require external insecticide application, but Bt toxin is spread in their pollen. An early study found that Bt corn pollen may be harmful to monarch caterpillars (figure **21.3.*n***), but only at concentrations that are seldom reached in nature. Follow-up studies found that most of Bt corn grown did not harm monarchs; however, the one strain of Bt corn did was consequently removed from the market.



Figure **21.3.*n***: An early study suggested that pollen containing Bt toxin can harm beneficial and native insects, like this monarch caterpillar. However, without Bt crops, farmers are more likely to spray insecticides, circulating more harmful chemicals than pollen from Bt crops does. Image by Judy Gallagher (CC-BY).

Through interbreeding, or hybridization, genetically modified crops might share their transgenes with wild relatives. This could affect the genetics of those wild relatives and have unforeseen consequences on their populations and could even have implications for the larger ecosystem. For example, if a gene engineered to confer herbicide resistance were to pass from a genetically modified crop to a wild relative, it might transform the wild species into a **superweed** – a species that could not be controlled by herbicide. Its rampant growth could then displace other wild species and the wildlife that depends on it, thus inflecting ecological harm.

Not only could escaped genes alter weedy species, but they could also enter populations of native species. This could make some native species better competitors than they were previously, disrupting ecosystem dynamics. (They could potentially outcompete other native species with which they would otherwise coexist.)

While there is evidence of genetic transfer between genetically modified crops and wild relatives, there is not yet evidence of ecological harm from that transfer. Clearly, continued monitoring, especially for newly-developed crops, is warranted.

The escape of genetically modified animals has potential to disrupt ecosystems as well. For example, if AquaAdvantage salmon were to escape into natural ecosystem, as farmed fish often do, they could outcompete native salmon, including endangered species. Their genetic modification, which facilitates rapid growth, could result in a competitive advantage.

Health Concerns

In addition to environmental risks, some people are concerned about potential health risks of genetically modified crops because they feel that genetic modification alters the intrinsic properties, or essence, of an organism. As discussed above, however, it is known that both traditional breeding practices and modern genetic engineering produce permanent genetic changes. Furthermore, selective breeding actually has a larger and more unpredictable impact on a species's genetics because of its comparably crude nature.

To address these concerns (and others), the US National Academies of Sciences, Engineering, and Medicine (NASEM) published a comprehensive, 500-page report in 2016 that summarized the current scientific knowledge regarding genetically modified crops. The report, titled *Genetically Engineered Crops: Experiences and Prospects*, reviewed more than 900 research articles, in addition to public comments and expert testimony. NASEM's GE Crop Report found "no substantiated evidence of a difference in risks to human health between current commercially available genetically engineered (GE) crops and conventionally bred crops, nor did it find conclusive cause-and-effect evidence of environmental problems from the GE crops." Additionally, the UN's Food and Agriculture Organization has concluded that risks to human and animal health from the use of GMOs are negligible. The scientific consensus on genetically modified crops is quite clear: they are safe for human consumption.

The potential of genetically modified crops to be allergenic is one of the potential adverse health effects, and it should continue to be studied, especially because some scientific evidence indicates that animals fed genetically modified crops have been harmed. NASEM's GE Crop Report concluded that when developing new crops, it is the product that should be studied for potential health and environmental risks, not the process that achieved that product. What this means is, because both traditional breeding practices and modern genetic engineering produce new traits through genetic modification, they both present potential risks. Thus, for the safety of the environment and human health, both should be adequately studied.

Are Genetically Modified Crops the Solution We Need?

Significant resources, both financial and intellectual, have been allocated to answering the question: are genetically modified crops safe for human consumption? After many hundreds of scientific studies, the answer is yes. But a significant question still remains: are they necessary? Certainly, such as in instances like Hawaii's papaya, which were threatened with eradication due to an aggressive disease, genetic engineering was a quick and effective solution that would have been extremely difficult, if not impossible, to solve using traditional breeding practices.

However, in many cases, the early promises of genetically engineered crops – that they would improve nutritional quality of foods, confer disease resistance, and provide unparalleled advances in crop yields – have largely failed to come to fruition. NASEM's GE Crop Report states that while genetically modified crops have resulted in the reduction of agricultural loss from pests, reduced pesticide use, and reduced rates of injury from insecticides for farm workers, they have not increased the rate at which crop yields are advancing when compared to non-GE crops. Additionally, while there are some notable exceptions like golden rice or virus-resistant papayas, very few genetically engineered crops have been produced to increase nutritional capacity or to prevent plant disease that can devastate a farmer's income and reduce food security. The vast majority of genetically modified crops are

developed for only two purposes: to introduce herbicide resistance or pest resistance. Genetically modified crops are concentrated in developed countries, and their availability in developing countries, where they are perhaps most needed, is limited (figure **21.3.*o***).

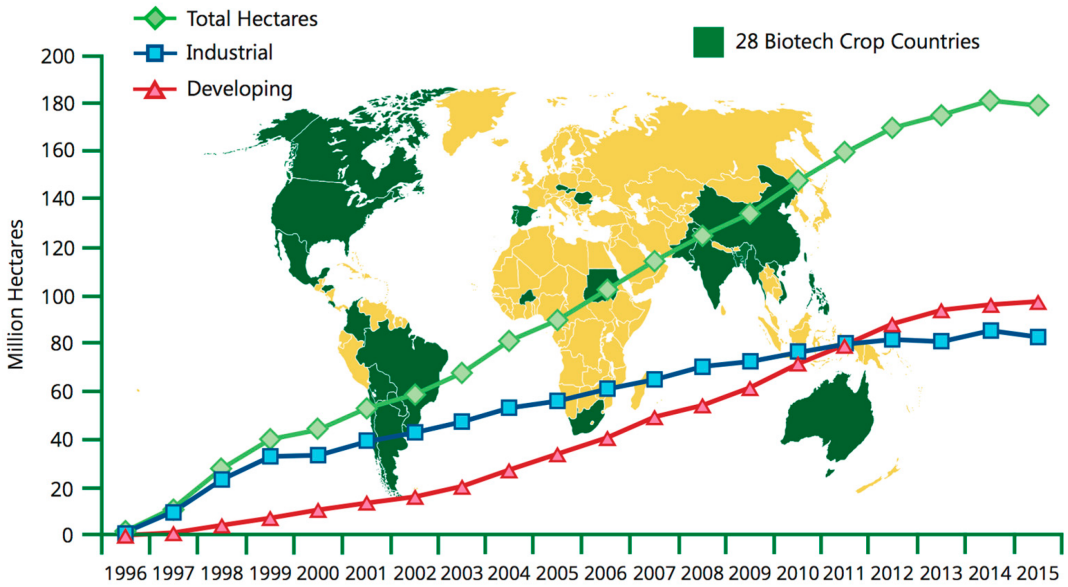


Figure **21.3.*o***: Global area of genetically modified crops in millions of hectares 1996–2015. Overall, the hectares of genetically modified crops has increased, and in 2011, developing countries surpassed industrial countries. By 2015, out of the 28 countries that grew biotech crops, 20 were developing, and only eight were developed countries. Latin American, African, and Asian farmers together grew 97.1 million hectares (54%) of the global 179.7 million biotech hectares, whereas industrial countries only planted 83 million hectares or 46%. Image and caption (modified) from Taheri, F., Azadi, H., & D'Haese, M. (2017). A World without Hunger: Organic or GM Crops? *Sustainability*, *9*(4), 580. doi:10.3390/su9040580. (CC-BY)

Suggested Supplementary Reading

NASEM. 2016. Genetically Engineered Crops: Experiences and Prospects.

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SECTION OVERVIEW

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21.4.2: Fossil Formation

21.4.3: Gaps in the Fossil Record

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21.4.8: Vestigial Structures

21.4.9: Biogeography and the Distribution of Species

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21.4.1: The Fossil Record as Evidence for Evolution

Learning Objectives

- Synthesize the contributions of the fossil record to our understanding of evolution

What Fossils Tell Us

Fossils are the preserved remains or traces of animals, plants, and other organisms from the past. Fossils range in age from 10,000 to 3.48 billion years old. The observation that certain fossils were associated with certain rock strata led 19th century geologists to recognize a geological timescale. Like extant organisms, fossils vary in size from microscopic, like single-celled bacteria, to gigantic, like dinosaurs and trees.



Figure **21.4.1.1**: "Sue" T-rex skeleton: The bones of this Tyrannosaurus rex were preserved through the process of permineralization, which suggests that this organism was covered by sediment soon after death.

Permineralization

Permineralization is a process of fossilization that occurs when an organism is buried. The empty spaces within an organism (spaces filled with liquid or gas during life) become filled with mineral-rich groundwater. Minerals precipitate from the groundwater, occupying the empty spaces. This process can occur in very small spaces, such as within the cell wall of a plant cell. Small-scale permineralization can produce very detailed fossils. For permineralization to occur, the organism must be covered by sediment soon after death, or soon after the initial decay process.

The degree to which the remains are decayed when covered determines the later details of the fossil. Fossils usually consist of the portion of the organisms that was partially mineralized during life, such as the bones and teeth of vertebrates or the chitinous or calcareous exoskeletons of invertebrates. However, other fossils contain traces of skin, feathers or even soft tissues.

Trace Fossils

Fossils may also consist of the marks left behind by the organism while it was alive, such as footprints or feces. These types of fossils are called trace fossils, or ichnofossils, as opposed to body fossils. Past life may also leave some markers that cannot be seen but can be detected in the form of biochemical signals; these are known as chemofossils or biomarkers.



Figure 21.4.1.1: Dinosaur footprints: Footprints are examples of trace fossils, which contribute to the fossil record.

The Fossil Record

The totality of fossils, both discovered and undiscovered, and their placement in fossiliferous (fossil-containing) rock formations and sedimentary layers (strata) is known as the fossil record. The fossil record was one of the early sources of data underlying the study of evolution and continues to be relevant to the history of life on Earth. The development of radiometric dating techniques in the early 20th century allowed geologists to determine the numerical or "absolute" age of various strata and their included fossils.

Evidence for Evolution

Fossils provide solid evidence that organisms from the past are not the same as those found today; fossils show a progression of evolution. Fossils, along with the comparative anatomy of present-day organisms, constitute the morphological, or anatomical, record. By comparing the anatomies of both modern and extinct species, paleontologists can infer the lineages of those species. This approach is most successful for organisms that had hard body parts, such as shells, bones or teeth. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years.

Key Points

- Fossils are the preserved remains or traces of animals, plants, and other organisms from the past.
- Fossils are important evidence for evolution because they show that life on earth was once different from life found on earth today.
- Usually only a portion of an organism is preserved as a fossil, such as body fossils (bones and exoskeletons), trace fossils (feces and footprints), and chemofossils (biochemical signals).
- Paleontologists can determine the age of fossils using methods like radiometric dating and categorize them to determine the evolutionary relationships between organisms.

Key Terms

- **biomarker**: A substance used as an indicator of a biological state, most commonly disease.
- **trace fossil**: A type of fossil reflecting the reworking of sediments and hard substrates by organisms including structures like burrows, trails, and impressions.
- **fossil record**: All discovered and undiscovered fossils and their placement in rock formations and sedimentary layers.
- **strata**: Layers of sedimentary rock.
- **fossiliferous**: Containing fossils.

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21.4.2: Fossil Formation

Learning Objectives

- Predict the conditions suitable to fossil formation

Fossil Formation

The process of a once living organism becoming a fossil is called fossilization. Fossilization is a very rare process, and of all the organisms that have lived on Earth, only a tiny percentage of them ever become fossils. To see why, imagine an antelope that dies on the African plain. Most of its body is quickly eaten by scavengers, and the remaining flesh is soon eaten by insects and bacteria, leaving behind only scattered bones. As the years go by, the bones are scattered and fragmented into small pieces, eventually turning into dust and returning their nutrients to the soil. As a result, it would be rare for any of the antelope's remains to actually be preserved as a fossil.

Fossilization can occur in many ways. Most fossils are preserved in one of five processes:

- preserved remains
- permineralization
- molds and casts
- replacement
- compression

Preserved Remains

The rarest form of fossilization is the preservation of original skeletal material and even soft tissue. For example, some insects have been preserved perfectly in amber, which is ancient tree sap. In addition, several mammoths and even a Neanderthal hunter have been discovered frozen in glaciers. These preserved remains allow scientists the rare opportunity to examine the skin, hair, and organs of ancient creatures. Scientists have collected DNA from these remains and compared the DNA sequences to those of modern creatures.



Figure **21.4.2.1**: Amber: The image depicts a gnat preserved in amber. A lot of insects have been found to be perfectly maintained in this ancient tree sap.

Permineralization

The most common method of fossilization is permineralization. After a bone, wood fragment, or shell is buried in sediment, it may be exposed to mineral-rich water that moves through the sediment. This water will deposit minerals, typically silica, into empty spaces, producing a fossil. Fossilized dinosaur bones, petrified wood, and many marine fossils were formed by permineralization.



Figure **21.4.2.1**: Permineralization: These fossils from the Road Canyon Formation (Middle Permian of Texas) have been silicified (replaced with silica), which is a form of permineralization.

Molds and Casts

In some cases, the original bone or shell dissolves away, leaving behind an empty space in the shape of the shell or bone. This depression is called a mold. Later, the space may be filled with other sediments to form a matching cast in the shape of the original organism. Many mollusks (bivalves, snails, and squid) are commonly found as molds and casts because their shells dissolve easily.

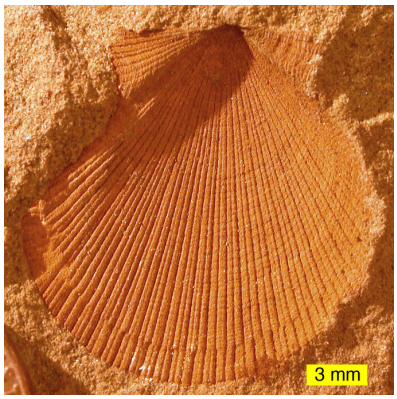


Figure **21.4.2.1**: Molds: The depression in the image is an external mold of a bivalve from the Logan Formation, Lower Carboniferous, Ohio

Replacement

In some cases, the original shell or bone dissolves away and is replaced by a different mineral. For example, shells that were originally calcite may be replaced by dolomite, quartz, or pyrite. If quartz fossils are surrounded by a calcite matrix, the calcite can be dissolved away by acid, leaving behind an exquisitely preserved quartz fossil. When permineralization and replacement occur together, the organism is said to have undergone petrification, the process of turning organic material into stone. However, replacement can occur without permineralization and vice versa.

Compression

Some fossils form when their remains are compressed by high pressure. This can leave behind a dark imprint of the fossil. Compression is most common for fossils of leaves and ferns but also can occur with other organisms.

Conditions for Fossilization

Following the death of an organism, several forces contribute to the dissolution of its remains. Decay, predators, or scavengers will typically rapidly remove the flesh. The hard parts, if they are separable at all, can be dispersed by predators, scavengers, or currents. The individual hard parts are subject to chemical weathering and erosion, as well as to splintering by predators or scavengers, which will crunch up bones for marrow and shells to extract the flesh inside. Also, an animal swallowed whole by a predator, such as a mouse swallowed by a snake, will have not just its flesh but some, and perhaps all, its bones destroyed by the gastric juices of the predator.

It would not be an exaggeration to say that the typical vertebrate fossil consists of a single bone, or tooth, or fish scale. The preservation of an intact skeleton with the bones in the relative positions they had in life requires a remarkable circumstances, such as burial in volcanic ash, burial in aeolian sand due to the sudden slumping of a sand dune, burial in a mudslide, burial by a turbidity current, and so forth. The mineralization of soft parts is even less common and is seen only in exceptionally rare chemical and biological conditions.

Key Points

- Preservation of remains in amber or other substances is the rarest from of fossilization; this mechanism allows scientists to study the skin, hair, and organs of ancient creatures.
- Permineralization, where minerals like silica fill the empty spaces of shells, is the most common form of fossilization.
- Molds form when shells or bones dissolve, leaving behind an empty depression; a cast is then formed when the depression is filled by sediment.
- Replacement occurs when the original shell or bone dissolves away and is replaced by a different mineral; when this occurs with permineralization, it is called petrification.
- In compression, the most common form of fossilization of leaves and ferns, a dark imprint of the fossil remains.
- Decay, chemical weathering, erosion, and predators are factors that deter fossilization.
- Fossilization of soft body parts is rare, and hard parts are better preserved when buried.

Key Terms

- **amber**: a hard, generally yellow to brown translucent fossil resin
- **permineralization**: form of fossilization in which minerals are deposited in the pores of bone and similar hard animal parts
- **petrification**: process by which organic material is converted into stone through the replacement of the original material and the filling of the original pore spaces with minerals

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21.4.3: Gaps in the Fossil Record

Learning Objectives

- Explain the gap in the fossil record

Incompleteness of the Fossil Record

Each fossil discovery represents a snapshot of the process of evolution. Because of the specialized and rare conditions required for a biological structure to fossilize, many important species or groups may never leave fossils at all. Even if they do leave fossils, humans may never find them—for example, if they are buried under hundreds of feet of ice in Antarctica. The number of species known about through the fossil record is less than 5% of the number of species alive today. Fossilized species may represent less than 1% of all the species that have ever lived.

Types of Fossils in the Fossil Record

The fossil record is very uneven and is mostly comprised of fossils of organisms with hard body parts, leaving most groups of soft-bodied organisms with little to no fossil record. Groups considered to have a good fossil record, including transitional fossils between these groups, are the vertebrates, the echinoderms, the brachiopods, and some groups of arthropods. Their hard bones and shells fossilize easily, unlike the bodies of organisms like cephalopods or jellyfish.

Romer's Gap

Romer's gap is an example of an apparent gap in the tetrapod fossil record used in the study of evolutionary biology. These gaps represent periods from which no relevant fossils have been found. Romer's gap is named after paleontologist Alfred Romer, who first recognized it. Romer's gap spanned from approximately 360 to 345 million years ago, corresponding to the first 15 million years of the Carboniferous Period.



Figure **21.4.3.1**: Romer's Gap: The bank of the Whiteadder Water in Scotland is one of the few known localities bearing fossils of tetrapods from Romer's gap.

There has been much debate over why there are so few fossils from this time period. Some scientists have suggested that the geochemistry of the time period caused bad conditions for fossil formation, so few organisms were fossilized. Another theory suggests that scientists have simply not yet discovered an excavation site for these fossils, due to inaccessibility or random chance.

Key Points

- The number of species known about through fossils is less than 1% of all species that have ever lived.
- Because hard body parts are more easily preserved than soft body parts, there are more fossils of animals with hard body parts, such as vertebrates, echinoderms, brachiopods, and some groups of arthropods.
- Very few fossils have been found in the period from 360 to 345 million years ago, known as Romer's gap. Theories to explain this include the period's geochemistry, errors in excavation, and limited vertebrate diversity.

Key Terms

- **transitional fossil**: Fossilized remains of a life form that exhibits traits common to both an ancestral group and its derived descendant group.
- **Romer's gap**: A period in the tetrapod fossil record (360 to 345 million years ago) from which excavators have not yet found relevant fossils.

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21.4.4: Carbon Dating and Estimating Fossil Age

Learning Objectives

- Summarize the available methods for dating fossils

Determining Fossil Ages

Paleontology seeks to map out how life evolved across geologic time. A substantial hurdle is the difficulty of working out fossil ages. There are several different methods for estimating the ages of fossils, including:

1. stratigraphy
2. biostratigraphy
3. carbon dating

Stratigraphy

Paleontologists rely on stratigraphy to date fossils. Stratigraphy is the science of understanding the strata, or layers, that form the sedimentary record. Strata are differentiated from each other by their different colors or compositions and are exposed in cliffs, quarries, and river banks. These rocks normally form relatively horizontal, parallel layers, with younger layers forming on top.

If a fossil is found between two layers of rock whose ages are known, the fossil's age is thought to be between those two known ages. Because rock sequences are not continuous, but may be broken up by faults or periods of erosion, it is difficult to match up rock beds that are not directly adjacent.



Figure **21.4.4.1**: Sedimentary layers: The layers of sedimentary rock, or strata, can be seen as horizontal bands of differently colored or differently structured materials exposed in this cliff. The deeper layers are older than the layers found at the top, which aids in determining the relative age of fossils found within the strata.

Biostratigraphy

Fossils of species that survived for a relatively short time can be used to match isolated rocks: this technique is called biostratigraphy. For instance, the extinct chordate *Eoplacognathus pseudoplanus* is thought to have existed during a short range in the Middle Ordovician period. If rocks of unknown age have traces of *E. pseudoplanus*, they have a mid-Ordovician age. Such index fossils must be distinctive, globally distributed, and occupy a short time range to be useful. Misleading results can occur if the index fossils are incorrectly dated.

Relative Dating

Stratigraphy and biostratigraphy can in general provide only relative dating (A was before B), which is often sufficient for studying evolution. This is difficult for some time periods, however, because of the barriers involved in matching rocks of the same age across continents. Family-tree relationships can help to narrow down the date when lineages first appeared. For example, if fossils of B date to X million years ago and the calculated "family tree" says A was an ancestor of B, then A must have evolved earlier.

It is also possible to estimate how long ago two living branches of a family tree diverged by assuming that DNA mutations accumulate at a constant rate. However, these “molecular clocks” are sometimes inaccurate and provide only approximate timing. For example, they are not sufficiently precise and reliable for estimating when the groups that feature in the Cambrian explosion first evolved, and estimates produced by different approaches to this method may vary as well.

Carbon Dating

Together with stratigraphic principles, radiometric dating methods are used in geochronology to establish the geological time scale. Beds that preserve fossils typically lack the radioactive elements needed for radiometric dating (” radiocarbon dating ” or simply “carbon dating”). The principle of radiocarbon dating is simple: the rates at which various radioactive elements decay are known, and the ratio of the radioactive element to its decay products shows how long the radioactive element has existed in the rock. This rate is represented by the half-life, which is the time it takes for half of a sample to decay.

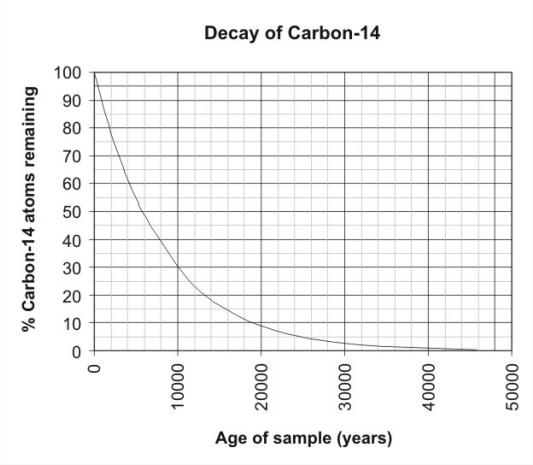


Figure **21.4.4.1**: Half-life of Carbon-14: Radiometric dating is a technique used to date materials such as rocks or carbon, usually based on a comparison between the observed abundance of a naturally occurring radioactive isotope and its decay products, using known decay rates.

The half-life of carbon-14 is 5,730 years, so carbon dating is only relevant for dating fossils less than 60,000 years old. Radioactive elements are common only in rocks with a volcanic origin, so the only fossil-bearing rocks that can be dated radiometrically are volcanic ash layers. Carbon dating uses the decay of carbon-14 to estimate the age of organic materials, such as wood and leather.

Key Points

- Determining the ages of fossils is an important step in mapping out how life evolved across geologic time.
- The study of stratigraphy enables scientists to determine the age of a fossil if they know the age of layers of rock that surround it.
- Biostratigraphy enables scientists to match rocks with particular fossils to other rocks with those fossils to determine age.
- Paleontology seeks to map out how life evolved across geologic time. A substantial hurdle is the difficulty of working out fossil ages.
- Scientists use carbon dating when determining the age of fossils that are less than 60,000 years old, and that are composed of organic materials such as wood or leather.

Key Terms

- **half-life**: The time required for half of the nuclei in a sample of a specific isotope to undergo radioactive decay.
- **stratigraphy**: The study of rock layers and the layering process.
- **radiocarbon dating**: A method of estimating the age of an artifact or biological vestige based on the relative amounts of various isotopes of carbon present in a sample.

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21.4.5: The Fossil Record and the Evolution of the Modern Horse

Learning Objectives

- Analyze the fossil record to understand the evolution of horses

Fossils provide evidence that organisms from the past are not the same as those found today, and demonstrate a progression of evolution. Scientists date and categorize fossils to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of forms over millions of years.

Case Study: Evolution of the Modern Horse

Highly detailed fossil records have been recovered for sequences in the evolution of modern horses. The fossil record of horses in North America is especially rich and contains transition fossils: fossils that show intermediate stages between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago, which gave rise to the first horse-like species 55 to 42 million years ago in the genus *Eohippus*.

The first equid fossil was found in the gypsum quarries in Montmartre, Paris in the 1820s. The tooth was sent to the Paris Conservatory, where Georges Cuvier identified it as a browsing equine related to the tapir. His sketch of the entire animal matched later skeletons found at the site. During the H.M.S. Beagle survey expedition, Charles Darwin had remarkable success with fossil hunting in Patagonia. In 1833 in Santa Fe, Argentina, he was “filled with astonishment” when he found a horse’s tooth in the same stratum as fossils of giant armadillos and wondered if it might have been washed down from a later layer, but concluded this was “not very probable.” In 1836, the anatomist Richard Owen confirmed the tooth was from an extinct species, which he subsequently named *Equus curvidens*.

The original sequence of species believed to have evolved into the horse was based on fossils discovered in North America in the 1870s by paleontologist Othniel Charles Marsh. The sequence, from *Eohippus* to the modern horse (*Equus*), was popularized by Thomas Huxley and became one of the most widely known examples of a clear evolutionary progression. The sequence of transitional fossils was assembled by the American Museum of Natural History into an exhibit that emphasized the gradual, “straight-line” evolution of the horse.

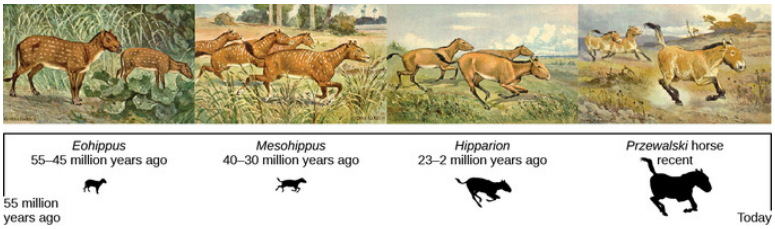


Figure 21.4.5.1: Horse evolution: This illustration shows an artist’s renderings of species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. One of the trends, depicted here, is the evolutionary tracking of a drying climate and increase in prairie versus forest habitat reflected in forms that are more adapted to grazing and predator escape through running.

Since then, as the number of equid fossils has increased, the actual evolutionary progression from *Eohippus* to *Equus* has been discovered to be much more complex and multibranched than was initially supposed. Detailed fossil information on the rate and distribution of new equid species has also revealed that the progression between species was not as smooth and consistent as was once believed.

Although some transitions were indeed gradual progressions, a number of others were relatively abrupt in geologic time, taking place over only a few million years. Both anagenesis, a gradual change in an entire population ‘s gene frequency, and cladogenesis, a population “splitting” into two distinct evolutionary branches, occurred, and many species coexisted with “ancestor” species at various times.

Adaptation for Grazing

The series of fossils tracks the change in anatomy resulting from a gradual drying trend that changed the landscape from a forested habitat to a prairie habitat. Early horse ancestors were originally specialized for tropical forests, while modern horses are now adapted to life on drier land. Successive fossils show the evolution of teeth shapes and foot and leg anatomy to a grazing habit with adaptations for escaping predators.

The horse belongs to the order Perissodactyla (odd-toed ungulates), the members of which all share hoofed feet and an odd number of toes on each foot, as well as mobile upper lips and a similar tooth structure. This means that horses share a common ancestry with tapirs and rhinoceroses. Later species showed gains in size, such as those of *Hipparion*, which existed from about 23 to 2 million years ago. The fossil record shows several adaptive radiations in the horse lineage, which is now much reduced to only one genus, *Equus*, with several species. Paleozoologists have been able to piece together a more complete outline of the modern horse's evolutionary lineage than that of any other animal.

Key Points

- A dog-like organism gave rise to the first horse ancestors 55-42 million years ago.
- The fossil record shows modern horses moved from tropical forests to prairie habitats, developed teeth, and grew in size.
- The first equid fossil was a tooth from the extinct species *Equus curvidens* found in Paris in the 1820s.
- Thomas Huxley popularized the evolutionary sequence of horses, which became one of the most common examples of clear evolutionary progression.
- Horse evolution was previously believed to be a linear progress, but after more fossils were discovered, it was determined the evolution of horses was more complex and multi-branched.
- Horses have evolved from gradual change (anagenesis) as well as abrupt progression and division (cladogenesis).

Key Terms

- **cladogenesis**: An evolutionary splitting event in which each branch and its smaller branches forms a clade.
- **equid**: A member of the horse family.
- **anagenesis**: Evolution of a new species through a large scale change in gene frequency so that the new species replaces the old, rather than branching to produce an additional species.

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21.4.6: Homologous Structures

Learning Objectives

- Describe the connection between evolution and the appearance of homologous structures

Homologous Structures

Homology is the relationship between structures or DNA derived from the most recent common ancestor. A common example of homologous structures in evolutionary biology are the wings of bats and the arms of primates. Although these two structures do not look similar or have the same function, genetically, they come from the same structure of the last common ancestor. Homologous traits of organisms are therefore explained by descent from a common ancestor.

It's important to note that defining two structures as homologous depends on what ancestor is being described as the common ancestor. If we go all the way back to the beginning of life, all structures are homologous!

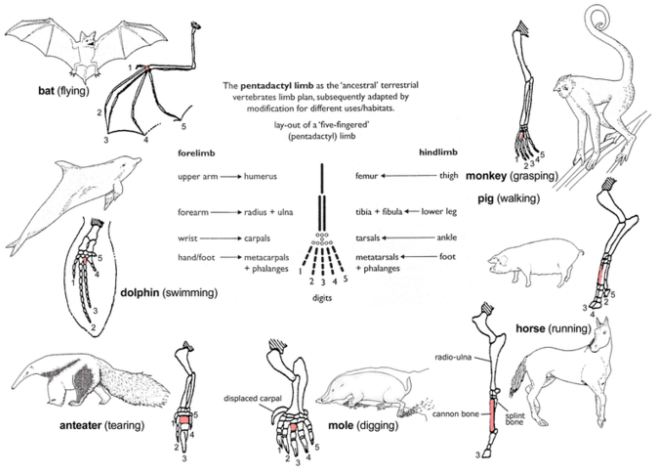


Figure **21.4.6.1**: Homology in the forelimbs of vertebrates: The principle of homology illustrated by the adaptive radiation of the forelimb of mammals. All conform to the basic pentadactyl pattern but are modified for different usages. The third metacarpal is shaded throughout; the shoulder is crossed-hatched.

In genetics, homology is measured by comparing protein or DNA sequences. Homologous gene sequences share a high similarity, supporting the hypothesis that they share a common ancestor.

Homology can also be partial: new structures can evolve through the combination of developmental pathways or parts of them. As a result, hybrid or mosaic structures can evolve that exhibit partial homologies. For example, certain compound leaves of flowering plants are partially homologous both to leaves and shoots because they combine some traits of leaves and some of shoots.

Paralogous Structures

Homologous sequences are considered paralogous if they were separated by a gene duplication event; if a gene in an organism is duplicated to occupy two different positions in the same genome, then the two copies are paralogous.

A set of sequences that are paralogous are called paralogs of each other. Paralogs typically have the same or similar function, but sometimes do not. It is considered that due to lack of the original selective pressure upon one copy of the duplicated gene, this copy is free to mutate and acquire new functions.

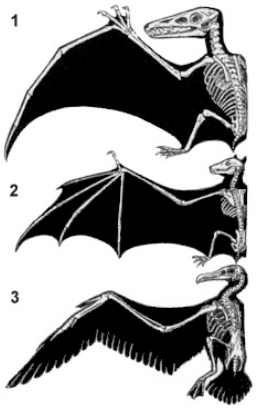


Figure **21.4.6.1**: Homology vs. analogy: The wings of pterosaurs (1), bats (2), and birds (3) are analogous as wings, but homologous as forelimbs. This is because they are similar characteristically and even functionally, but evolved from different ancestral roots.

Paralogous genes often belong to the same species, but not always. For example, the hemoglobin gene of humans and the myoglobin gene of chimpanzees are considered paralogs. This is a common problem in bioinformatics; when genomes of different species have been sequenced and homologous genes have been found, one can not immediately conclude that these genes have the same or similar function, as they could be paralogs whose function has diverged.

Analogous Structures

The opposite of homologous structures are analogous structures, which are physically similar structures between two taxa that evolved separately (rather than being present in the last common ancestor). Bat wings and bird wings evolved independently and are considered analogous structures. Genetically, a bat wing and a bird wing have very little in common; the last common ancestor of bats and birds did not have wings like either bats or birds. Wings evolved independently in each lineage after diverging from ancestors with forelimbs that were not used as wings (terrestrial mammals and theropod dinosaurs, respectively).

It is important to distinguish between different hierarchical levels of homology in order to make informative biological comparisons. In the above example, the bird and bat wings are analogous as wings, but homologous as forelimbs because the organ served as a forearm (not a wing) in the last common ancestor of tetrapods.

Analogy is different than homology. Although analogous characteristics are superficially similar, they are not homologous because they are phylogenetically independent. The wings of a maple seed and the wings of an albatross are analogous but not homologous (they both allow the organism to travel on the wind, but they didn't both develop from the same structure). Analogy is commonly also referred to as homoplasy.

Key Points

- Homology is a relationship defined between structures or DNA derived from a common ancestor and illustrates descent from a common ancestor.
- Analogous structures are physically (but not genetically) similar structures that were not present the last common ancestor.
- Homology can also be partial; new structures can evolve through the combination or parts of developmental pathways.
- Analogy may also be referred to as homoplasy, which is further divided into parallelism, reversal, and convergence.

Key Terms

- **homology**: A correspondence of structures in two life forms with a common evolutionary origin, such as flippers and hands.
- **analogy**: The relationship between characteristics that are apparently similar but did not develop from the same structure
- **homoplasy**: A correspondence between the parts or organs of different species acquired as the result of parallel evolution or convergence.

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21.4.7: Convergent Evolution

Learning Objectives

- Predict the circumstances supporting convergent evolution of two species

Convergent Evolution

Sometimes, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called convergent evolution, where similar traits evolve independently in species that do not share a recent common ancestry.

Examples of Convergent Evolution

Convergent evolution describes the independent evolution of similar features in species of different lineages. The two species came to the same function, flying, but did so separately from each other. They have "converged" on this useful trait. Both sharks and dolphins have similar body forms, yet are only distantly related: sharks are fish and dolphins are mammals. Such similarities are a result of both populations being exposed to the same selective pressures. Within both groups, changes that aid swimming have been favored. Thus, over time, they developed similar appearances (morphology), even though they are not closely related.

One of the most well-known examples of convergent evolution is the camera eye of cephalopods (e.g., octopus), vertebrates (e.g., mammals), and cnidaria (e.g., box jellies). Their last common ancestor had at most a very simple photoreceptive spot, but a range of processes led to the progressive refinement of this structure to the advanced camera eye. There is, however, one subtle difference: the cephalopod eye is "wired" in the opposite direction, with blood and nerve vessels entering from the back of the retina, rather than the front as in vertebrates.

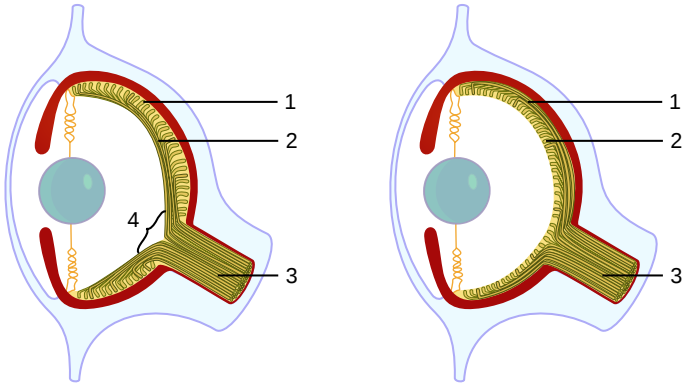


Figure **21.4.7.1**: Eye evolution: Vertebrates and octopuses developed the camera eye independently. In the vertebrate version the nerve fibers pass in front of the retina, and there is a blind spot (4) where the nerves pass through the retina. In the octopus version, the eye is constructed the "right way out," with the nerves attached to the rear of the retina. This means that octopuses do not have a blind spot.

Convergent evolution is similar to, but distinguishable from, the phenomenon of parallel evolution. Parallel evolution occurs when two independent but similar species evolve in the same direction and thus independently acquire similar characteristics; for example, gliding frogs have evolved in parallel from multiple types of tree frog.

Analogous Structures

Traits arising through convergent evolution are analogous structures, in contrast to homologous structures, which have a common origin, but not necessarily similar function. The British anatomist Richard Owen was the first scientist to recognize the fundamental difference between analogies and homologies. Bat and pterosaur wings are an example of analogous structures, while the bat wing is homologous to human and other mammal forearms, sharing an ancestral state despite serving different functions.

Divergent Evolution

The opposite of convergent evolution is divergent evolution, whereby related species evolve different traits. On a molecular level, this can happen due to random mutation unrelated to adaptive changes.

Key Points

- Examples of convergent evolution include the relationship between bat and insect wings, shark and dolphin bodies, and vertebrate and cephalopod eyes.
- Analogous structures arise from convergent evolution, but homologous structures do not.
- Convergent evolution is the opposite of divergent evolution, in which related species evolve different traits.
- Convergent evolution is similar to parallel evolution, in which two similar but independent species evolve in the same direction and independently acquire similar characteristics.

Key Terms

- **parallel evolution**: the development of a similar trait in related, but distinct, species descending from the same ancestor, but from different clades
- **convergent evolution**: a trait of evolution in which species not of similar recent origin acquire similar properties due to natural selection
- **divergent evolution**: the process by which a species with similar traits become groups that are tremendously different from each other over many generations
- **morphology**: the form and structure of an organism

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21.4.8: Vestigial Structures

Learning Objectives

- Discuss the connection between evolution and the existence of vestigial structures

What Are Vestigial Structures?

Some organisms possess structures with no apparent function which appear to be residual parts from a past ancestor. For example, some snakes have pelvic bones despite having no legs because they descended from reptiles that did have legs. Another example of a structure with no function is the human vermiform appendix. These unused structures without function are called vestigial structures. Other examples of vestigial structures are wings (which may have other functions) on flightless birds like the ostrich, leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.

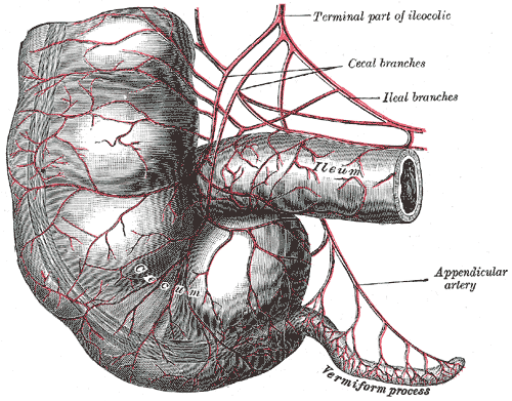


Figure **21.4.8.1**: Vestigial appendix: In humans the vermiform appendix is a vestigial structure; it has lost much of its ancestral function.

There are also several reflexes and behaviors that are considered to be vestigial. The formation of goose bumps in humans under stress is a vestigial reflex its function in human ancestors was to raise the body's hair, making the ancestor appear larger and scaring off predators. The arrector pili muscle, which is a band of smooth muscle that connects the hair follicle to connective tissue, contracts and creates the goose bumps on skin.

Vestigial Structures in Evolution

Vestigial structures are often homologous to structures that function normally in other species. Therefore, vestigial structures can be considered evidence for evolution, the process by which beneficial heritable traits arise in populations over an extended period of time. The existence of vestigial traits can be attributed to changes in the environment and behavior patterns of the organism in question. As the function of the trait is no longer beneficial for survival, the likelihood that future offspring will inherit the "normal" form of it decreases. In some cases the structure becomes detrimental to the organism.

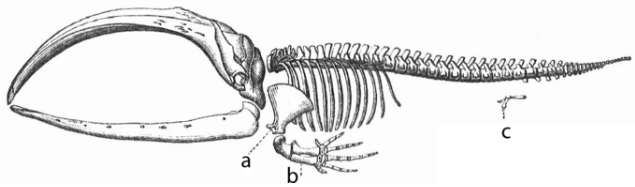


Figure **21.4.8.1**: Whale Skeleton: The pelvic bones in whales are also a good example of vestigial evolution (whales evolved from four-legged land mammals and secondarily lost their hind legs). Letter c in the picture indicates the undeveloped hind legs of a baleen whale.

If there are no selection pressures actively lowering the fitness of the individual, the trait will persist in future generations unless the trait is eliminated through genetic drift or other random events.

Although in many cases the vestigial structure is of no direct harm, all structures require extra energy in terms of development, maintenance, and weight and are also a risk in terms of disease (e.g., infection, cancer). This provides some selective pressure for

the removal of parts that do not contribute to an organism's fitness, but a structure that is not directly harmful will take longer to be 'phased out' than one that is. Some vestigial structures persist due to limitations in development, such that complete loss of the structure could not occur without major alterations of the organism's developmental pattern, and such alterations would likely produce numerous negative side-effects.

The vestigial versions of a structure can be compared to the original version of the structure in other species in order to determine the homology of the structure. Homologous structures indicate common ancestry with those organisms that have a functional version of the structure. Vestigial traits can still be considered adaptations because an adaptation is often defined as a trait that has been favored by natural selection. Adaptations, therefore, need not be adaptive, as long as they were at some point.

Key Points

- Structures that have no apparent function and appear to be residual parts from a past ancestor are called vestigial structures.
- Examples of vestigial structures include the human appendix, the pelvic bone of a snake, and the wings of flightless birds.
- Vestigial structures can become detrimental, but in most cases these structures are harmless; however, these structures, like any other structure, require extra energy and are at risk for disease.
- Vestigial structures, especially non-harmful ones, take a long time to be phased out since eliminating them would require major alterations that could result in negative side effects.

Key Terms

- **vestigial structure**: Genetically determined structures or attributes that have lost most or all of their ancestral function in a given species.
- **adaptation**: A modification of something or its parts that makes it more fit for existence under the conditions of its current environment.

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21.4.9: Biogeography and the Distribution of Species

Learning Objectives

- Relate biogeography and the distribution of species

Distribution of Species

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors, such as temperature and rainfall, vary based on latitude and elevation, primarily. As these abiotic factors change, the composition of plant and animal communities also changes.

Patterns of Species Distribution

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An endemic species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Since species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia.



Figure **21.4.9.1**: Australia: Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal.

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of Proteaceae in Australia, southern Africa, and South America is best explained by the plant family's presence there prior to the southern supercontinent Gondwana breaking up.

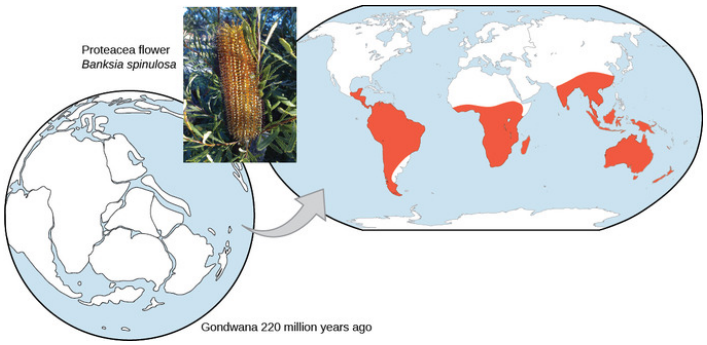


Figure 21.4.9.1: Biogeography: The Proteacea family of plants evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in red).

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Key Points

- Biogeography is the study of geological species distribution, which is influenced by both biotic and abiotic factors.
- Some species are endemic and are only found in a particular region, while others are generalists and are distributed worldwide.
- Species that evolved before the breakup of continents are distributed worldwide.
- Species that evolved after the breakup of continents are found in only certain regions of the planet.

Key Terms

- **endemic**: unique to a particular area or region; not found in other places
- **generalist**: species which can thrive in a wide variety of environmental conditions
- **Pangaea**: supercontinent that included all the landmasses of the earth before the Triassic period and that broke up into Laurasia and Gondwana

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21.5: Anatomical Evidence of Evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, identifying patterns in nature that were consistent with evolution and since Darwin our understanding has become clearer and broader.

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today; fossils show a progression of evolution. Scientists determine the age of fossils and categorize them all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past, and shows the evolution of form over millions of years (Figure **21.5.1**). For example, highly detailed fossil records have been recovered for sequences of species in the evolution of whales and modern horses. The fossil record of horses in North America is especially rich and many contain transition fossils: those showing intermediate anatomy between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago that gave rise to the first horse-like species 55 to 42 million years ago in the genus *Eohippus*. The series of fossils tracks the change in anatomy resulting from a gradual drying trend that changed the landscape from a forested one to a prairie. Successive fossils show the evolution of teeth shapes and foot and leg anatomy to a grazing habit, with adaptations for escaping predators, for example in species of *Mesohippus* found from 40 to 30 million years ago. Later species showed gains in size, such as those of *Hipparion*, which existed from about 23 to 2 million years ago. The fossil record shows several adaptive radiations in the horse lineage, which is now much reduced to only one genus, *Equus*, with several species.

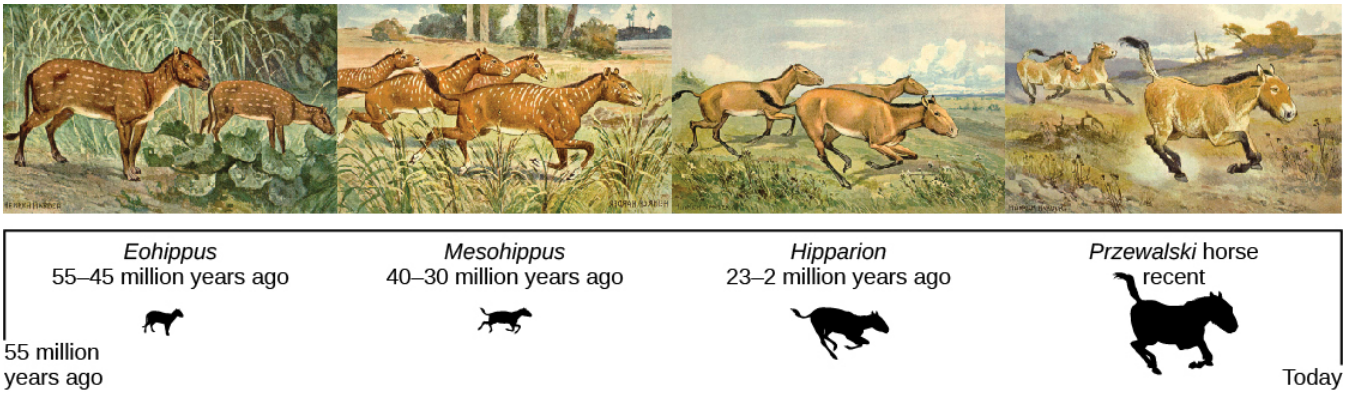


Figure 21.5.1: This illustration shows an artist's renderings of these species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. One of the trends, depicted here is the evolutionary tracking of a drying climate and increase in prairie versus forest habitat reflected in forms that are more adapted to grazing and predator escape through running. Przewalski's horse is one of a few living species of horse.

Anatomy and Embryology

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction (Figure **21.5.2**). That similarity results from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout, evidence of descent from a common ancestor. Scientists call these synonymous parts homologous structures. Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past ancestor. For example, some snakes have pelvic bones despite having no legs because they descended from reptiles that did have legs. These unused structures without function are called vestigial structures. Other examples of vestigial structures are wings on flightless birds (which may have other functions), leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.

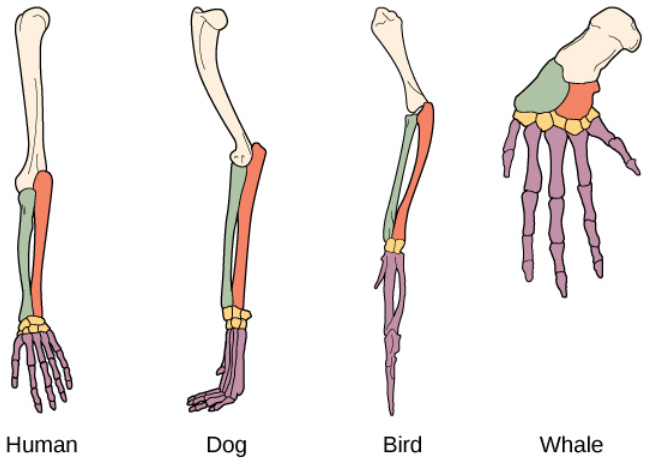


Figure 21.5.2: The similar construction of these appendages indicates that these organisms share a common ancestor.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan (a bird), living in the arctic region have temporary white coverings during winter to blend with the snow and ice (Figure **21.5.3**). The similarity occurs not because of common ancestry, indeed one covering is of fur and the other of feathers, but because of similar selection pressures—the benefits of not being seen by predators.



Figure 21.5.3: The white winter coat of (a) the arctic fox and (b) the ptarmigan's plumage are adaptations to their environments. (credit a: modification of work by Keith Morehouse)

Embryology, the study of the development of the anatomy of an organism to its adult form also provides evidence of relatedness between now widely divergent groups of organisms. Structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits at some point in their early development. These disappear in the adults of terrestrial groups, but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by the time of birth. The reason embryos of unrelated species are often similar is that mutational changes that affect the organism during embryonic development can cause amplified differences in the adult, even while the embryonic similarities are preserved.

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea

(about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, for example the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of Proteaceae in Australia, southern Africa, and South America is best explained by the plant family's presence there prior to the southern supercontinent Gondwana breaking up (Figure **21.5.4**).

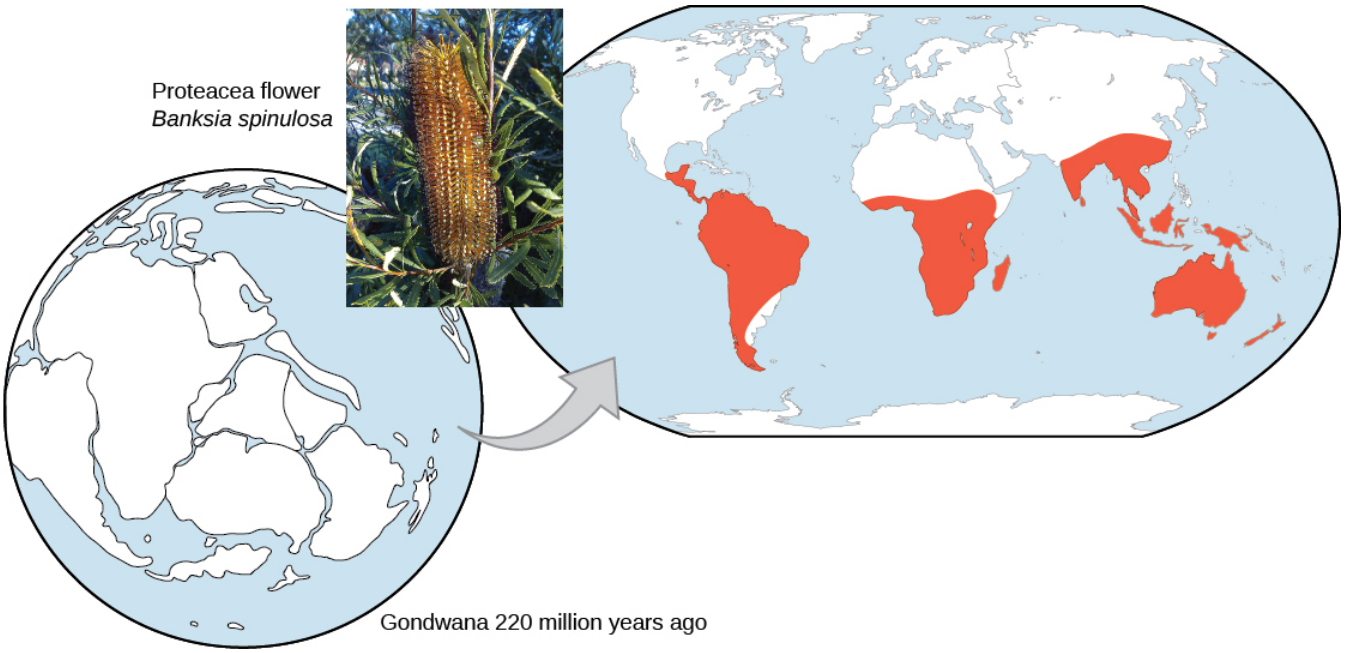


Figure 21.5.4: The Proteacea family of plants evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in red). (credit "Proteacea flower": modification of work by "dorofofoto"/Flickr)

The great diversification of the marsupials in Australia and the absence of other mammals reflects that island continent's long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents migration of species to other regions. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all found nowhere else but on their island, yet display distant relationships to ancestral species on mainlands.

Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material and of the near universality of the genetic code and the machinery of DNA replication and expression. Fundamental divisions in life between the three domains are reflected in major structural differences in otherwise conservative structures such as the components of ribosomes and the structures of membranes. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences—exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events. These duplications are a kind of mutation in which an entire gene is added as an extra copy (or many copies) in the genome. These duplications allow the free modification of one copy by mutation, selection, and drift, while the second copy continues to produce a functional protein. This allows the original function for the protein to be kept, while evolutionary forces tweak the copy until it functions in a new way.

Section Summary

The evidence for evolution is found at all levels of organization in living things and in the extinct species we know about through fossils. Fossils provide evidence for the evolutionary change through now extinct forms that led to modern species. For example,

there is a rich fossil record that shows the evolutionary transitions from horse ancestors to modern horses that document intermediate forms and a gradual adaptation to changing ecosystems. The anatomy of species and the embryological development of that anatomy reveal common structures in divergent lineages that have been modified over time by evolution. The geographical distribution of living species reflects the origins of species in particular geographic locations and the history of continental movements. The structures of molecules, like anatomical structures, reflect the relationships of living species and match patterns of similarity expected from descent with modification.

Glossary

vestigial structure

a physical structure present in an organism but that has no apparent function and appears to be from a functional structure in a distant ancestor

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SECTION OVERVIEW

21.6: Convergent Evolution and the Biogeographical Record

Learning Objectives

- Predict the circumstances supporting convergent evolution of two species

Convergent Evolution

Sometimes, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called convergent evolution, where similar traits evolve independently in species that do not share a recent common ancestry.

Examples of Convergent Evolution

Convergent evolution describes the independent evolution of similar features in species of different lineages. The two species came to the same function, flying, but did so separately from each other. They have "converged" on this useful trait. Both sharks and dolphins have similar body forms, yet are only distantly related: sharks are fish and dolphins are mammals. Such similarities are a result of both populations being exposed to the same selective pressures. Within both groups, changes that aid swimming have been favored. Thus, over time, they developed similar appearances (morphology), even though they are not closely related.

One of the most well-known examples of convergent evolution is the camera eye of cephalopods (e.g., octopus), vertebrates (e.g., mammals), and cnidaria (e.g., box jellies). Their last common ancestor had at most a very simple photoreceptive spot, but a range of processes led to the progressive refinement of this structure to the advanced camera eye. There is, however, one subtle difference: the cephalopod eye is "wired" in the opposite direction, with blood and nerve vessels entering from the back of the retina, rather than the front as in vertebrates.

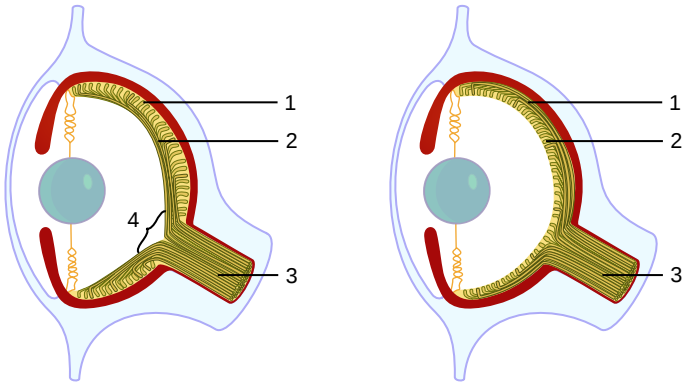


Figure **21.6.1**: Eye evolution: Vertebrates and octopuses developed the camera eye independently. In the vertebrate version the nerve fibers pass in front of the retina, and there is a blind spot (4) where the nerves pass through the retina. In the octopus version, the eye is constructed the "right way out," with the nerves attached to the rear of the retina. This means that octopuses do not have a blind spot.

Convergent evolution is similar to, but distinguishable from, the phenomenon of parallel evolution. Parallel evolution occurs when two independent but similar species evolve in the same direction and thus independently acquire similar characteristics; for example, gliding frogs have evolved in parallel from multiple types of tree frog.

Analogous Structures

Traits arising through convergent evolution are analogous structures, in contrast to homologous structures, which have a common origin, but not necessarily similar function. The British anatomist Richard Owen was the first scientist to recognize the fundamental

difference between analogies and homologies. Bat and pterosaur wings are an example of analogous structures, while the bat wing is homologous to human and other mammal forearms, sharing an ancestral state despite serving different functions.

Divergent Evolution

The opposite of convergent evolution is divergent evolution, whereby related species evolve different traits. On a molecular level, this can happen due to random mutation unrelated to adaptive changes.

Key Points

- Examples of convergent evolution include the relationship between bat and insect wings, shark and dolphin bodies, and vertebrate and cephalopod eyes.
- Analogous structures arise from convergent evolution, but homologous structures do not.
- Convergent evolution is the opposite of divergent evolution, in which related species evolve different traits.
- Convergent evolution is similar to parallel evolution, in which two similar but independent species evolve in the same direction and independently acquire similar characteristics.

Key Terms

- **parallel evolution**: the development of a similar trait in related, but distinct, species descending from the same ancestor, but from different clades
- **convergent evolution**: a trait of evolution in which species not of similar recent origin acquire similar properties due to natural selection
- **divergent evolution**: the process by which a species with similar traits become groups that are tremendously different from each other over many generations
- **morphology**: the form and structure of an organism

21.6.1: Biogeographical Record

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21.6.1: Biogeographical Record

Learning Objectives

- Relate biogeography and the distribution of species

Distribution of Species

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors, such as temperature and rainfall, vary based on latitude and elevation, primarily. As these abiotic factors change, the composition of plant and animal communities also changes.

Patterns of Species Distribution

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An endemic species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Since species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia.



Figure **21.6.1.1**: Australia: Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal.

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of Proteaceae in Australia, southern Africa, and South America is best explained by the plant family's presence there prior to the southern supercontinent Gondwana breaking up.

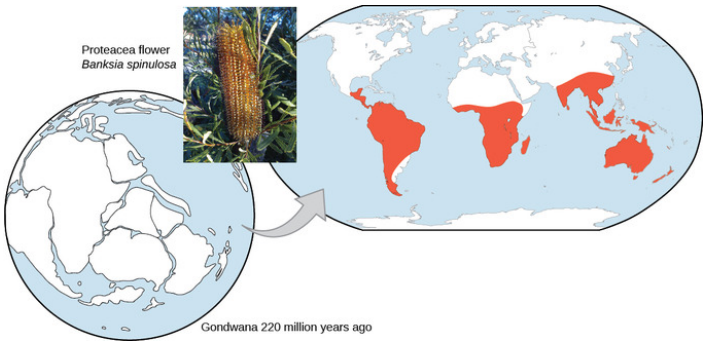


Figure 21.6.1.1: Biogeography: The Proteacea family of plants evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in red).

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Key Points

- Biogeography is the study of geological species distribution, which is influenced by both biotic and abiotic factors.
- Some species are endemic and are only found in a particular region, while others are generalists and are distributed worldwide.
- Species that evolved before the breakup of continents are distributed worldwide.
- Species that evolved after the breakup of continents are found in only certain regions of the planet.

Key Terms

- **endemic**: unique to a particular area or region; not found in other places
- **generalist**: species which can thrive in a wide variety of environmental conditions
- **Pangaea**: supercontinent that included all the landmasses of the earth before the Triassic period and that broke up into Laurasia and Gondwana

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21.7: Darwin's Critics

Although the theory of evolution initially generated some controversy, by 20 years after the publication of *On the Origin of Species* it was almost universally accepted by biologists, particularly younger biologists. Nevertheless, the theory of evolution is a difficult concept and misconceptions about how it works abound. In addition, there are those that reject it as an explanation for the diversity of life.

CONCEPT IN ACTION

This website addresses some of the main misconceptions associated with the theory of evolution.

Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word "theory" with the way scientists use the word. In science, a "theory" is understood to be a concept that has been extensively tested and supported over time. We have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes what scientists understand to be facts about the world. In the same way, the theory of evolution describes facts about the living world. As such, a theory in science has survived significant efforts to discredit it by scientists, who are naturally skeptical. While theories can sometimes be overturned or revised, this does not lessen their weight but simply reflects the constantly evolving state of scientific knowledge. In contrast, a "theory" in common vernacular means a guess or suggested explanation for something. This meaning is more akin to the concept of a "hypothesis" used by scientists, which is a tentative explanation for something that is proposed to either be supported or disproved. When critics of evolution say evolution is "just a theory," they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mischaracterization. If this were the case, geneticist Theodosius Dobzhansky would not have said that "nothing in biology makes sense, except in the light of evolution."[1]

Individuals Evolve

An individual is born with the genes it has—these do not change as the individual ages. Therefore, an individual cannot evolve or adapt through natural selection. Evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, but this is called development; it involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking about the evolution of a characteristic, it is probably best to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time, and then measures the average bill size in the population several years later after there has been a strong selective pressure, this average value may be different as a result of evolution. Although some individuals may survive from the first time to the second, those individuals will still have the same bill size. However, there may be enough new individuals with different bill sizes to change the average bill size.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics complain that it cannot explain the origin of life. The theory does not try to explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies—the origin of species. It does not shed light on the beginnings of life including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, over a very long time, and presumably just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things. The early stages of life included the formation of organic molecules such as carbohydrates, amino acids, or nucleotides. If these were formed from inorganic precursors today, they would simply be broken down by living things. The early stages of life also probably included more complex aggregations of molecules into enclosed structures with an internal environment, a boundary layer of some form, and the external environment. Such structures, if they were formed now, would be quickly consumed or broken down by living organisms.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA or RNA, either within a cell or within a pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Organisms Evolve on Purpose

Statements such as "organisms evolve in response to a change in an environment," are quite common. There are two easy misunderstandings possible with such a statement. First of all, the statement must not be understood to mean that individual organisms evolve, as was discussed above. The statement is shorthand for "a population evolves in response to a changing environment." However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and, therefore, producing proportionately more offspring than other phenotypes. This results in change in the population if the characters are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select for a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects for individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic application.

In a larger sense, evolution is also not goal directed. Species do not become "better" over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species. This kind of language is common in popular literature. Certain organisms, ourselves included, are described as the "pinnacle" of evolution, or "perfected" by evolution. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at some point in the future. This holds equally well for a species of insect as it does the human species.

Evolution Is Controversial among Scientists

The theory of evolution was controversial when it was first proposed in 1859, yet within 20 years virtually every working biologist had accepted evolution as the explanation for the diversity of life. The rate of acceptance was extraordinarily rapid, partly because Darwin had amassed an impressive body of evidence. The early controversies involved both scientific arguments against the theory and the arguments of religious leaders. It was the arguments of the biologists that were resolved after a short time, while the arguments of religious leaders have persisted to this day.

The theory of evolution replaced the predominant theory at the time that species had all been specially created within relatively recent history. Despite the prevalence of this theory, it was becoming increasingly clear to naturalists during the nineteenth century that it could no longer explain many observations of geology and the living world. The persuasiveness of the theory of evolution to these naturalists lay in its ability to explain these phenomena, and it continues to hold extraordinary explanatory power to this day. Its continued rejection by some religious leaders results from its replacement of special creation, a tenet of their religious belief. These leaders cannot accept the replacement of special creation by a mechanistic process that excludes the actions of a deity as an explanation for the diversity of life including the origins of the human species. It should be noted, however, that most of the major denominations in the United States have statements supporting the acceptance of evidence for evolution as compatible with their theologies.

The nature of the arguments against evolution by religious leaders has evolved over time. One current argument is that the theory is still controversial among biologists. This claim is simply not true. The number of working scientists who reject the theory of evolution, or question its validity and say so, is small. A Pew Research poll in 2009 found that 97 percent of the 2500 scientists polled believe species evolve.[2] The support for the theory is reflected in signed statements from many scientific societies such as the American Association for the Advancement of Science, which includes working scientists as members. Many of the scientists

that reject or question the theory of evolution are non-biologists, such as engineers, physicians, and chemists. There are no experimental results or research programs that contradict the theory. There are no papers published in peer-reviewed scientific journals that appear to refute the theory. The latter observation might be considered a consequence of suppression of dissent, but it must be remembered that scientists are skeptics and that there is a long history of published reports that challenged scientific orthodoxy in unpopular ways. Examples include the endosymbiotic theory of eukaryotic origins, the theory of group selection, the microbial cause of stomach ulcers, the asteroid-impact theory of the Cretaceous extinction, and the theory of plate tectonics. Research with evidence and ideas with scientific merit are considered by the scientific community. Research that does not meet these standards is rejected.

Other Theories Should Be Taught

A common argument from some religious leaders is that alternative theories to evolution should be taught in public schools. Critics of evolution use this strategy to create uncertainty about the validity of the theory without offering actual evidence. In fact, there are no viable alternative scientific theories to evolution. The last such theory, proposed by Lamarck in the nineteenth century, was replaced by the theory of natural selection. A single exception was a research program in the Soviet Union based on Lamarck's theory during the early twentieth century that set that country's agricultural research back decades. Special creation is not a viable alternative scientific theory because it is not a scientific theory, since it relies on an untestable explanation. Intelligent design, despite the claims of its proponents, is also not a scientific explanation. This is because intelligent design posits the existence of an unknown designer of living organisms and their systems. Whether the designer is unknown or supernatural, it is a cause that cannot be measured; therefore, it is not a scientific explanation. There are two reasons not to teach nonscientific theories. First, these explanations for the diversity of life lack scientific usefulness because they do not, and cannot, give rise to research programs that promote our understanding of the natural world. Experiments cannot test non-material explanations for natural phenomena. For this reason, teaching these explanations as science in public schools is not in the public interest. Second, in the United States, it is illegal to teach them as science because the U.S. Supreme Court and lower courts have ruled that the teaching of religious belief, such as special creation or intelligent design, violates the establishment clause of the First Amendment of the U.S. Constitution, which prohibits government sponsorship of a particular religion.

The theory of evolution and science in general is, by definition, silent on the existence or non-existence of the spiritual world. Science is only able to study and know the material world. Individual biologists have sometimes been vocal atheists, but it is equally true that there are many deeply religious biologists. Nothing in biology precludes the existence of a god, indeed biology as a science has nothing to say about it. The individual biologist is free to reconcile her or his personal and scientific knowledge as they see fit. The Voices for Evolution project (http://ncse.com/voices), developed through the National Center for Science Education, works to gather the diversity of perspectives on evolution to advocate it being taught in public schools.

Section Summary

The theory of evolution is a difficult concept and misconceptions abound. The factual nature of evolution is often challenged by wrongly associating the scientific meaning of a theory with the vernacular meaning. Evolution is sometimes mistakenly interpreted to mean that individuals evolve, when in fact only populations can evolve as their gene frequencies change over time. Evolution is often assumed to explain the origin of life, which it does not speak to. It is often spoken in goal-directed terms by which organisms change through intention, and selection operates on mutations present in a population that have not arisen in response to a particular environmental stress. Evolution is often characterized as being controversial among scientists; however, it is accepted by the vast majority of working scientists. Critics of evolution often argue that alternative theories to evolution should be taught in public schools; however, there are no viable alternative scientific theories to evolution. The alternative religious beliefs should not be taught as science because it cannot be proven, and in the United States it is unconstitutional. Science is silent on the question of the existence of a god while scientists are able to reconcile religious belief and scientific knowledge.

Footnotes

1. 1 Theodosius Dobzhansky. "Biology, Molecular and Organismic." *American Zoologist* 4, no. 4 (1964): 449.
2. 2 Pew Research Center for the People & the Press, *Public Praises Science; Scientists Fault Public, Media* (Washington, DC, 2009), 37.Contributors

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SECTION OVERVIEW

22.1.1: Understanding Evolution

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22.1.1.1: What is Evolution?

Learning Objectives

- Describe the historical influences on Darwin's theory of evolution

Introduction: Evolution

All species of living organisms, including bacteria and chimpanzees, evolved at some point from a different species. Although it may seem that living things today stay the same, this is not the case: evolution is a gradual and ongoing process.

The theory of evolution is the unifying theory of biology, meaning it is the framework within which biologists ask questions about the living world. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote that "nothing makes sense in biology except in the light of evolution." The tenet that all species have evolved and diversified from a common ancestor is the foundation from which we approach all questions in biology. It provides a direction for predictions about living things, which has been validated through extensive scientific experimentation.

Evolution by natural selection describes a mechanism for the change of species over time. Well before Darwin began to explore the concept of evolution, the idea that species change over time had already been suggested and debated. The view that species are static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks who expressed ideas about evolution. During the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc Comte de Buffon who observed that various geographic regions have different plant and animal populations, even when the environments are similar. It was also accepted that there are extinct species.



Figure **22.1.1.1.1**: Evolution by Natural Selection: All organisms are products of evolution adapted to their environment. (a) Saguaro (Carnegiea gigantea) can soak up 750 liters of water in a single rain storm, enabling these cacti to survive the dry conditions of the Sonoran desert in Mexico and the Southwestern United States. (b) The Andean semiaquatic lizard (Potamites montanicola), discovered in Peru in 2010, lives between 1,570 to 2,100 meters in elevation and, unlike most lizards, is nocturnal and swims. Scientists still do not know how these cold-blood animals are able to move in the cold (10 to 15°C) temperatures of the Andean night.

During this time, a Scottish naturalist named James Hutton proposed that geological change occurs gradually by the accumulation of small changes over long periods of time. This theory contrasted with the predominant view of the time: that the geology of the planet is a consequence of catastrophic events that occurred during a relatively brief past. During the nineteenth century, Hutton's views were popularized by the geologist Charles Lyell, who was a friend of Charles Darwin. Lyell's ideas, in turn, influenced Darwin's concept of evolution. The greater age of the earth proposed by Lyell supported the gradual evolution that Darwin proposed, and the slow process of geological change provided an analogy for the gradual change in species.

In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a different mechanism for evolutionary change. This mechanism is now referred to as an inheritance of acquired characteristics. This idea states that modifications in an individual are caused by its environment, or the use or disuse of a structure during its lifetime, and that these changes can be inherited by its offspring, bringing about change in a species. While this mechanism for evolutionary change was discredited, Lamarck's ideas were an important influence on the concept of evolution.

Key Points

- Ancient Greeks expressed ideas about evolution, which were reintroduced in the eighteenth century by Georges-Louis Leclerc Comte de Buffon who observed different environments had different plant and animal populations.

- James Hutton proposed that geological changes occur gradually over time via the accumulation of small changes rather than through large catastrophic events.
- Charles Lyell popularized James Hutton's theory; this theory of incremental change influenced Darwin's theory of evolution.
- Jean-Baptiste Lamarck proposed the theory of the inheritance of acquired characterstics; this theory has now been discredited, but it served as an important influence on the theory of evolution.

Key Terms

- **evolution**: the change in the genetic composition of a population over successive generations
- **inheritance of acquired characteristics**: hypothesis that physiological changes acquired over the life of an organism may be transmitted to its offspring

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22.1.1.2: Charles Darwin and Natural Selection

Learning Objectives

- Explain how natural selection can lead to evolution

Charles Darwin and Natural Selection

In the mid-nineteenth century, the mechanism for evolution was independently conceived of and described by two naturalists: Charles Darwin and Alfred Russel Wallace. Importantly, each naturalist spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world to places like South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, as with Wallace's later journeys to the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands west of Ecuador. On these islands, Darwin observed that species of organisms on different islands were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with a unique beak shape. The species on the islands had a graded series of beak sizes and shapes with very small differences between the most similar. He observed that these finches closely resembled another finch species on the mainland of South America. Darwin imagined that the island species might be modified from one of the original mainland species. Upon further study, he realized that the varied beaks of each finch helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks for breaking seeds, while insect-eating finches had spear-like beaks for stabbing their prey.

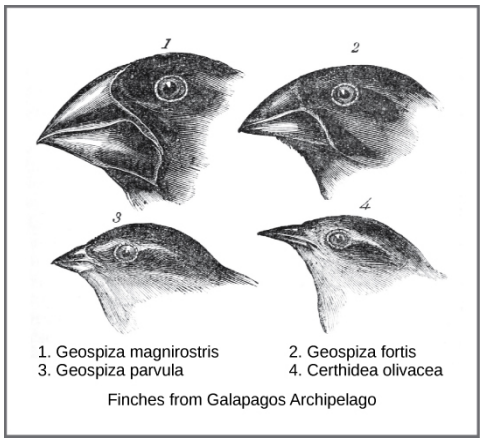


Figure **22.1.1.2.1**: Beak Shape Among Finch Species: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources.

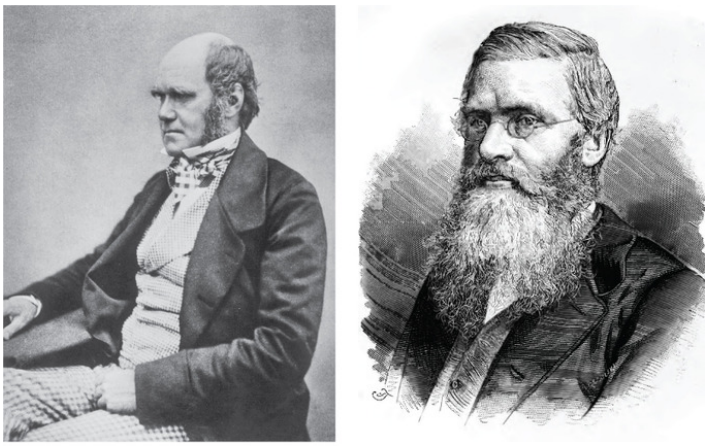
Natural Selection

Wallace and Darwin observed similar patterns in other organisms and independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. Natural selection, also known as "survival of the fittest," is the more prolific reproduction of individuals with favorable traits that survive environmental change because of those traits. This leads to evolutionary change, the trait becoming predominant within a population. For example, Darwin observed that a population of giant tortoises found in the Galapagos Archipelago have longer necks than those that lived on other islands with dry lowlands. These tortoises were "selected" because they could reach more leaves and access more food than those with short necks. In times of drought, when fewer leaves would be available, those that could reach more leaves had a better chance to eat and survive than those that could not reach the food source. Consequently, long-necked tortoises would more probably be reproductively successful and pass the long-necked trait to their offspring. Over time, only long-necked tortoises would be present in the population.

Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, most characteristics of organisms are inherited, or passed from parent to offspring, although *how* traits were inherited was unknown. Second, more offspring are produced than are able to survive. The capacity for reproduction in all organisms outstrips the availability of resources

to support their numbers. Thus, there is competition for those resources in each generation. Both Darwin and Wallace were influenced by an essay written by economist Thomas Malthus who discussed this principle in relation to human populations. Third, Darwin and Wallace reasoned that offspring with the inherited characteristics that allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over successive generations in a process that Darwin called descent with modification. Ultimately, natural selection leads to greater adaptation of the population to its local environment; it is the only mechanism known for adaptive evolution.

Papers by Darwin and Wallace presenting the idea of natural selection were read together in 1858 before the Linnean Society in London. The following year, Darwin's book, *On the Origin of Species*, was published. His book outlined his arguments for evolution by natural selection.



(a) (b)

Figure **22.1.1.2.1**: Charles Darwin and Alfred Wallace: Both (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Key Points

- Wallace traveled to Brazil to collect and observe insects from the Amazon rainforest.
- Darwin observed that finches in the Galápagos Islands had different beaks than finches in South America; these adaptations equiped the birds to acquire specific food sources.
- Wallace and Darwin observed similar patterns in the variation of organisms and independently developed the same explanation for how such variations could occur over time, a mechanism Darwin called natural selection.
- According to natural selection, also known as "survival of the fittest," individuals with traits that enable them to survive are more reproductively successful; this leads to those traits becoming predominant within a population.
- Natural selection is an inevitable outcome of three principles: most characteristics are inherited, more offspring are produced than are able to survive, and offspring with more favorable characteristics will survive and have more offspring than those individuals with less favorable traits.

Key Terms

- **natural selection**: a process in which individual organisms or phenotypes that possess favorable traits are more likely to survive and reproduce
- **descent with modification**: change in populations over generations

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22.1.1.3: The Galapagos Finches and Natural Selection

Learning Objectives

- Describe how finches provide visible evidence of evolution

Visible Evidence of Ongoing Evolution: Darwin's Finches

From 1831 to 1836, Darwin traveled around the world, observing animals on different continents and islands. On the Galapagos Islands, Darwin observed several species of finches with unique beak shapes. He observed these finches closely resembled another finch species on the mainland of South America and that the group of species in the Galápagos formed a graded series of beak sizes and shapes, with very small differences between the most similar. Darwin imagined that the island species might be all species modified from one original mainland species. In 1860, he wrote, "seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."

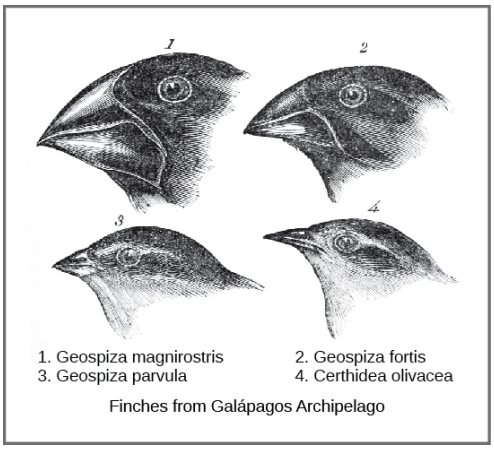


Figure **22.1.1.3.1**: Darwin's Finches: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources. This illustration shows the beak shapes for four species of ground finch: 1. *Geospiza magnirostris* (the large ground finch), 2. *G. fortis* (the medium ground finch), 3. *G. parvula* (the small tree finch), and 4. *Certhidea olivacea* (the green-warbler finch).

Natural Selection

Darwin called this mechanism of change natural selection. Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, the characteristics of organisms are inherited, or passed from parent to offspring. Second, more offspring are produced than are able to survive; in other words, resources for survival and reproduction are limited. The capacity for reproduction in all organisms exceeds the availability of resources to support their numbers. Thus, there is a competition for those resources in each generation. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Out of these three principles, Darwin reasoned that offspring with inherited characteristics that allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called "descent with modification," or evolution.

Studies of Natural Selection After Darwin

Demonstrations of evolution by natural selection can be time consuming. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of the operation of natural selection. The Grants found changes from one generation to the next in the beak shapes of the medium ground finches on the Galápagos island of Daphne Major.

The medium ground finch feeds on seeds. The birds have inherited variation in the bill shape with some individuals having wide, deep bills and others having thinner bills. Large-billed birds feed more efficiently on large, hard seeds, whereas smaller billed birds

feed more efficiently on small, soft seeds. During 1977, a drought period altered vegetation on the island. After this period, the number of seeds declined dramatically; the decline in small, soft seeds was greater than the decline in large, hard seeds. The large-billed birds were able to survive better than the small-billed birds the following year.

The year following the drought when the Grants measured beak sizes in the much-reduced population, they found that the average bill size was larger. This was clear evidence for natural selection of bill size caused by the availability of seeds. The Grants had studied the inheritance of bill sizes and knew that the surviving large-billed birds would tend to produce offspring with larger bills, so the selection would lead to evolution of bill size. Subsequent studies by the Grants have demonstrated selection on and evolution of bill size in this species in response to other changing conditions on the island. The evolution has occurred both to larger bills, as in this case, and to smaller bills when large seeds became rare.

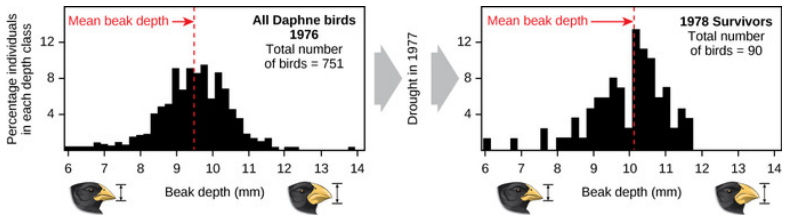


Figure **22.1.1.3.1**: Finches of Daphne Major: A drought on the Galápagos island of Daphne Major in 1977 reduced the number of small seeds available to finches, causing many of the small-beaked finches to die. This caused an increase in the finches' average beak size between 1976 and 1978.

Key Points

- Darwin observed the Galapagos finches had a graded series of beak sizes and shapes and predicted these species were modified from one original mainland species.
- Darwin called differences among species natural selection, which is caused by the inheritance of traits, competition between individuals, and the variation of traits.
- Offspring with inherited characteristics that allow them to best compete will survive and have more offspring than those individuals with variations that are less able to compete.
- Large-billed finches feed more efficiently on large, hard seeds, whereas smaller billed finches feed more efficiently on small, soft seeds.
- When small, soft seeds become rare, large-billed finches will survive better, and there will be more larger-billed birds in the following generation; when large, hard seeds become rare, the opposite will occur.

Key Terms

- **natural selection**: a process in which individual organisms or phenotypes that possess favorable traits are more likely to survive and reproduce
- **evolution**: the change in the genetic composition of a population over successive generations

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22.1.1.4: Processes and Patterns of Evolution

Learning Objectives

- Explain why only heritable variation can be acted upon by natural selection

Processes and Patterns of Evolution

Variation

Natural selection can only take place if there is variation, or differences, among individuals in a population. Importantly, these differences must have some genetic basis; otherwise, the selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons, such as an individual being taller due to better nutrition rather than different genes.

Genetic diversity within a population comes from two main mechanisms: mutation and sexual reproduction. Mutation, a change in the DNA sequence, is the ultimate source of new alleles, or new genetic variation in any population. The genetic changes caused by mutation can have one of three outcomes:

- Many mutations will have no effect on the fitness of the phenotype; these are called neutral mutations.
- A mutation may affect the phenotype of the organism in a way that gives it reduced fitness (a lower likelihood of survival or fewer offspring).
- A mutation may produce a phenotype with a beneficial effect on fitness. Different mutations will have a range of effects on the fitness of an organism that expresses them in their phenotype, from a small effect to a great effect.

Sexual reproduction also leads to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each of the offspring. However, sexual reproduction can not lead to new genes, but rather provides a new combination of genes in a given individual.

Adaptations

A heritable trait that aids the survival and reproduction of an organism in its present environment is called an adaptation. Scientists describe groups of organisms becoming adapted to their environment when a change in the range of genetic variation occurs over time that increases or maintains the “fitness” of the population to its environment. The webbed feet of platypuses are an adaptation for swimming. The snow leopards’ thick fur is an adaptation for living in the cold. The cheetahs’ fast speed is an adaptation for catching prey.

Whether or not a trait is favorable depends on the environmental conditions at the time. The same traits are not always selected because environmental conditions can change. For example, consider a species of plant that grew in a moist climate and did not need to conserve water. Large leaves were selected because they allowed the plant to obtain more energy from the sun. Large leaves require more water to maintain than small leaves, and the moist environment provided favorable conditions to support large leaves. After thousands of years, the climate changed and the area no longer had excess water. The direction of natural selection shifted so that plants with small leaves were selected because those populations were able to conserve water to survive the new environmental conditions.

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. When two species evolve in diverse directions from a common point, it is called divergent evolution. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments and adaptation to different kinds of pollinators.



(a) (b)

Figure **22.1.1.4.1**: Flowering Plants: Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star (Liatrus spicata) and the (b) purple coneflower (Echinacea purpurea) vary in appearance, yet both share a similar basic morphology.

In other cases, similar phenotypes evolve independently in distantly-related species. For example, flight has evolved in both bats and insects; they both have structures we refer to as wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called convergent evolution, where similar traits evolve independently in species that do not share a recent common ancestry. The two species came to the same function, flying, but did so separately from each other.

These physical changes occur over enormous spans of time and help explain how evolution occurs. Natural selection acts on individual organisms, which in turn can shape an entire species. Although natural selection may work in a single generation on an individual, it can take thousands or even millions of years for the genotype of an entire species to evolve. It is over these large time spans that life on earth has changed and continues to change.

Key Points

- Genetic variation within a population is a result of mutations and sexual reproduction.
- A mutation may be neutral, reduce an organism's fitness, or increase an organism's fitness.
- An adaptation is a heritable trait that increases the survival and rate of reproduction of an organism in its present environment.
- Divergent evolution describes the process in which two species evolve in diverse directions from a common point.
- Convergent evolution is the process in which similar traits evolve independently in species that do not share a recent common ancestry.

Key Terms

- **adaptation**: modification of something or its parts that makes it more fit for existence under the conditions of its current environment
- **divergent evolution**: the process by which a species with similar traits become groups that are tremendously different from each other over many generations
- **convergent evolution**: a trait of evolution in which species not of similar recent origin acquire similar properties due to natural selection

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22.1.1.5: Evidence of Evolution

Learning Objectives

- Explain the development of the theory of evolution

Evidence of Evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, to identifying patterns in nature that were consistent with evolution. Since Darwin, our understanding has become clearer and broader.

Fossils, Anatomy, and Embryology

Fossils provide solid evidence that organisms from the past are not the same as those found today; they show a progression of evolution. Scientists calculate the age of fossils and categorize them to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years. For example, scientists have recovered highly-detailed records showing the evolution of humans and horses. The whale flipper shares a similar morphology to appendages of birds and mammals, indicating that these species share a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout. Scientists call these synonymous parts homologous structures.

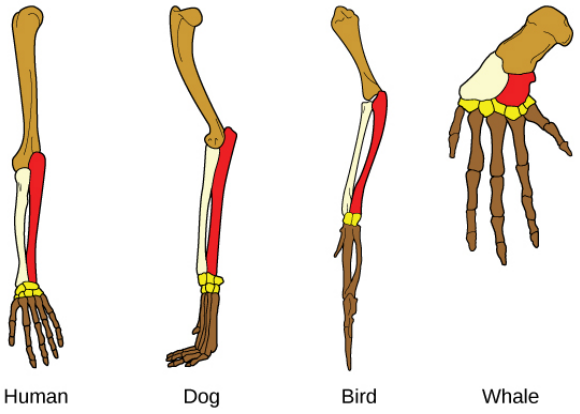


Figure **22.1.1.5.1**: Common Ancestors: The similar construction of these appendages indicates that these organisms share a common ancestor.



Figure **22.1.1.5.1**: Evolution of Humans and Horses: (a) In this display, fossil hominids are arranged from oldest (bottom) to newest (top). As hominids evolved, the shape of the skull changed. (b) An artist's rendition of extinct species of the genus Equus reveals that these ancient species resembled the modern horse (Equus ferus), but varied in size.

Some structures exist in organisms that have no apparent function at all, appearing to be residual parts from a common ancestor. These unused structures (such as wings on flightless birds, leaves on some cacti, and hind leg bones in whales) are vestigial.

Embryology, the study of the development of the anatomy of an organism to its adult form, provides evidence for evolution as embryo formation in widely-divergent groups of organisms tends to be conserved. Structures that are absent in the adults of some groups often appear in their embryonic forms, disappearing by the time the adult or juvenile form is reached. For example, all

vertebrate embryos, including humans, exhibit gill slits and tails at some point in their early development. These disappear in the adults of terrestrial groups, but are maintained in adults of aquatic groups, such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by birth.

Another form of evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan living in the arctic region, have been selected for seasonal white phenotypes during winter to blend with the snow and ice. These similarities occur not because of common ancestry, but because of similar selection pressures: the benefits of not being seen by predators.



(a) (b)

Figure **22.1.1.5.1**: Adaptations: Winter Coats: The white winter coat of the (a) arctic fox and the (b) ptarmigan's plumage are adaptations to their environments.

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia compared to that of the southern continents that formed from the supercontinent Gondwana.

The great diversification of marsupials in Australia and the absence of other mammals reflect Australia's long isolation. Australia has an abundance of endemic species (those found nowhere else) which is typical of islands whose isolation by expanses of water prevents species from migrating. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all unique to their one point of origin, yet they display distant relationships to ancestral species on mainlands.

Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material, in the near universality of the genetic code, and in the machinery of DNA replication and expression. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences. This is exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplications that allow the free modification of one copy by mutation, selection, or drift (changes in a population ‘s gene pool resulting from chance), while the second copy continues to produce a functional protein.

Key Points

- Fossils serve to highlight the differences and similarities between current and extinct species, showing the evolution of form over time.

- Similar anatomy across different species highlights their common origin and can be seen in homologous and vestigial structures.
- Embryology provides evidence for evolution since the embryonic forms of divergent groups are extremely similar.
- The natural distribution of species across different continents supports evolution; species that evolved before the breakup of the supercontinent are distributed worldwide, whereas species that evolved more recently are more localized.
- Molecular biology indicates that the molecular basis for life evolved very early and has been maintained with little variation across all life on the planet.

Key Terms

- **homologous structure**: the traits of organisms that result from sharing a common ancestor; such traits often have similar embryological origins and development
- **biogeography**: the study of the geographical distribution of living things
- **vestigial structure**: genetically determined structures or attributes that have apparently lost most or all of their ancestral function in a given species

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22.1.1.6: Misconceptions of Evolution

Learning Objectives

- Discuss misconceptions about the theory of evolution

Misconceptions of Evolution

Although the theory of evolution generated controversy when it was first proposed, it was almost universally accepted by biologists within 20 years of the publication of *On the Origin of Species*. Nevertheless, the theory of evolution is a difficult concept and misconceptions about it abound.

Evolution is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word "theory" with the way scientists use the word. In science, a "theory" is understood to be a body of thoroughly-tested and verified explanations for a set of observations of the natural world. Scientists have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes understood facts about the world. In the same way, the theory of evolution describes facts about the living world. A theory in science has also survived significant efforts to discredit it by scientists. In contrast, a "theory" in common vernacular is a word meaning a guess or suggested explanation; this meaning is more akin to the scientific concept of "hypothesis. " When critics of evolution say evolution is "just a theory," they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mis-characterization.

Individuals Evolve

Evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, obviously, but this is called development and involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking about the evolution of a characteristic, it is probably best to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium-ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time and then measures the average bill size in that population several years later, this average value *of the population* will be different as a result of evolution.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. The theory of evolution explains how populations change over time. It does not shed light on the beginnings of life, including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on earth are a particularly difficult problem because it occurred a very long time ago and, presumably, it occurred just once. However, while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties. Once a mechanism of inheritance was in place in the form of a molecule like DNA, either within a cell or pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the expense of inefficient reproducers.

Organisms Evolve on Purpose

Statements such as "organisms evolve in response to a change in an environment" may lead to the misunderstanding that evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and, therefore, producing proportionately more offspring than other phenotypes. This results in change in the population if the characteristics are genetically determined.

It is important to understand that the variation that natural selection works on is already present in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, probably at a low

frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotics.

In a larger sense, evolution is not goal directed. Species do not become “better” over time; they track their changing environment with adaptations that maximize their reproduction. The characteristics that evolve in a species are a function of preexisting variation and the environment, both of which are constantly changing non-directionally. A trait that is fit in one environment at one time may also be fatal at some point in the future.

Evolution = Natural Selection

The terms “evolution” and “natural selection” are often conflated, as the two concepts are closely related. They are not, however, synonymous. Natural selection refers to the process by which organisms better suited for their environment are more likely to survive and produce offspring, thereby proliferating those favorable genetics in a population. Evolution is defined more broadly as any change in the genetic makeup of a population over time. As expounded by Darwin, natural selection is a major driving force of evolution, but it is not the only one.

Genetic drift, for example, is another mechanism by which evolution may occurs. Genetic drift occurs when allelic frequency is altered due to random sampling. It is evolution by chance, and the smaller the population, the more significant the effects on genetic distribution due to sampling error. For example, a population bottleneck, which occurs when an event such as a natural disaster dramatically reduces the size of a population, can result in the elimination or significant reduction of a trait within a population, regardless of how beneficial that trait may be to survival or reproduction. Thus evolution can occur without natural selection.



Figure **22.1.1.6.1**: Misconceptions of Evolution: Lamarckian evolution and giraffes: Lamarck’s hypothesis for how evolution worked stated that organisms could pass on traits they had acquired during their lifetime to the progeny, such as giraffes gaining a long neck because their parents needed to reach high food.

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Key Points

- Attacks on the theory of evolution sometimes take issue with the word “theory”, which in the vernacular means a guess or suggested explanation. In scientific language, “theory” indicates a body of thoroughly-tested and verified explanations for a set of observations of the natural world.
- Evolution does not take place on an individual level; evolution is the average change of a characteristic within an entire population.
- Evolution does not explain the origin of life; the theory of evolution instead explains how populations change over time and how traits are selected in order to increase the fitness of a population.
- Favorable traits do not arise as a result of the environment as these traits are already present; individuals with favorable traits are more likely to survive and, thus, will have greater fitness than individuals with less desirable traits.
- Evolution and natural selection are not synonymous. Natural selection is just one mechanism by which evolution occurs.

Key Terms

- **theory**: a well-substantiated explanation of some aspect of the natural world based on knowledge that has been repeatedly confirmed through observation and experimentation

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CHAPTER OVERVIEW

22.1.2: Formation of New Species

Topic hierarchy

22.1.2.1: The Biological Species Concept

22.1.2.2: Reproductive Isolation

22.1.2.3: Speciation

22.1.2.4: Allopatric Speciation

22.1.2.5: Sympatric Speciation

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22.1.2.1: The Biological Species Concept

Learning Objectives

- Explain the biological species concept

Species and the Ability to Reproduce

A species is a group of individual organisms that interbreed and produce fertile, viable offspring. According to this definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile offspring.

Members of the same species share both external and internal characteristics which develop from their DNA. The closer relationship two organisms share, the more DNA they have in common, just like people and their families. People's DNA is likely to be more like their father or mother's DNA than their cousin's or grandparent's DNA. Organisms of the same species have the highest level of DNA alignment and, therefore, share characteristics and behaviors that lead to successful reproduction.

Species' appearance can be misleading in suggesting an ability or inability to mate. For example, even though domestic dogs (*Canis lupus familiaris*) display phenotypic differences, such as size, build, and coat, most dogs can interbreed and produce viable puppies that can mature and sexually reproduce.



Figure **22.1.2.1.1**: Interbreeding in Dogs: Dogs of different breeds still have the ability to reproduce. The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo.

In other cases, individuals may appear similar although they are not members of the same species. For example, even though bald eagles (*Haliaeetus leucocephalus*) and African fish eagles (*Haliaeetus vocifer*) are both birds and eagles, each belongs to a separate species group. If humans were to artificially intervene and fertilize the egg of a bald eagle with the sperm of an African fish eagle and a chick did hatch, that offspring, called a hybrid (a cross between two species), would probably be infertile: unable to successfully reproduce after it reached maturity. Different species may have different genes that are active in development; therefore, it may not be possible to develop a viable offspring with two different sets of directions. Thus, even though hybridization may take place, the two species still remain separate.



Figure **22.1.2.1.1**: Species Similarity & Reproduction: Species that appear similar may not be able to reproduce. The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species.

Populations of species share a gene pool: a collection of all the variants of genes in the species. Again, the basis to any changes in a group or population of organisms must be genetic for this is the only way to share and pass on traits. When variations occur within a species, they can only be passed to the next generation along two main pathways: asexual reproduction or sexual reproduction. The change will be passed on asexually simply if the reproducing cell possesses the changed trait. For the changed trait to be

passed on by sexual reproduction, a gamete, such as a sperm or egg cell, must possess the changed trait. In other words, sexually-reproducing organisms can experience several genetic changes in their body cells, but if these changes do not occur in a sperm or egg cell, the changed trait will never reach the next generation. Only heritable traits can evolve. Therefore, reproduction plays a paramount role for genetic change to take root in a population or species. In short, organisms must be able to reproduce with each other to pass new traits to offspring.

Key Points

- Members of the same species are similar both in their external appearance and their internal physiology; the closer the relationship between two organisms, the more similar they will be in these features.
- Some species can look very dissimilar, such as two very different breeds of dogs, but can still mate and produce viable offspring, which signifies that they belong to the same species.
- Some species may look very similar externally, but can be dissimilar enough in their genetic makeup that they cannot produce viable offspring and are, therefore, different species.
- Mutations can occur in any cell of the body, but if a change does not occur in a sperm or egg cell, it cannot be passed on to the organism's offspring.

Key Terms

- **species**: a group of organsms that, in nature, are capable of mating and producing viable, fertile offspring
- **hybrid**: offspring resulting from cross-breeding different entities, e.g. two different species or two purebred parent strains
- **gene pool**: the complete set of unique alleles that would be found by inspecting the genetic material of every living member of a species or population

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22.1.2.2: Reproductive Isolation

Learning Objectives

- Explain how reproductive isolation can result in speciation

Reproductive Isolation

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were to be brought together, mating would be improbable, but if mating did occur, offspring would be non-viable or infertile. Many types of diverging characters may affect reproductive isolation, the ability to interbreed, of the two populations. Reproductive isolation is a collection of mechanisms, behaviors, and physiological processes that prevent the members of two different species that cross or mate from producing offspring, or which ensure that any offspring that may be produced is not fertile.

Scientists classify reproductive isolation in two groups: prezygotic barriers and postzygotic barriers. Recall that a zygote is a fertilized egg: the first cell of the development of an organism that reproduces sexually. Therefore, a prezygotic barrier is a mechanism that blocks reproduction from taking place; this includes barriers that prevent fertilization when organisms attempt reproduction. A postzygotic barrier occurs after zygote formation; this includes organisms that don't survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, called temporal isolation, can act as a form of reproductive isolation. For example, two species of frogs inhabit the same area, but one reproduces from January to March, whereas the other reproduces from March to May.



(a) (b)

Figure **22.1.2.2.1**: Temporal isolation: These two related frog species exhibit temporal reproductive isolation. (a) Rana aurora breeds earlier in the year than (b) Rana boylii.

In some cases, populations of a species move to a new habitat and take up residence in a place that no longer overlaps with other populations of the same species; this is called habitat isolation. Reproduction with the parent species ceases and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, the forces of natural selection, mutation, and genetic drift will likely result in the divergence of the two groups.

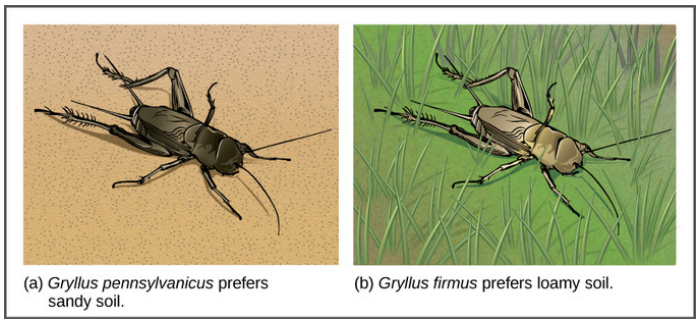


Figure 22.1.2.2.1: Habitat isolation: Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) Gryllus pennsylvanicus prefers sandy soil, while the cricket (b) Gryllus firmus prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated.

Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction from taking place. For example, male fireflies use specific light patterns to attract females. Various species display their lights differently; if a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells prevent fertilization from taking place; this is called a gametic barrier. Similarly, in some cases, closely-related organisms try to mate, but their reproductive structures simply do not fit together. For example, damselfly males of different species have differently-shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together..

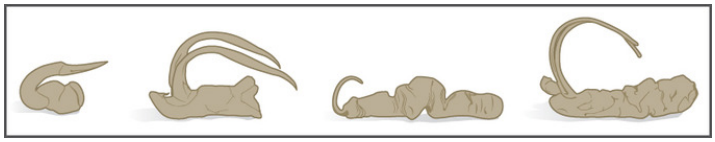


Figure 22.1.2.2.1: Differences in reproductive structures in male damselflies: The shape of the male reproductive organ varies among male damselfly species and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.

In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary in length and diameter, which prevents the plant from being cross-pollinated with a different species.



Figure 22.1.2.2.1: Reproductive isolation in plants: Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds.

When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages; this is called hybrid inviability. In another postzygotic situation, reproduction leads to the birth and growth of a hybrid that is sterile and unable to reproduce offspring of their own; this is called hybrid sterility.

Key Points

- Reproductive isolation can be either prezygotic (barriers that prevent fertilization) or postzygotic (barriers that occur after zygote formation such as organisms that die as embryos or those that are born sterile).
- Some species may be prevented from mating with each other by the incompatibility of their anatomical mating structures, or a resulting offspring may be prevented by the incompatibility of their gametes.

- Postzygotic barriers include the creation of hybrid individuals that do not survive past the embryonic stages (hybrid inviability) or the creation of a hybrid that is sterile and unable to produce offspring (hybrid sterility).
- Temporal isolation can result in species that are physically similar and may even live in the same habitat, but if their breeding schedules do not overlap then interbreeding will never occur.
- Behavioral isolation, in which the behaviors involved in mating are so unique as to prevent mating, is a prezygotic barrier that can cause two otherwise-compatible species to be uninterested in mating with each other.
- Behavioral isolation, in which the behaviors involved in mating are so unique as to prevent mating, is a prezygotic barrier that can cause two otherwise compatible species to be uninterested in mating with each other.

Key Terms

- **reproductive isolation**: a collection of mechanisms, behaviors, and physiological processes that prevent two different species that mate from producing offspring, or which ensure that any offspring produced is not fertile
- **temporal isolation**: factors that prevent potentially fertile individuals from meeting that reproductively isolate the members of distinct species
- **behavioral isolation**: the presence or absence of a specific behavior that prevents reproduction between two species from taking place
- **prezygotic barrier**: a mechanism that blocks reproduction from taking place by preventing fertilization
- **postzygotic barrier**: a mechanism that blocks reproduction after fertilization and zygote formation
- **hybrid inviability**: a situation in which a mating between two individuals creates a hybrid that does not survive past the embryonic stages
- **hybrid sterility**: a situation in which a mating between two individuals creates a hybrid that is sterile

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22.1.2.3: Speciation

Learning Objectives

- Define speciation and discuss the ways in which it may occur

Speciation

The biological definition of species, which works for sexually-reproducing organisms, is a group of actually or potentially interbreeding individuals. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. In fact, the presence in nature of hybrids between similar species suggests that they may have descended from a single interbreeding species: the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet, there must be mechanisms for speciation: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species*, which bears some resemblance to the more modern phylogenetic diagram of elephant evolution. The diagram shows that as one species changes over time, it branches repeatedly to form more than one new species as long as the population survives or until the organism becomes extinct.

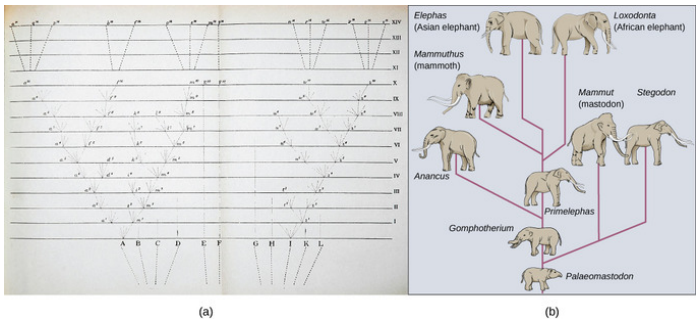


Figure **22.1.2.3.1**: The Evolution of Species: The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the Palaeomastodon, a species that lived in Egypt 35–50 million years ago.

For speciation to occur, two new populations must be formed from one original population; they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories: allopatric speciation and sympatric speciation. Allopatric speciation (allo- = "other"; -patric = "homeland") involves geographic separation of populations from a parent species and subsequent evolution. Sympatric speciation (sym- = "same"; -patric = "homeland") involves speciation occurring within a parent species remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely; multiple events can be conceptualized as single splits occurring close in time.

Key Points

- For the majority of species, the definition of a species is a group of animals that can potentially interbreed, although some different species are capable of producing hybrid offspring.
- Darwin was the first to envision speciation as the branching of two or more new species from one ancestral species; indicated by a diagram he made that bears a striking resemblance to modern-day phylogenetic diagrams.
- For a new species to be formed from an old species, certain events or changes must occur such that the new population is no longer capable of interbreeding with the old one.
- Speciation can occur either through allopatric speciation, when a population is geographically separated from one another, or through sympatric speciation, in which the two new species are not geographically separated.

- Speciation, the formation of two species from one original species, occurs as one species changes over time and branches to form more than one new species.

Key Terms

- **sympatric**: living in the same territory without interbreeding
- **allopatric**: not living in the same territory; geographically isolated and thus unable to crossbreed
- **speciation**: the process by which new distinct species evolve

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22.1.2.4: Allopatric Speciation

Learning Objectives

- Give examples of allopatric speciation

Allopatric Speciation

A geographically-continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous, that free-flow of alleles is prevented. When that separation continues for a period of time, the two populations are able to evolve along different trajectories. This is known as allopatric speciation. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ causing natural selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion forming a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are individuals from each population would fly back and forth, continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be improbable; therefore, speciation would be probably occur.

Biologists group allopatric processes into two categories: dispersal and vicariance. Dispersal occurs when a few members of a species move to a new geographical area, while vicariance occurs when a natural situation arises to physically divide organisms.

Scientists have documented numerous cases of allopatric speciation. For example, along the west coast of the United States, two separate sub-species of spotted owls exist. The northern spotted owl has genetic and phenotypic differences from its close relative, the Mexican spotted owl, which lives in the south.



Figure **22.1.2.4.1**: Allopatric speciation due to geographic separation: The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation.

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more probable it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would generally have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south causing the types of organisms in each ecosystem differ, as do their behaviors and habits. Also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, resulting in speciation.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area with each finding a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. This is called adaptive radiation because many adaptations evolve from a single point of origin, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved.

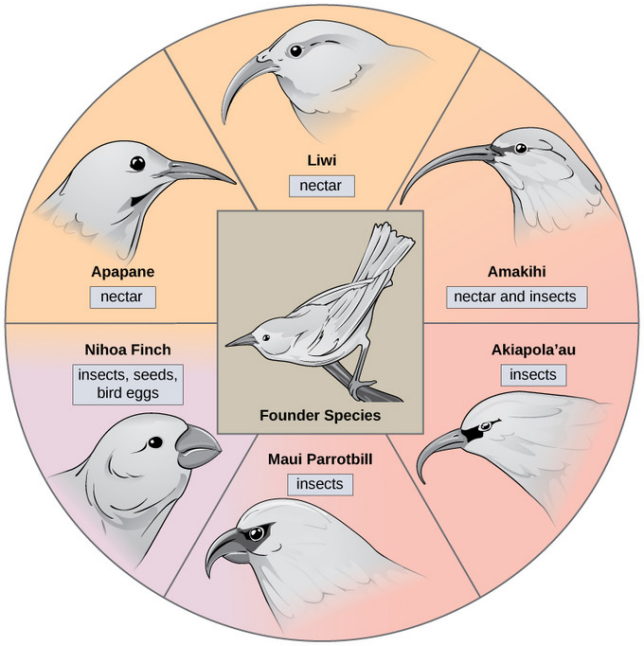


Figure **22.1.2.4.1**: Adaptive Radiation: The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

In Hawaiian honeycreepers, the response to natural selection based on specific food sources in each new habitat led to the evolution of a different beak suited to the specific food source. The seed-eating birds have a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects.

Key Points

- When a population is geographically continuous, the allele frequencies among its members are similar; however, when a population becomes separated, the allele frequencies between the two groups can begin to vary.
- If the separation between groups continues for a long period of time, the differences between their alleles can become more and more pronounced due to differences in climate, predation, food sources, and other factors, eventually leading to the formation of a new species.
- Geographic separation between populations can occur in many ways; the severity of the separation depends on the travel capabilities of the species.
- Allopatric speciation events can occur either by dispersal, when a few members of a species move to a new geographical area, or by vicariance, when a natural situation, such as the formation of a river or valley, physically divide organisms.
- When a population disperses throughout an area, into new, different and often isolated habitats, multiple speciation events can occur in which the single original species gives rise to many new species; this phenomenon is called adaptive radiation.

Key Terms

- **vicariance**: the separation of a group of organisms by a geographic barrier, resulting in differentiation of the original group into new varieties or species
- **adaptive radiation**: the diversification of species into separate forms that each adapt to occupy a specific environmental niche

- **dispersal**: the movement of a few members of a species to a new geographical area, resulting in differentiation of the original group into new varieties or species

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22.1.2.5: Sympatric Speciation

Learning Objectives

- Give examples of sympatric speciation

Sympatric Speciation

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. The process of speciation within the same space is called sympatric speciation. The prefix “sym” means same, so “sympatric” means “same homeland” in contrast to “allopatric” meaning “other homeland.” A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a serious chromosomal error during cell division. In a normal cell division event, chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has too many or too few individual chromosomes in a condition called aneuploidy.

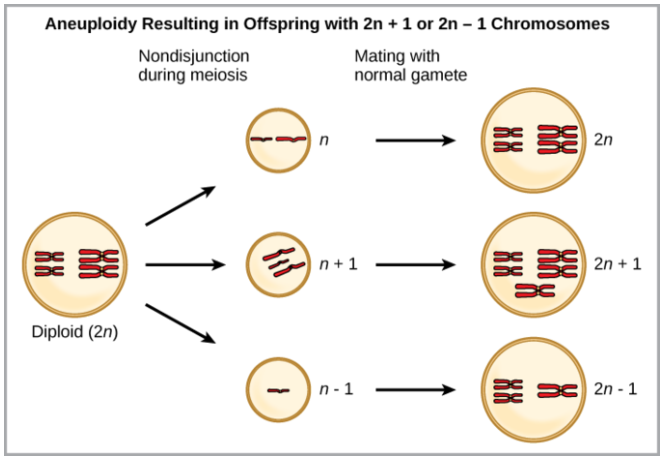


Figure 22.1.2.5.1: Aneuploidy of chromosomes: Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have 2n+1 or 2n-1 chromosomes

Polyploidy is a condition in which a cell or organism has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation, or the inability to interbreed with normal individuals, of an individual in the polyploidy state. In some cases, a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called autopolyploidy. The prefix “auto-” means “self,” so the term means multiple chromosomes from one’s own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.

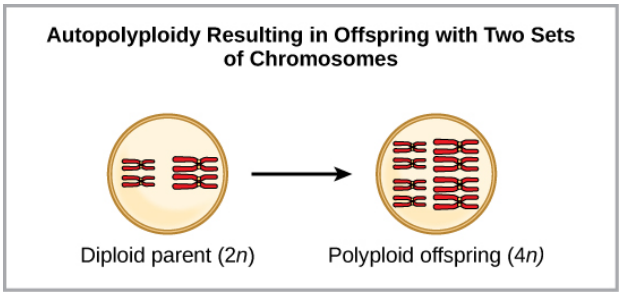


Figure 22.1.2.5.1: The generation of autopolyploidy: Autopolyploidy results when meiosis is not followed by cytokinesis.

For example, if a plant species with 2n = 6 produces autopolyploid gametes that are also diploid (2n = 6, when they should be n = 3), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes produced by this plant species. However, they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with

4n: a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species.

The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an allopolyploid. The prefix “allo-” means “other” (recall from allopatric). Therefore, an allopolyploid occurs when gametes from two different species combine. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

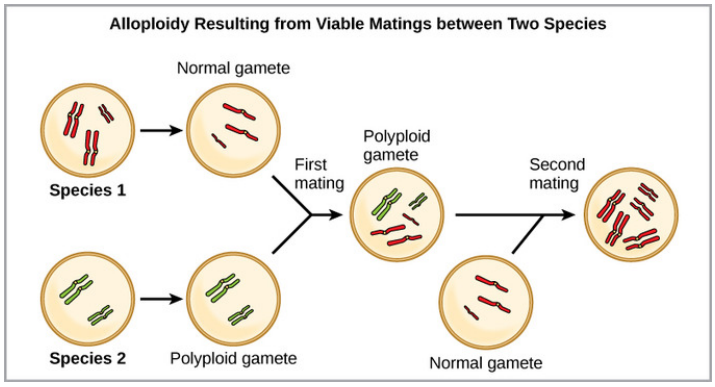


Figure **22.1.2.5.1**: The generation of allopolyploidy: Alloploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. (Animals with any of the types of chromosomal aberrations described here are unlikely to survive and produce normal offspring.) Scientists have discovered more than half of all plant species studied relate back to a species evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

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Key Points

- Sympatric speciation can occur when one individual develops an abnormal number of chromosomes, either extra chromosomes (polyploidy) or fewer, such that viable interbreeding can no longer occur.
- When the extra sets of chromosomes in a polyploid originate with the individual because their own gametes do not undergo cytokinesis after meiosis, the result is autopolyploidy.
- When individuals of two different species reproduce to form a viable offspring, such that the extra chromosomes come from two different species, the result is an allopolyploid.
- Once a species develops an abnormal number of chromosomes, it can then only interbreed with members of the population that have the same abnormal number, which can lead to the development of a new species.

Key Terms

- **sympatric speciation**: the process through which new species evolve from a single ancestral species while inhabiting the same geographic region
- **autopolyploid**: having more than two sets of chromosomes, derived from the same species, as a result of redoubling
- **allopolyploid**: having multiple complete sets of chromosomes derived from different species

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SECTION OVERVIEW

22.1.3: Hybrid Zones and Rates of Speciation

Topic hierarchy

22.1.3.1: Hybrid Zones

22.1.3.2: Varying Rates of Speciation

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22.1.3.1: Hybrid Zones

Learning Objectives

- Discuss how the fitness of a hybrid will lead to changes in the hybrid zone over time

Reconnection After Speciation

Speciation occurs over a span of evolutionary time. When a new species arises, there is a transition period during which the closely-related species continue to interact.

After speciation, two species may recombine or even continue interacting indefinitely. Individual organisms will mate with any nearby individual with which they are capable of breeding. An area where two closely-related species continue to interact and reproduce, forming hybrids, is called a hybrid zone. Over time, the hybrid zone may change depending on the fitness strength and the reproductive barriers of the hybrids.

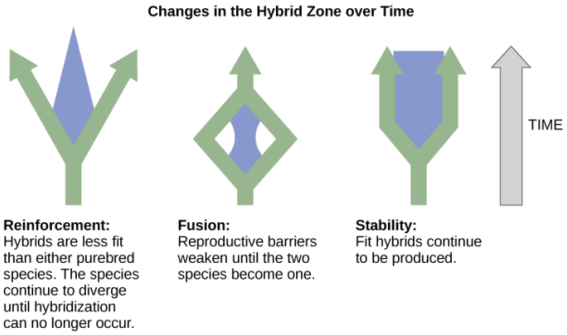


Figure **22.1.3.1.1**: Speciation and the Hybrid Zone: After speciation has occurred, the two separate-but-closely-related species may continue to produce offspring in an area called the hybrid zone. Reinforcement, fusion, or stability may result, depending on reproductive barriers and the relative fitness of the hybrids.

Hybrids can have less fitness, more fitness, or about the same fitness level as the purebred parents. Usually, hybrids tend to be less fit; therefore, reproduction to produce hybrids will diminish over time, which nudges the two species to diverge further in a process called reinforcement. This term is used because the low success of the hybrids reinforces the original speciation. If the hybrids are less fit than the parents, reinforcement of speciation occurs, and the species will continue to diverge until they can no longer mate and produce viable offspring.

If the hybrids are as fit or more fit than the parents, or the reproductive barriers weaken, the two species may fuse back into one species (reconnection). For a hybrid form to persist, it will generally have to be able to exploit the available resources better than either parent species, with which, in most cases, it will have to compete.

Over time, via a process called hybrid speciation, the hybrids themselves can become a separate species. Reproductive isolation between hybrids and their parents was once thought to be particularly difficult to achieve; thus, hybrid species were thought to be extremely rare. With DNA analysis becoming more accessible in the 1990s, hybrid speciation has been shown to be a fairly common phenomenon, particularly in plants.

Scientists have also observed that sometimes two species will remain separate, but continue to interact to produce some hybrid individuals; this is classified as stability because no real net change is taking place. For a hybrid zone to be stable, the offspring produced by the hybrids have to be less fit than members of the parent species.

Key Points

- After speciation, or sufficient evolutionary change for one species to become two distinct species, the two species may continue to co-habitate and interact.
- The area in which two closely-related species interact and reproduce is known as the hybrid zone; their offspring are known as hybrids.

- Depending on the fitness of the hybrid offspring relative to the parents, the two species may either stay as two distinct species (reinforcement), or become one species again (reconnection).

Key Terms

- **hybrid zone**: an area where the ranges of two interbreeding species meet and interbreed
- **hybrid speciation**: the formation of a new species as the direct result of mating between members of two existing species
- **reconnection**: a convergence of two species over time

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22.1.3.2: Varying Rates of Speciation

Learning Objectives

- Explain how the interaction of an organism's population size in association with environmental changes can lead to different rates of speciation

Varying Rates of Speciation

Scientists around the world study speciation, documenting observations both of living organisms and those found in the fossil record. As their ideas take shape and as research reveals new details about how life evolves, they develop models to help explain rates of speciation. In terms of how quickly speciation occurs, two patterns are currently observed: the gradual speciation model and the punctuated equilibrium model.

In the gradual speciation model, species diverge gradually over time in small steps. In the punctuated equilibrium model, a new species changes quickly from the parent species and then remains largely unchanged for long periods of time afterward. This early change model is called punctuated equilibrium, because it begins with a punctuated or periodic change and then remains in balance afterward. While punctuated equilibrium suggests a faster tempo, it does not necessarily exclude gradualism.

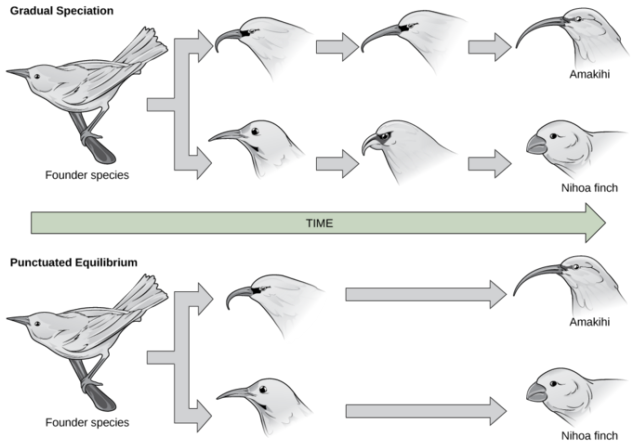


Figure **22.1.3.2.1**: Graduated Speciation vs Punctuated Equilibrium: In (a) gradual speciation, species diverge at a slow, steady pace as traits change incrementally. In (b) punctuated equilibrium, species diverge quickly and then remain unchanged for long periods of time.

The primary influencing factor on changes in speciation rate is environmental conditions. Under some conditions, selection occurs quickly or radically. Consider a species of snails that had been living with the same basic form for many thousands of years. Layers of their fossils would appear similar for a long time. When a change in the environment takes place, such as a drop in the water level, a small number of organisms are separated from the rest in a brief period of time, essentially forming one large and one tiny population. The tiny population faces new environmental conditions. Because its gene pool quickly became so small, any variation that surfaces and that aids in surviving the new conditions becomes the predominant form.

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Key Points

- In the gradual speciation model, species diverge slowly over time in small steps while in the punctuated equilibrium model, a new species diverges rapidly from the parent species.
- The two key influencing factors on the change in speciation rate are the environmental conditions and the population size.
- Gradual speciation is most likely to occur in large populations that live in a stable environment, while the punctuation equilibrium model is more likely to occur in a small population with rapid environmental change.

Key Terms

- **punctuated equilibrium**: a theory of evolution holding that evolutionary change tends to be characterized by long periods of stability, with infrequent episodes of very fast development
- **gradualism**: in evolutionary biology, belief that evolution proceeds at a steady pace, without the sudden development of new species or biological features from one generation to the next

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SECTION OVERVIEW

22.1.4: Evolution of Genomes

Topic hierarchy

22.1.4.1: Genomic Similiarities between Distant Species

22.1.4.2: Genome Evolution

22.1.4.3: Whole-Genome Duplication

22.1.4.4: Gene Duplications and Divergence

22.1.4.5: Noncoding DNA

22.1.4.6: Variations in Size and Number of Genes

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22.1.4.1: Genomic Similiarities between Distant Species

Learning Objectives

- Discuss the evolutionary implications of observed genome similarities between distant species

Genomic Similarities Between Distant Species

Genetic distance refers to the genetic divergence between species or between populations within a species. Smaller genetic distances indicate that the populations have more similar genes, which indicates they are closely related; they have a recent common ancestor, or recent interbreeding has taken place. Genetic distance is useful in reconstructing the history of populations. For example, evidence from genetic distance suggests that humans arrived in America about 30,000 years ago. By examining the difference between allele frequencies between the populations, genetic distance can estimate how long ago the two populations were together.

Phylogenetic Relationships

Phylogeny describes the relationships of an organism, such as the relationship with its ancestors and the species it is most closely related. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different. The use of advanced genomic analysis has allowed us to establish phylogenetic trees, which map the relationship between species at a genetic and molecular level. The ability to use these technologies has established previously unknown relationships and has contributed to a more complex evolutionary history. These technologies have established genomic similarities between distant species by establishing genetic distances. In addition, the mechanisms by which genomic similarities between distant species occur can include horizontal gene transfer.

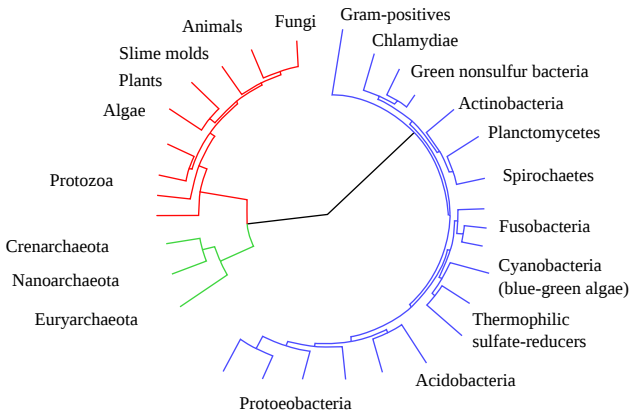


Figure **22.1.4.1.1**: Tree of Life: Diagrammatic representation of the divergence of modern taxonomic groups from their common ancestor. This shows the genomic similarities that can exist between distant species based on their relationship with this ancestor.

Horizontal Gene Transfer

Horizontal gene transfer (HGT), also known as lateral gene transfer, is the transfer of genes between unrelated species. Genes have been shown to be passed between species which are only distantly related using standard phylogeny, thus adding a layer of complexity to the understanding of phylogenetic relationships. The various ways that HGT occurs in prokaryotes is important to understanding phylogenies. Although at present, HGT is not viewed as important to eukaryotic evolution, HGT does occur in this domain as well. Finally, as an example of the ultimate gene transfer, theories of genome fusion between symbiotic or endosymbiotic organisms have been proposed to explain an event of great importance—the evolution of the first eukaryotic cell, without which humans could not have come into existence.

The mechanism of HGT has been shown to be quite common in the prokaryotic domains of Bacteria and Archaea, significantly changing the way their evolution is viewed. The majority of evolutionary models, such as in the endosymbiont theory, propose that

eukaryotes descended from multiple prokaryotes, which makes HGT all the more important to understanding the phylogenetic relationships of all extant and extinct species. These gene transfers between species are the major mechanism whereby bacteria acquire resistance to antibiotics. Classically, this type of transfer has been thought to occur by three different mechanisms: transformation, transduction and conjugation.

Although it is easy to see how prokaryotes exchange genetic material by HGT, it was initially thought that this process was absent in eukaryotes, followed by the idea that the gene transfers between multicellular eukaryotes should be more difficult. In spite of this fact, HGT between distantly related organisms has been demonstrated in several eukaryotic species.

In animals, a particularly interesting example of HGT occurs within the aphid species. Aphids are insects that vary in color based on carotenoid content. Carotenoids are pigments made by a variety of plants, fungi, and microbes, and they serve a variety of functions in animals, who obtain these chemicals from their food. Humans require carotenoids to synthesize vitamin A, and we obtain them by eating orange fruits and vegetables: carrots, apricots, mangoes, and sweet potatoes. On the other hand, aphids have acquired the ability to make the carotenoids on their own. According to DNA analysis, this ability is due to the transfer of fungal genes into the insect by HGT, presumably as the insect consumed fungi for food.



Figure **22.1.4.1.1**: Horizontal Gene Transfer in Animals: (a) Red aphids get their color from red carotenoid pigment. Genes necessary to make this pigment are present in certain fungi, and scientists speculate that aphids acquired these genes through HGT after consuming fungi for food. If genes for making carotenoids are inactivated by mutation, the aphids revert back to (b) their green color. Red coloration makes the aphids a lot more conspicuous to predators, but evidence suggests that red aphids are more resistant to insecticides than green ones. Thus, red aphids may be more fit to survive in some environments than green ones.

Key Points

- Genomic similarities between distant species can be explained by the theory that all organisms share a common ancestor.
- Genomic similarities between distant species can be analysed using genomic analysis tools to create phylogenetic trees that explain these relationships.
- Genetic distance is used to explain the genetic divergence between species or between populations within a species and can indicate how closely related they are and whether they have a recent common ancestor or recent interbreeding has taken place.
- Horizontal gene transfer (HGT) occurs when two unrelated species exchange genes, usually two prokaryotes, although HGT occurs in some eurokaryotes as well.

Key Terms

- **conjugation**: the temporary fusion of organisms, especially as part of sexual reproduction
- **phylogeny**: the evolutionary history of an organism
- **horizontal gene transfer**: the transfer of genetic material from one organism to another one that is not its offspring; especially common among bacteria
- **transformation**: the alteration of a bacterial cell caused by the transfer of DNA from another, especially if pathogenic
- **transduction**: horizontal gene transfer mechanism in prokaryotes where genes are transferred using a virus

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22.1.4.2: Genome Evolution

Learning Objectives

- Explain the importance of genomic changes in an evolutionary context

Accumulating Changes Over Time

The evolution of the genome is characterized by the accumulation of changes. The analysis of genomes and their changes in sequence or size over time involves various fields. There are various mechanisms that have contributed to genome evolution and these include gene and genome duplications, polyploidy, mutation rates, transposable elements, pseudogenes, exon shuffling and genomic reduction and gene loss. The concepts of gene and whole-genome duplication are discussed as their own independent concepts, thus, the focus will be on other mechanisms.

Mutation Rates

Mutation rates differ between species and even between different regions of the genome of a single species. Spontaneous mutations often occur which can cause various changes in the genome. Mutations can result in the addition or deletion of one or more nucleotide bases. A change in the code can result in a frameshift mutation which causes the entire code to be read in the wrong order and thus often results in a protein becoming non-functional. A mutation in a promoter region, enhancer region or a region coding for transcription factors can also result in either a loss of function or and upregulation or downregulation in transcription of that gene. Mutations are constantly occurring in an organism's genome and can cause either a negative effect, positive effect or no effect at all.

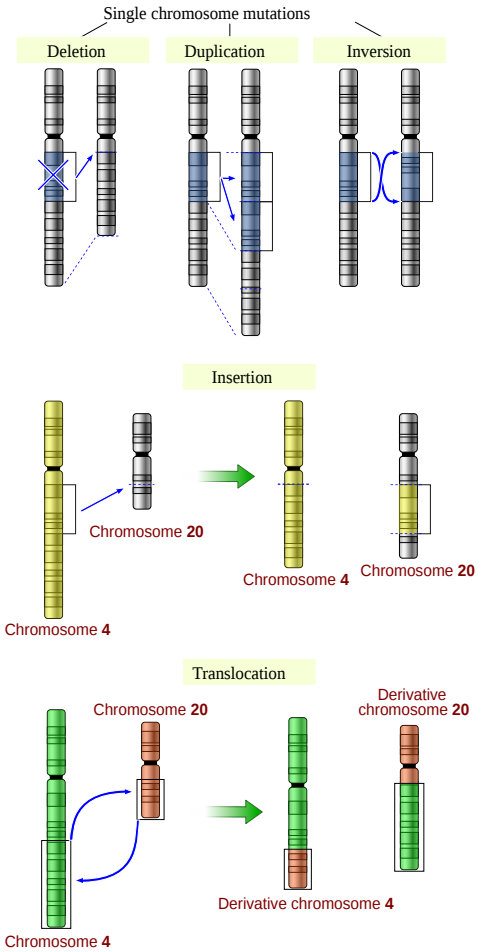


Figure **22.1.4.2.1**: Chromosomal Mutations: Chromosomal mutations over time can accumulate and promote diversity and evolution if a produced trait is favorable.

Transposable Elements

Transposable elements are regions of DNA that can be inserted into the genetic code through one of two mechanisms. These mechanisms work similarly to “cut-and-paste” and “copy-and-paste” functionalities in word processing programs. The “cut-and-paste” mechanism works by excising DNA from one place in the genome and inserting itself into another location in the code. The “copy-and-paste” mechanism works by making a genetic copy or copies of a specific region of DNA and inserting these copies elsewhere in the code. The most common transposable element in the human genome is the Alu sequence, which is present in the genome over one million times.

Pseudogenes

Often a result of spontaneous mutation, pseudogenes are dysfunctional genes derived from previously functional gene relatives. There are many mechanisms by which a functional gene can become a pseudogene including the deletion or insertion of one or multiple nucleotides. This can result in a shift of reading frame, causing the gene to longer code for the expected protein, a premature stop codon or a mutation in the promoter region. Often cited examples of pseudogenes within the human genome include the once functional olfactory gene families. Over time, many olfactory genes in the human genome became pseudogenes and were no longer able to produce functional proteins, explaining the poor sense of smell humans possess in comparison to their mammalian relatives.

Exon Shuffling

Exon shuffling is a mechanism by which new genes are created. This can occur when two or more exons from different genes are combined together or when exons are duplicated. Exon shuffling results in new genes by altering the current intron-exon structure. This can occur by any of the following processes: transposon mediated shuffling, sexual recombination or illegitimate recombination. Exon shuffling may introduce new genes into the genome that can be either selected against and deleted or selectively favored and conserved.

Genome Reduction and Gene Loss

Many species exhibit genome reduction when subsets of their genes are not needed anymore. This typically happens when organisms adapt to a parasitic life style, e.g. when their nutrients are supplied by a host. As a consequence, they lose the genes need to produce these nutrients. In many cases, there are both free living and parasitic species that can be compared and their lost genes identified. Good examples are the genomes of Mycobacterium tuberculosis and Mycobacterium leprae, the latter of which has a dramatically reduced genome. Another beautiful example are endosymbiont species. For instance, Polynucleobacter necessarius was first described as a cytoplasmic endosymbiont of the ciliate Euplotes aediculatus. The latter species dies soon after being cured of the endosymbiont. In the few cases in which P. necessarius is not present, a different and rarer bacterium apparently supplies the same function. No attempt to grow symbiotic P. necessarius outside their hosts has yet been successful, strongly suggesting that the relationship is obligate for both partners. Yet, closely related free-living relatives of P. necessarius have been identified. The endosymbionts have a significantly reduced genome when compared to their free-living relatives (1.56 Mbp vs. 2.16 Mbp).

Key Points

- Gene and whole genome duplications have contributed accumulations that have contributed to genome evolution.
- Mutations are constantly occurring in an organism’s genome and can cause either a negative effect, positive effect or no effect at all; however, it will still result in changes to the genome.
- Transposable elements are regions of DNA that can be inserted into the genetic code and will causes changes within the genome.
- Pseudogenes are dysfunctional genes derived from previously functional gene relatives and will become a pseudogene by deletion or insertion of one or multiple nucleotides.
- Exon shuffling occurs when two or more exons from different genes are combined together or when exons are duplicated, and will result in new genes.
- Species can also exhibit genome reduction when subsets of their genes are not needed anymore.

Key Terms

- **intron**: a portion of a split gene that is included in pre-RNA transcripts but is removed during RNA processing and rapidly degraded
- **exon**: a region of a transcribed gene present in the final functional RNA molecule
- **pseudogene**: a segment of DNA that is part of the genome of an organism, and which is similar to a gene but does not code for a gene product

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22.1.4.3: Whole-Genome Duplication

Learning Objectives

- State the evolutionary implications of whole-genome duplication

Whole-Genome Duplication

Gene duplication is the process by which a region of DNA coding for a gene creates additional copies of the gene. Similar to gene duplication, whole-genome duplication is the process by which an organism's entire genetic information is copied, once or multiple times, which is known as polyploidy. This may provide an evolutionary benefit to the organism by supplying it with multiple copies of a gene, thus, creating a greater possibility of functional and selectively favored genes.

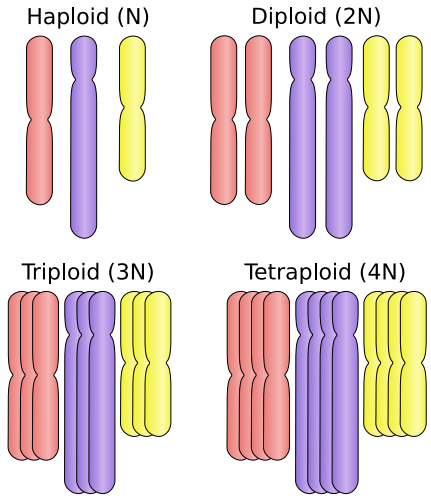


Figure **22.1.4.3.1**: Polyploidy: This image shows haploid (single), diploid (double), triploid (triple), and tetraploid (quadruple) sets of chromosomes. Triploid and tetraploid chromosomes are examples of polyploidy.

Evolutionary importance

Paleopolyploidization events lead to massive cellular changes, including doubling of the genetic material, changes in gene expression and increased cell size. Gene loss during diploidization is not completely random, but heavily selected. Genes from large gene families are duplicated. On the other hand, individual genes are not duplicated. Overall, paleopolyploidy can have both short-term and long-term evolutionary effects on an organism's fitness in the natural environment.

Genome diversity

Genome doubling provides organisms with redundant alleles that can evolve freely with little selection pressure. The duplicated genes can undergo neofunctionalization or subfunctionalization which could help the organism adapt to the new environment or survive different stress conditions.

Speciation

Sympatric speciation can begin with a chromosomal error during meiosis or the formation of a hybrid individual with too many chromosomes, such as polyploidy which can occur during whole-genome duplication. Scientists have identified types of polyploidy that can lead to reproductive isolation of an individual in the polyploid state. In some cases a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called autopolyploidy. The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an allopolyploid. The prefix "allo" means "other" (recall from allopatric); therefore, an allopolyploid occurs when gametes from two different species combine.

It has been suggested that many polyploidization events created new species, via a gain of adaptive traits, or by sexual incompatibility with their diploid counterparts. An example would be the recent speciation of allopolyploid Spartina — S. anglica;

the polyploid plant is so successful that it is listed as an invasive species in many regions.

Evidence of Whole-Genome Duplication

In 1997, Wolfe & Shields gave evidence for an ancient duplication of the *Saccharomyces cerevisiae* (Yeast) genome. It was initially noted that this yeast genome contained many individual gene duplications. Wolfe & Shields hypothesized that this was actually the result of an entire genome duplication in the yeast's distant evolutionary history. They found 32 pairs of homologous chromosomal regions, accounting for over half of the yeast's genome. They also noted that although homologs were present, they were often located on different chromosomes. Based on these observations, they determined that *Saccharomyces cerevisiae* underwent a whole-genome duplication soon after its evolutionary split from *Kluyveromyces*, a genus of ascomycetous yeasts. Over time, many of the duplicate genes were deleted and rendered non-functional. A number of chromosomal rearrangements broke the original duplicate chromosomes into the current manifestation of homologous chromosomal regions.

Key Points

- Whole- genome duplication can provide an evolutionary advantage by providing the organism with multiple copies of a gene that is considered favorable.
- Whole-genome duplication can result in divergence and formation of new species over time.
- Whole-genome duplication can result in mutation and cause disease if the genes are rendered non-functional.

Key Terms

- **polyploidy**: having more than the usual two homologous sets of chromosomes
- **palaeopolyploidization**: the development of polyploid organisms in the geologic past
- **sympatric speciation**: the process through which new species evolve from a single ancestral species while inhabiting the same geographic region

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22.1.4.4: Gene Duplications and Divergence

Learning Objectives

- Explain the mechanisms of gene duplication and divergence

Gene Duplication

Gene duplication is the process by which a region of DNA coding for a gene is copied. Gene duplication can occur as the result of an error in recombination or through a retrotransposition event. Duplicate genes are often immune to the selective pressure under which genes normally exist. This can result in a large number of mutations accumulating in the duplicate gene code. This may render the gene non-functional or in some cases confer some benefit to the organism. There are multiple mechanisms by which gene duplication can occur.

Ectopic Recombination

Duplications can arise from unequal crossing-over that occurs during meiosis between misaligned homologous chromosomes. The product of this recombination is a duplication at the site of the exchange and a reciprocal deletion. Ectopic recombination is typically mediated by sequence similarity at the duplicate breakpoints, which form direct repeats. Repetitive genetic elements, such as transposable elements, offer one source of repetitive DNA that can facilitate recombination, and they are often found at duplication breakpoints in plants and mammals.

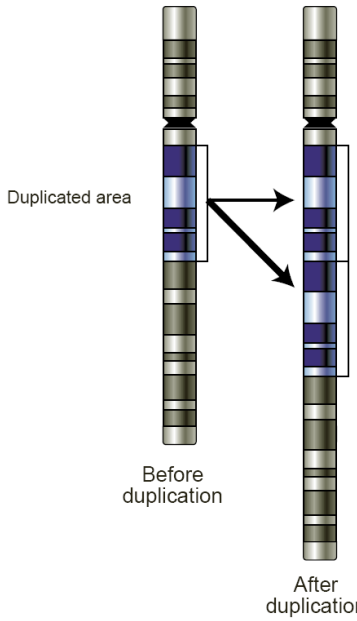


Figure **22.1.4.4.1**: Gene Duplication: This figure indicates a schematic of a region of a chromosome before and after a duplication event. Ectopic recombination is typically mediated by sequence similarity at the duplicate breakpoints, which form direct repeats.

Replication Slippage

Replication slippage is an error in DNA replication, which can produce duplications of short genetic sequences. During replication, DNA polymerase begins to copy the DNA, and at some point during the replication process, the polymerase dissociates from the DNA and replication stalls. When the polymerase reattaches to the DNA strand, it aligns the replicating strand to an incorrect position and incidentally copies the same section more than once. Replication slippage is also often facilitated by repetitive sequence but requires only a few bases of similarity.

Retrotransposition

During cellular invasion by a replicating retroelement or retrovirus, viral proteins copy their genome by reverse transcribing RNA to DNA. If viral proteins attach irregularly to cellular mRNA, they can reverse-transcribe copies of genes to create retrogenes. Retrogenes usually lack intronic sequence and often contain poly A sequences that are also integrated into the genome. Many retrogenes display changes in gene regulation in comparison to their parental gene sequences, which sometimes results in novel functions.

Aneuploidy

Aneuploidy occurs when nondisjunction at a single chromosome results in an abnormal number of chromosomes. Aneuploidy is often harmful and in mammals regularly leads to spontaneous abortions. Some aneuploid individuals are viable. For example, trisomy 21 in humans leads to Down syndrome, but it is not fatal. Aneuploidy often alters gene dosage in ways that are detrimental to the organism and therefore, will not likely spread through populations.

Gene duplication as an evolutionary event

Gene duplications are an essential source of genetic novelty that can lead to evolutionary innovation. Duplication creates genetic redundancy and if one copy of a gene experiences a mutation that affects its original function, the second copy can serve as a ‘spare part’ and continue to function correctly. Thus, duplicate genes accumulate mutations faster than a functional single-copy gene, over generations of organisms, and it is possible for one of the two copies to develop a new and different function. This is an examples of neofunctionalization.

Gene duplication is believed to play a major role in evolution; this stance has been held by members of the scientific community for over 100 years. It has been argued that gene duplication is the most important evolutionary force since the emergence of the universal common ancestor.

Another possible fate for duplicate genes is that both copies are equally free to accumulate degenerative mutations, so long as any defects are complemented by the other copy. This leads to a neutral “subfunctionalization” model, in which the functionality of the original gene is distributed among the two copies. Neither gene can be lost, as both now perform important non-redundant functions, but ultimately neither is able to achieve novel functionality. Subfunctionalization can occur through neutral processes in which mutations accumulate with no detrimental or beneficial effects. However, in some cases subfunctionalization can occur with clear adaptive benefits. If an ancestral gene is pleiotropic and performs two functions, often times neither one of these two functions can be changed without affecting the other function. In this way, partitioning the ancestral functions into two separate genes can allow for adaptive specialization of subfunctions, thereby providing an adaptive benefit.

Divergence

Genetic divergence is the process in which two or more populations of an ancestral species accumulate independent genetic changes through time, often after the populations have become reproductively isolated for some period of time. In some cases, subpopulations living in ecologically distinct peripheral environments can exhibit genetic divergence from the remainder of a population, especially where the range of a population is very large. The genetic differences among divergent populations can involve silent mutations (that have no effect on the phenotype) or give rise to significant morphological and/or physiological changes. Genetic divergence will always accompany reproductive isolation, either due to novel adaptations via selection and/or due to genetic drift, and is the principal mechanism underlying speciation.

Genetic drift or allelic drift is the change in the frequency of a gene variant (allele) in a population due to random sampling. The alleles in the offspring are a sample of those in the parents, and chance has a role in determining whether a given individual survives and reproduces. A population’s allele frequency is the fraction of the copies of one gene that share a particular form. Genetic drift may cause gene variants to disappear completely and thereby reduce genetic variation. When there are few copies of an allele, the effect of genetic drift is larger, and when there are many copies the effect is smaller. These changes in gene frequency can contribute to divergence.

Divergent evolution is usually a result of diffusion of the same species to different and isolated environments, which blocks the gene flow among the distinct populations allowing differentiated fixation of characteristics through genetic drift and natural selection.Divergent evolution can also be applied to molecular biology characteristics. This could apply to a pathway in two or

more organisms or cell types. This can apply to genes and proteins, such as nucleotide sequences or protein sequences that are derived from two or more homologous genes. Both orthologous genes (resulting from a speciation event) and paralogous genes (resulting from gene duplication within a population) can be said to display divergent evolution.

Key Points

- Ectopic recombination occurs when there is an unequal crossing-over and the product of this recombination are a duplication at the site of the exchange and a reciprocal deletion.
- Gene duplications do not always result in detrimental mutations; they can contribute to divergent evolution, which causes genetic differences between groups to develop and eventually form new species.
- Replication slippage can occur when there is an error during DNA replication and duplications of short genetic sequences are produced.
- Retrotranspositions occur when a retrovirus copies their genome by reverse transcribing RNA to DNA and aberrantly attach to cellular mRNA and reverse transcribe copies of genes to create retrogenes.
- Aneuploidy can occur when there is a nondisjunction even at a single chromosome thus, the result is an abnormal number of chromosomes.
- Genetic divergence can occur by mechanisms such as genetic drift which contibute to the accumulation of independent genetic changes of two or more populations derived from a common ancestor.

Key Terms

- **paralogous**: having a similar structure indicating divergence from a common ancestral gene
- **nondisjunction**: the failure of chromosome pairs to separate properly during meiosis
- **retrogene**: a DNA gene copied back from RNA by reverse transcription
- **genetic drift**: an overall shift of allele distribution in an isolated population, due to random fluctuations in the frequencies of individual alleles of the genes

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22.1.4.5: Noncoding DNA

Learning Objectives

- Summarize the importance of noncoding DNA

Noncoding DNA

In genomics and related disciplines, noncoding DNA sequences are components of an organism's DNA that do not encode protein sequences. Some noncoding DNA is transcribed into functional noncoding RNA molecules (e.g. transfer RNA, ribosomal RNA, and regulatory RNAs), while others are not transcribed or give rise to RNA transcripts of unknown function. The amount of noncoding DNA varies greatly among species. For example, over 98% of the human genome is noncoding DNA, while only about 2% of a typical bacterial genome is noncoding DNA.

Initially, a large proportion of noncoding DNA had no known biological function and was therefore sometimes referred to as "junk DNA", particularly in the lay press. However, many types of noncoding DNA sequences do have important biological functions, including the transcriptional and translational regulation of protein-coding sequences, origins of DNA replication, centromeres, telomeres, scaffold attachment regions (SARs), genes for functional RNAs, and many others. Other noncoding sequences have likely, but as-yet undetermined, functions. Some sequences may have no biological function for the organism, such as endogenous retroviruses.

Genomic Variation between Organisms

The amount of total genomic DNA varies widely between organisms, and the proportion of coding and noncoding DNA within these genomes varies greatly as well. More than 98% of the human genome does not encode protein sequences, including most sequences within introns and most intergenic DNA. While overall genome size, and by extension the amount of noncoding DNA, are correlated to organism complexity, there are many exceptions. For example, the genome of the unicellular Polychaos dubium (formerly known as Amoeba dubia) has been reported to contain more than 200 times the amount of DNA in humans. The pufferfish Takifugu rubripes genome is only about one eighth the size of the human genome, yet seems to have a comparable number of genes; approximately 90% of the Takifugu genome is noncoding DNA.

In 2013, a new "record" for most efficient genome was discovered. Utricularia gibba, a bladderwort plant, has only 3% noncoding DNA. The extensive variation in nuclear genome size among eukaryotic species is known as the C-value enigma or C-value paradox. Most of the genome size difference appears to lie in the noncoding DNA. About 80 percent of the nucleotide bases in the human genome may be transcribed, but transcription does not necessarily imply function.



Figure 22.1.4.5.1: Utricularia gibba flower: Utricularia gibba has 3% noncoding DNA, which is low for flowering plants. This 3% has given this plant the title the 'most efficient' genome.

Key Points

- In the human genome, over 98% of DNA is classified as noncoding DNA and can be transcribed to regulatory noncoding RNAs (i.e. tRNAs, rRNAs), origins of DNA replication, centromeres, telomeres and scaffold attachment regions (SARs).
- Noncoding regions are most commonly referred to as 'junk DNA', however, this term is misleading as noncoding DNA does have functional importance.
- The proportion of coding and noncoding DNA within organisms varies and the amount of noncoding DNA typically correlates with organism complexity, though there are many notable exceptions.

Key Terms

- **intergenic**: describing the noncoding sections of nucleic acid between genes
- **noncoding**: DNA which does not code for protein
- **intron**: a portion of a split gene that is included in pre-RNA transcripts but is removed during RNA processing and rapidly degraded

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22.1.4.6: Variations in Size and Number of Genes

Learning Objectives

- Describe how variations in the size and number of genes can arise through evolutionary mechanisms

Variations in Size and Number of Genes

Genetic diversity refers to any variation in the nucleotides, genes, chromosomes, or whole genomes of organisms. Genetic diversity at its most elementary level is represented by differences in the sequences of nucleotides (adenine, cytosine, guanine, and thymine) that form the DNA (deoxyribonucleic acid) within the cells of the organism. The DNA is contained in the chromosomes present within the cell; some chromosomes are contained within specific organelles in the cell (for example, the chromosomes of mitochondria and chloroplast). Nucleotide variation is measured for discrete sections of the chromosomes, called genes. Thus, each gene compromises a hereditary section of DNA that occupies a specific place of the chromosome, and controls a particular characteristic of an organism.

Chromosomes

Most organisms are diploid, having two sets of chromosomes, and therefore two copies (called alleles) of each gene. However, some organisms can be haploid, triploid, or tetraploid (having one, three, or four sets of chromosomes respectively). Within any single organism, there may be variation between the two (or more) alleles for each gene. This variation is introduced either through mutation of one of the alleles, or as a result of sexual reproduction.

During sexual reproduction, offspring inherit alleles from both parents and these alleles might be slightly different, especially if there has been migration or hybridization of organisms, so that the parents may come from different populations and gene pools. Also, when the offspring's chromosomes are copied after fertilization, genes can be exchanged in a process called sexual recombination. Harmless mutations and sexual recombination may allow the evolution of new characteristics.

Genome Size and Number

Genome size is usually measured in base pairs (or bases in single-stranded DNA or RNA). The C-value is another measure of genome size. The C-value refers to the amount, in picograms, of DNA contained within a haploid nucleus (e.g. a gamete) or one half the amount in a diploid somatic cell of a eukaryotic organism. In some cases (notably among diploid organisms), the terms C-value and genome size are used interchangeably, however in polyploids the C-value may represent two or more genomes contained within the same nucleus.

Different species can have different numbers of genes within the entire DNA or genome of the organism. However, a greater total number of genes might not correspond with a greater observable complexity in the anatomy and physiology of the organism (i.e. greater phenotypic complexity). For example, the predicted size of the human genome is not much larger than the genomes of some invertebrates and plants, and may even be smaller than the Indian rice genome. In humans, more proteins are encoded per gene than in other species. In prokaryotic genomes, research has shown that there is a significant positive correlation between the C-value of prokaryotes and the amount of genes that compose the genome. This indicates that gene number is the main factor influencing the size of the prokaryotic genome.

Genes vs Genome Size

In eukaryotic organisms, there is a paradox observed, namely that the number of genes that make up the genome does not correlate with genome size. In other words, the genome size is much larger than would be expected given the total number of protein coding genes. Genome size can increase by duplication, insertion, or polyploidization and the process of recombination can lead to both DNA loss or gain. It is also possible that genomes can shrink due to deletions.

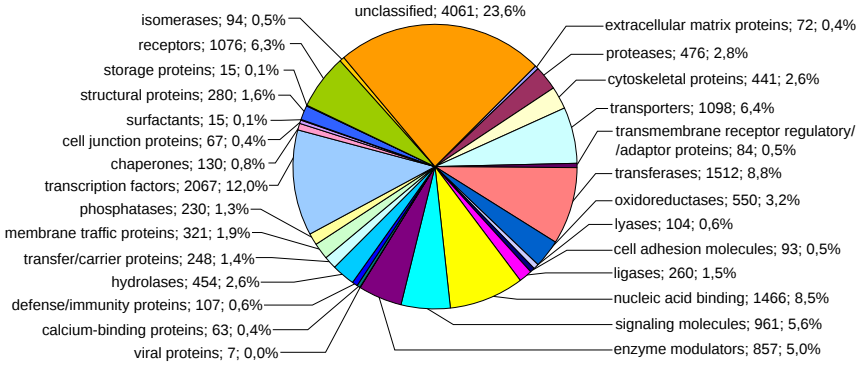


Figure **22.1.4.6.1**: Gene variation in the Genome: This figure represents the human genome, categorized by function of each gene product, given both as number of genes and as percentage of all genes. Importantly, genome size does not necessarily correlate with complexity.

A famous example for such gene decay is the genome of Mycobacterium leprae, the causative agent of leprosy. M.leprae has lost many once-functional genes over time due to the formation of pseudogenes. This is evident in looking at its closest ancestor Mycobacterium tuberculosis. M. leprae lives inside and replicates inside of a host and due to this arrangement it does not have a need for many of the genes it once carried which allowed it to live and prosper outside of the host. Thus over time these genes have lost their function through mechanisms such as mutation causing them to become pseudogenes. It is beneficial to an organism to rid itself of non-essential genes because it makes replicating its DNA much faster and more energy-efficient.

An example of increasing genome size over time is seen in filamentous plant pathogens. These plant pathogen genomes have been growing larger over the years due to repeat-driven expansion. The repeat-rich regions contain genes coding for host interaction proteins. With the addition of more and more repeats to these regions the plants increase the possibility of developing new virulence factors through mutation and other forms of genetic recombination. In this way it is beneficial for these plant pathogens to have larger genomes.

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Key Points

- Harmless mutations and sexual recombination of chromosomes may allow the evolution of new characteristics.
- Genome size can be affected by various events, including duplication, insertion, recombination, deletion and polyploidization events.
- Genome size can be affected by evolution of an organism and result is an increased or decreased need for specific genes for survival based on behavior.
- The human genome exemplifies the concept that complexity does not always correlate with an increase in genome size; there are fewer protein coding genes present than expected relative to the genome size.

Key Terms

- **polyploidization**: hybridization that leads to polyploidy
- **pseudogene**: a segment of DNA that is part of the genome of an organism, and which is similar to a gene but does not code for a gene product
- **genome**: the cell's complete genetic information packaged as a double-stranded DNA molecule

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SECTION OVERVIEW

22.1.5: Evidence of Evolution

Topic hierarchy

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22.1.5.2: Fossil Formation

22.1.5.3: Gaps in the Fossil Record

22.1.5.4: Carbon Dating and Estimating Fossil Age

22.1.5.5: The Fossil Record and the Evolution of the Modern Horse

22.1.5.6: Homologous Structures

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22.1.5.8: Vestigial Structures

22.1.5.9: Biogeography and the Distribution of Species

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22.1.5.1: The Fossil Record as Evidence for Evolution

Learning Objectives

- Synthesize the contributions of the fossil record to our understanding of evolution

What Fossils Tell Us

Fossils are the preserved remains or traces of animals, plants, and other organisms from the past. Fossils range in age from 10,000 to 3.48 billion years old. The observation that certain fossils were associated with certain rock strata led 19th century geologists to recognize a geological timescale. Like extant organisms, fossils vary in size from microscopic, like single-celled bacteria, to gigantic, like dinosaurs and trees.



Figure **22.1.5.1.1**: "Sue" T-rex skeleton: The bones of this Tyrannosaurus rex were preserved through the process of permineralization, which suggests that this organism was covered by sediment soon after death.

Permineralization

Permineralization is a process of fossilization that occurs when an organism is buried. The empty spaces within an organism (spaces filled with liquid or gas during life) become filled with mineral-rich groundwater. Minerals precipitate from the groundwater, occupying the empty spaces. This process can occur in very small spaces, such as within the cell wall of a plant cell. Small-scale permineralization can produce very detailed fossils. For permineralization to occur, the organism must be covered by sediment soon after death, or soon after the initial decay process.

The degree to which the remains are decayed when covered determines the later details of the fossil. Fossils usually consist of the portion of the organisms that was partially mineralized during life, such as the bones and teeth of vertebrates or the chitinous or calcareous exoskeletons of invertebrates. However, other fossils contain traces of skin, feathers or even soft tissues.

Trace Fossils

Fossils may also consist of the marks left behind by the organism while it was alive, such as footprints or feces. These types of fossils are called trace fossils, or ichnofossils, as opposed to body fossils. Past life may also leave some markers that cannot be seen but can be detected in the form of biochemical signals; these are known as chemofossils or biomarkers.



Figure 22.1.5.1.1: Dinosaur footprints: Footprints are examples of trace fossils, which contribute to the fossil record.

The Fossil Record

The totality of fossils, both discovered and undiscovered, and their placement in fossiliferous (fossil-containing) rock formations and sedimentary layers (strata) is known as the fossil record. The fossil record was one of the early sources of data underlying the study of evolution and continues to be relevant to the history of life on Earth. The development of radiometric dating techniques in the early 20th century allowed geologists to determine the numerical or "absolute" age of various strata and their included fossils.

Evidence for Evolution

Fossils provide solid evidence that organisms from the past are not the same as those found today; fossils show a progression of evolution. Fossils, along with the comparative anatomy of present-day organisms, constitute the morphological, or anatomical, record. By comparing the anatomies of both modern and extinct species, paleontologists can infer the lineages of those species. This approach is most successful for organisms that had hard body parts, such as shells, bones or teeth. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years.

Key Points

- Fossils are the preserved remains or traces of animals, plants, and other organisms from the past.
- Fossils are important evidence for evolution because they show that life on earth was once different from life found on earth today.
- Usually only a portion of an organism is preserved as a fossil, such as body fossils (bones and exoskeletons), trace fossils (feces and footprints), and chemofossils (biochemical signals).
- Paleontologists can determine the age of fossils using methods like radiometric dating and categorize them to determine the evolutionary relationships between organisms.

Key Terms

- **biomarker**: A substance used as an indicator of a biological state, most commonly disease.
- **trace fossil**: A type of fossil reflecting the reworking of sediments and hard substrates by organisms including structures like burrows, trails, and impressions.
- **fossil record**: All discovered and undiscovered fossils and their placement in rock formations and sedimentary layers.
- **strata**: Layers of sedimentary rock.
- **fossiliferous**: Containing fossils.

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22.1.5.2: Fossil Formation

Learning Objectives

- Predict the conditions suitable to fossil formation

Fossil Formation

The process of a once living organism becoming a fossil is called fossilization. Fossilization is a very rare process, and of all the organisms that have lived on Earth, only a tiny percentage of them ever become fossils. To see why, imagine an antelope that dies on the African plain. Most of its body is quickly eaten by scavengers, and the remaining flesh is soon eaten by insects and bacteria, leaving behind only scattered bones. As the years go by, the bones are scattered and fragmented into small pieces, eventually turning into dust and returning their nutrients to the soil. As a result, it would be rare for any of the antelope's remains to actually be preserved as a fossil.

Fossilization can occur in many ways. Most fossils are preserved in one of five processes:

- preserved remains
- permineralization
- molds and casts
- replacement
- compression

Preserved Remains

The rarest form of fossilization is the preservation of original skeletal material and even soft tissue. For example, some insects have been preserved perfectly in amber, which is ancient tree sap. In addition, several mammoths and even a Neanderthal hunter have been discovered frozen in glaciers. These preserved remains allow scientists the rare opportunity to examine the skin, hair, and organs of ancient creatures. Scientists have collected DNA from these remains and compared the DNA sequences to those of modern creatures.



Figure **22.1.5.2.1**: Amber: The image depicts a gnat preserved in amber. A lot of insects have been found to be perfectly maintained in this ancient tree sap.

Permineralization

The most common method of fossilization is permineralization. After a bone, wood fragment, or shell is buried in sediment, it may be exposed to mineral-rich water that moves through the sediment. This water will deposit minerals, typically silica, into empty spaces, producing a fossil. Fossilized dinosaur bones, petrified wood, and many marine fossils were formed by permineralization.



Figure **22.1.5.2.1**: Permineralization: These fossils from the Road Canyon Formation (Middle Permian of Texas) have been silicified (replaced with silica), which is a form of permineralization.

Molds and Casts

In some cases, the original bone or shell dissolves away, leaving behind an empty space in the shape of the shell or bone. This depression is called a mold. Later, the space may be filled with other sediments to form a matching cast in the shape of the original organism. Many mollusks (bivalves, snails, and squid) are commonly found as molds and casts because their shells dissolve easily.

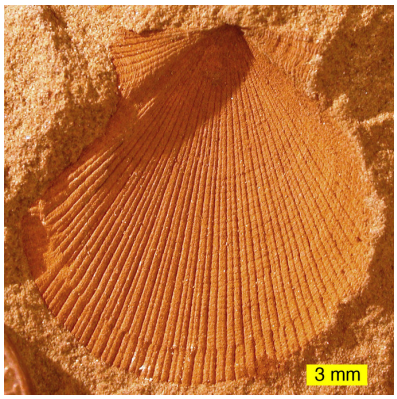


Figure **22.1.5.2.1**: Molds: The depression in the image is an external mold of a bivalve from the Logan Formation, Lower Carboniferous, Ohio

Replacement

In some cases, the original shell or bone dissolves away and is replaced by a different mineral. For example, shells that were originally calcite may be replaced by dolomite, quartz, or pyrite. If quartz fossils are surrounded by a calcite matrix, the calcite can be dissolved away by acid, leaving behind an exquisitely preserved quartz fossil. When permineralization and replacement occur together, the organism is said to have undergone petrification, the process of turning organic material into stone. However, replacement can occur without permineralization and vice versa.

Compression

Some fossils form when their remains are compressed by high pressure. This can leave behind a dark imprint of the fossil. Compression is most common for fossils of leaves and ferns but also can occur with other organisms.

Conditions for Fossilization

Following the death of an organism, several forces contribute to the dissolution of its remains. Decay, predators, or scavengers will typically rapidly remove the flesh. The hard parts, if they are separable at all, can be dispersed by predators, scavengers, or currents. The individual hard parts are subject to chemical weathering and erosion, as well as to splintering by predators or scavengers, which will crunch up bones for marrow and shells to extract the flesh inside. Also, an animal swallowed whole by a predator, such as a mouse swallowed by a snake, will have not just its flesh but some, and perhaps all, its bones destroyed by the gastric juices of the predator.

It would not be an exaggeration to say that the typical vertebrate fossil consists of a single bone, or tooth, or fish scale. The preservation of an intact skeleton with the bones in the relative positions they had in life requires a remarkable circumstances, such as burial in volcanic ash, burial in aeolian sand due to the sudden slumping of a sand dune, burial in a mudslide, burial by a turbidity current, and so forth. The mineralization of soft parts is even less common and is seen only in exceptionally rare chemical and biological conditions.

Key Points

- Preservation of remains in amber or other substances is the rarest from of fossilization; this mechanism allows scientists to study the skin, hair, and organs of ancient creatures.
- Permineralization, where minerals like silica fill the empty spaces of shells, is the most common form of fossilization.
- Molds form when shells or bones dissolve, leaving behind an empty depression; a cast is then formed when the depression is filled by sediment.
- Replacement occurs when the original shell or bone dissolves away and is replaced by a different mineral; when this occurs with permineralization, it is called petrification.
- In compression, the most common form of fossilization of leaves and ferns, a dark imprint of the fossil remains.
- Decay, chemical weathering, erosion, and predators are factors that deter fossilization.
- Fossilization of soft body parts is rare, and hard parts are better preserved when buried.

Key Terms

- **amber**: a hard, generally yellow to brown translucent fossil resin
- **permineralization**: form of fossilization in which minerals are deposited in the pores of bone and similar hard animal parts
- **petrification**: process by which organic material is converted into stone through the replacement of the original material and the filling of the original pore spaces with minerals

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22.1.5.3: Gaps in the Fossil Record

Learning Objectives

- Explain the gap in the fossil record

Incompleteness of the Fossil Record

Each fossil discovery represents a snapshot of the process of evolution. Because of the specialized and rare conditions required for a biological structure to fossilize, many important species or groups may never leave fossils at all. Even if they do leave fossils, humans may never find them—for example, if they are buried under hundreds of feet of ice in Antarctica. The number of species known about through the fossil record is less than 5% of the number of species alive today. Fossilized species may represent less than 1% of all the species that have ever lived.

Types of Fossils in the Fossil Record

The fossil record is very uneven and is mostly comprised of fossils of organisms with hard body parts, leaving most groups of soft-bodied organisms with little to no fossil record. Groups considered to have a good fossil record, including transitional fossils between these groups, are the vertebrates, the echinoderms, the brachiopods, and some groups of arthropods. Their hard bones and shells fossilize easily, unlike the bodies of organisms like cephalopods or jellyfish.

Romer's Gap

Romer's gap is an example of an apparent gap in the tetrapod fossil record used in the study of evolutionary biology. These gaps represent periods from which no relevant fossils have been found. Romer's gap is named after paleontologist Alfred Romer, who first recognized it. Romer's gap spanned from approximately 360 to 345 million years ago, corresponding to the first 15 million years of the Carboniferous Period.



Figure **22.1.5.3.1**: Romer's Gap: The bank of the Whiteadder Water in Scotland is one of the few known localities bearing fossils of tetrapods from Romer's gap.

There has been much debate over why there are so few fossils from this time period. Some scientists have suggested that the geochemistry of the time period caused bad conditions for fossil formation, so few organisms were fossilized. Another theory suggests that scientists have simply not yet discovered an excavation site for these fossils, due to inaccessibility or random chance.

Key Points

- The number of species known about through fossils is less than 1% of all species that have ever lived.
- Because hard body parts are more easily preserved than soft body parts, there are more fossils of animals with hard body parts, such as vertebrates, echinoderms, brachiopods, and some groups of arthropods.
- Very few fossils have been found in the period from 360 to 345 million years ago, known as Romer's gap. Theories to explain this include the period's geochemistry, errors in excavation, and limited vertebrate diversity.

Key Terms

- **transitional fossil**: Fossilized remains of a life form that exhibits traits common to both an ancestral group and its derived descendant group.
- **Romer's gap**: A period in the tetrapod fossil record (360 to 345 million years ago) from which excavators have not yet found relevant fossils.

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22.1.5.4: Carbon Dating and Estimating Fossil Age

Learning Objectives

- Summarize the available methods for dating fossils

Determining Fossil Ages

Paleontology seeks to map out how life evolved across geologic time. A substantial hurdle is the difficulty of working out fossil ages. There are several different methods for estimating the ages of fossils, including:

1. stratigraphy
2. biostratigraphy
3. carbon dating

Stratigraphy

Paleontologists rely on stratigraphy to date fossils. Stratigraphy is the science of understanding the strata, or layers, that form the sedimentary record. Strata are differentiated from each other by their different colors or compositions and are exposed in cliffs, quarries, and river banks. These rocks normally form relatively horizontal, parallel layers, with younger layers forming on top.

If a fossil is found between two layers of rock whose ages are known, the fossil's age is thought to be between those two known ages. Because rock sequences are not continuous, but may be broken up by faults or periods of erosion, it is difficult to match up rock beds that are not directly adjacent.



Figure **22.1.5.4.1**: Sedimentary layers: The layers of sedimentary rock, or strata, can be seen as horizontal bands of differently colored or differently structured materials exposed in this cliff. The deeper layers are older than the layers found at the top, which aids in determining the relative age of fossils found within the strata.

Biostratigraphy

Fossils of species that survived for a relatively short time can be used to match isolated rocks: this technique is called biostratigraphy. For instance, the extinct chordate *Eoplacognathus pseudoplanus* is thought to have existed during a short range in the Middle Ordovician period. If rocks of unknown age have traces of *E. pseudoplanus*, they have a mid-Ordovician age. Such index fossils must be distinctive, globally distributed, and occupy a short time range to be useful. Misleading results can occur if the index fossils are incorrectly dated.

Relative Dating

Stratigraphy and biostratigraphy can in general provide only relative dating (A was before B), which is often sufficient for studying evolution. This is difficult for some time periods, however, because of the barriers involved in matching rocks of the same age across continents. Family-tree relationships can help to narrow down the date when lineages first appeared. For example, if fossils of B date to X million years ago and the calculated "family tree" says A was an ancestor of B, then A must have evolved earlier.

It is also possible to estimate how long ago two living branches of a family tree diverged by assuming that DNA mutations accumulate at a constant rate. However, these “molecular clocks” are sometimes inaccurate and provide only approximate timing. For example, they are not sufficiently precise and reliable for estimating when the groups that feature in the Cambrian explosion first evolved, and estimates produced by different approaches to this method may vary as well.

Carbon Dating

Together with stratigraphic principles, radiometric dating methods are used in geochronology to establish the geological time scale. Beds that preserve fossils typically lack the radioactive elements needed for radiometric dating (” radiocarbon dating ” or simply “carbon dating”). The principle of radiocarbon dating is simple: the rates at which various radioactive elements decay are known, and the ratio of the radioactive element to its decay products shows how long the radioactive element has existed in the rock. This rate is represented by the half-life, which is the time it takes for half of a sample to decay.

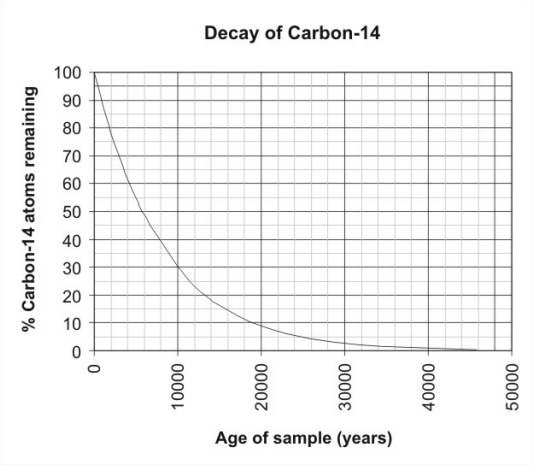


Figure 22.1.5.4.1: Half-life of Carbon-14: Radiometric dating is a technique used to date materials such as rocks or carbon, usually based on a comparison between the observed abundance of a naturally occurring radioactive isotope and its decay products, using known decay rates.

The half-life of carbon-14 is 5,730 years, so carbon dating is only relevant for dating fossils less than 60,000 years old. Radioactive elements are common only in rocks with a volcanic origin, so the only fossil-bearing rocks that can be dated radiometrically are volcanic ash layers. Carbon dating uses the decay of carbon-14 to estimate the age of organic materials, such as wood and leather.

Key Points

- Determining the ages of fossils is an important step in mapping out how life evolved across geologic time.
- The study of stratigraphy enables scientists to determine the age of a fossil if they know the age of layers of rock that surround it.
- Biostratigraphy enables scientists to match rocks with particular fossils to other rocks with those fossils to determine age.
- Paleontology seeks to map out how life evolved across geologic time. A substantial hurdle is the difficulty of working out fossil ages.
- Scientists use carbon dating when determining the age of fossils that are less than 60,000 years old, and that are composed of organic materials such as wood or leather.

Key Terms

- **half-life**: The time required for half of the nuclei in a sample of a specific isotope to undergo radioactive decay.
- **stratigraphy**: The study of rock layers and the layering process.
- **radiocarbon dating**: A method of estimating the age of an artifact or biological vestige based on the relative amounts of various isotopes of carbon present in a sample.

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22.1.5.5: The Fossil Record and the Evolution of the Modern Horse

Learning Objectives

- Analyze the fossil record to understand the evolution of horses

Fossils provide evidence that organisms from the past are not the same as those found today, and demonstrate a progression of evolution. Scientists date and categorize fossils to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of forms over millions of years.

Case Study: Evolution of the Modern Horse

Highly detailed fossil records have been recovered for sequences in the evolution of modern horses. The fossil record of horses in North America is especially rich and contains transition fossils: fossils that show intermediate stages between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago, which gave rise to the first horse-like species 55 to 42 million years ago in the genus *Eohippus*.

The first equid fossil was found in the gypsum quarries in Montmartre, Paris in the 1820s. The tooth was sent to the Paris Conservatory, where Georges Cuvier identified it as a browsing equine related to the tapir. His sketch of the entire animal matched later skeletons found at the site. During the H.M.S. Beagle survey expedition, Charles Darwin had remarkable success with fossil hunting in Patagonia. In 1833 in Santa Fe, Argentina, he was “filled with astonishment” when he found a horse’s tooth in the same stratum as fossils of giant armadillos and wondered if it might have been washed down from a later layer, but concluded this was “not very probable.” In 1836, the anatomist Richard Owen confirmed the tooth was from an extinct species, which he subsequently named *Equus curvidens*.

The original sequence of species believed to have evolved into the horse was based on fossils discovered in North America in the 1870s by paleontologist Othniel Charles Marsh. The sequence, from *Eohippus* to the modern horse (*Equus*), was popularized by Thomas Huxley and became one of the most widely known examples of a clear evolutionary progression. The sequence of transitional fossils was assembled by the American Museum of Natural History into an exhibit that emphasized the gradual, “straight-line” evolution of the horse.

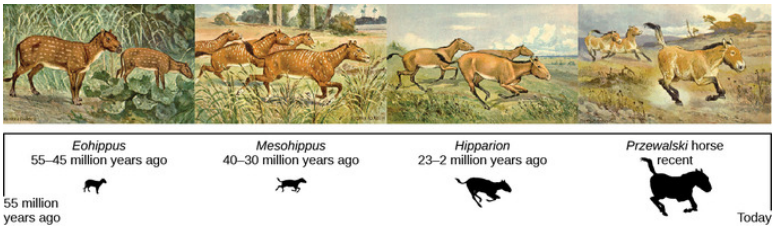


Figure 22.1.5.5.1: Horse evolution: This illustration shows an artist’s renderings of species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. One of the trends, depicted here, is the evolutionary tracking of a drying climate and increase in prairie versus forest habitat reflected in forms that are more adapted to grazing and predator escape through running.

Since then, as the number of equid fossils has increased, the actual evolutionary progression from *Eohippus* to *Equus* has been discovered to be much more complex and multibranched than was initially supposed. Detailed fossil information on the rate and distribution of new equid species has also revealed that the progression between species was not as smooth and consistent as was once believed.

Although some transitions were indeed gradual progressions, a number of others were relatively abrupt in geologic time, taking place over only a few million years. Both anagenesis, a gradual change in an entire population ‘s gene frequency, and cladogenesis, a population “splitting” into two distinct evolutionary branches, occurred, and many species coexisted with “ancestor” species at various times.

Adaptation for Grazing

The series of fossils tracks the change in anatomy resulting from a gradual drying trend that changed the landscape from a forested habitat to a prairie habitat. Early horse ancestors were originally specialized for tropical forests, while modern horses are now adapted to life on drier land. Successive fossils show the evolution of teeth shapes and foot and leg anatomy to a grazing habit with adaptations for escaping predators.

The horse belongs to the order Perissodactyla (odd-toed ungulates), the members of which all share hoofed feet and an odd number of toes on each foot, as well as mobile upper lips and a similar tooth structure. This means that horses share a common ancestry with tapirs and rhinoceroses. Later species showed gains in size, such as those of *Hipparion*, which existed from about 23 to 2 million years ago. The fossil record shows several adaptive radiations in the horse lineage, which is now much reduced to only one genus, *Equus*, with several species. Paleozoologists have been able to piece together a more complete outline of the modern horse's evolutionary lineage than that of any other animal.

Key Points

- A dog-like organism gave rise to the first horse ancestors 55-42 million years ago.
- The fossil record shows modern horses moved from tropical forests to prairie habitats, developed teeth, and grew in size.
- The first equid fossil was a tooth from the extinct species *Equus curvidens* found in Paris in the 1820s.
- Thomas Huxley popularized the evolutionary sequence of horses, which became one of the most common examples of clear evolutionary progression.
- Horse evolution was previously believed to be a linear progress, but after more fossils were discovered, it was determined the evolution of horses was more complex and multi-branched.
- Horses have evolved from gradual change (anagenesis) as well as abrupt progression and division (cladogenesis).

Key Terms

- **cladogenesis**: An evolutionary splitting event in which each branch and its smaller branches forms a clade.
- **equid**: A member of the horse family.
- **anagenesis**: Evolution of a new species through a large scale change in gene frequency so that the new species replaces the old, rather than branching to produce an additional species.

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22.1.5.6: Homologous Structures

Learning Objectives

- Describe the connection between evolution and the appearance of homologous structures

Homologous Structures

Homology is the relationship between structures or DNA derived from the most recent common ancestor. A common example of homologous structures in evolutionary biology are the wings of bats and the arms of primates. Although these two structures do not look similar or have the same function, genetically, they come from the same structure of the last common ancestor. Homologous traits of organisms are therefore explained by descent from a common ancestor.

It's important to note that defining two structures as homologous depends on what ancestor is being described as the common ancestor. If we go all the way back to the beginning of life, all structures are homologous!

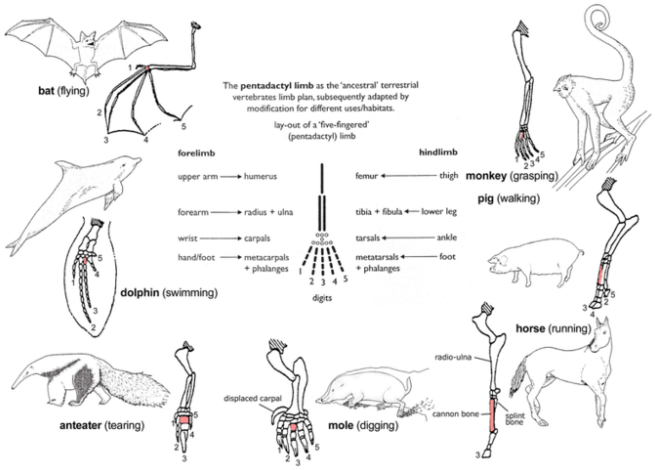


Figure **22.1.5.6.1**: Homology in the forelimbs of vertebrates: The principle of homology illustrated by the adaptive radiation of the forelimb of mammals. All conform to the basic pentadactyl pattern but are modified for different usages. The third metacarpal is shaded throughout; the shoulder is crossed-hatched.

In genetics, homology is measured by comparing protein or DNA sequences. Homologous gene sequences share a high similarity, supporting the hypothesis that they share a common ancestor.

Homology can also be partial: new structures can evolve through the combination of developmental pathways or parts of them. As a result, hybrid or mosaic structures can evolve that exhibit partial homologies. For example, certain compound leaves of flowering plants are partially homologous both to leaves and shoots because they combine some traits of leaves and some of shoots.

Paralogous Structures

Homologous sequences are considered paralogous if they were separated by a gene duplication event; if a gene in an organism is duplicated to occupy two different positions in the same genome, then the two copies are paralogous.

A set of sequences that are paralogous are called paralogs of each other. Paralogs typically have the same or similar function, but sometimes do not. It is considered that due to lack of the original selective pressure upon one copy of the duplicated gene, this copy is free to mutate and acquire new functions.

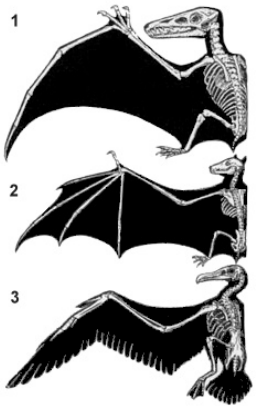


Figure **22.1.5.6.1**: Homology vs. analogy: The wings of pterosaurs (1), bats (2), and birds (3) are analogous as wings, but homologous as forelimbs. This is because they are similar characteristically and even functionally, but evolved from different ancestral roots.

Paralogous genes often belong to the same species, but not always. For example, the hemoglobin gene of humans and the myoglobin gene of chimpanzees are considered paralogs. This is a common problem in bioinformatics; when genomes of different species have been sequenced and homologous genes have been found, one can not immediately conclude that these genes have the same or similar function, as they could be paralogs whose function has diverged.

Analogous Structures

The opposite of homologous structures are analogous structures, which are physically similar structures between two taxa that evolved separately (rather than being present in the last common ancestor). Bat wings and bird wings evolved independently and are considered analogous structures. Genetically, a bat wing and a bird wing have very little in common; the last common ancestor of bats and birds did not have wings like either bats or birds. Wings evolved independently in each lineage after diverging from ancestors with forelimbs that were not used as wings (terrestrial mammals and theropod dinosaurs, respectively).

It is important to distinguish between different hierarchical levels of homology in order to make informative biological comparisons. In the above example, the bird and bat wings are analogous as wings, but homologous as forelimbs because the organ served as a forearm (not a wing) in the last common ancestor of tetrapods.

Analogy is different than homology. Although analogous characteristics are superficially similar, they are not homologous because they are phylogenetically independent. The wings of a maple seed and the wings of an albatross are analogous but not homologous (they both allow the organism to travel on the wind, but they didn't both develop from the same structure). Analogy is commonly also referred to as homoplasy.

Key Points

- Homology is a relationship defined between structures or DNA derived from a common ancestor and illustrates descent from a common ancestor.
- Analogous structures are physically (but not genetically) similar structures that were not present the last common ancestor.
- Homology can also be partial; new structures can evolve through the combination or parts of developmental pathways.
- Analogy may also be referred to as homoplasy, which is further divided into parallelism, reversal, and convergence.

Key Terms

- **homology**: A correspondence of structures in two life forms with a common evolutionary origin, such as flippers and hands.
- **analogy**: The relationship between characteristics that are apparently similar but did not develop from the same structure
- **homoplasy**: A correspondence between the parts or organs of different species acquired as the result of parallel evolution or convergence.

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22.1.5.7: Convergent Evolution

Learning Objectives

- Predict the circumstances supporting convergent evolution of two species

Convergent Evolution

Sometimes, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called convergent evolution, where similar traits evolve independently in species that do not share a recent common ancestry.

Examples of Convergent Evolution

Convergent evolution describes the independent evolution of similar features in species of different lineages. The two species came to the same function, flying, but did so separately from each other. They have "converged" on this useful trait. Both sharks and dolphins have similar body forms, yet are only distantly related: sharks are fish and dolphins are mammals. Such similarities are a result of both populations being exposed to the same selective pressures. Within both groups, changes that aid swimming have been favored. Thus, over time, they developed similar appearances (morphology), even though they are not closely related.

One of the most well-known examples of convergent evolution is the camera eye of cephalopods (e.g., octopus), vertebrates (e.g., mammals), and cnidaria (e.g., box jellies). Their last common ancestor had at most a very simple photoreceptive spot, but a range of processes led to the progressive refinement of this structure to the advanced camera eye. There is, however, one subtle difference: the cephalopod eye is "wired" in the opposite direction, with blood and nerve vessels entering from the back of the retina, rather than the front as in vertebrates.

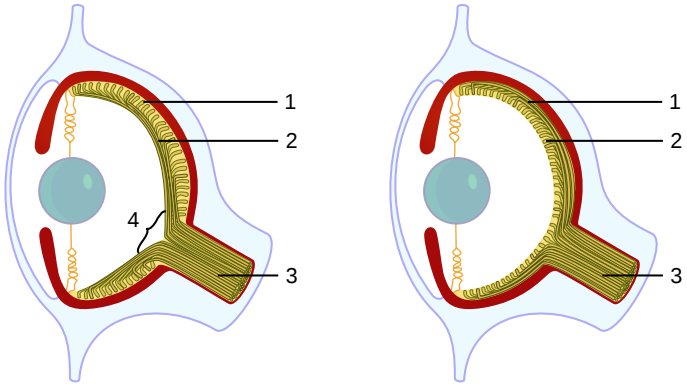


Figure **22.1.5.7.1**: Eye evolution: Vertebrates and octopuses developed the camera eye independently. In the vertebrate version the nerve fibers pass in front of the retina, and there is a blind spot (4) where the nerves pass through the retina. In the octopus version, the eye is constructed the "right way out," with the nerves attached to the rear of the retina. This means that octopuses do not have a blind spot.

Convergent evolution is similar to, but distinguishable from, the phenomenon of parallel evolution. Parallel evolution occurs when two independent but similar species evolve in the same direction and thus independently acquire similar characteristics; for example, gliding frogs have evolved in parallel from multiple types of tree frog.

Analogous Structures

Traits arising through convergent evolution are analogous structures, in contrast to homologous structures, which have a common origin, but not necessarily similar function. The British anatomist Richard Owen was the first scientist to recognize the fundamental difference between analogies and homologies. Bat and pterosaur wings are an example of analogous structures, while the bat wing is homologous to human and other mammal forearms, sharing an ancestral state despite serving different functions.

Divergent Evolution

The opposite of convergent evolution is divergent evolution, whereby related species evolve different traits. On a molecular level, this can happen due to random mutation unrelated to adaptive changes.

Key Points

- Examples of convergent evolution include the relationship between bat and insect wings, shark and dolphin bodies, and vertebrate and cephalopod eyes.
- Analogous structures arise from convergent evolution, but homologous structures do not.
- Convergent evolution is the opposite of divergent evolution, in which related species evolve different traits.
- Convergent evolution is similar to parallel evolution, in which two similar but independent species evolve in the same direction and independently acquire similar characteristics.

Key Terms

- **parallel evolution**: the development of a similar trait in related, but distinct, species descending from the same ancestor, but from different clades
- **convergent evolution**: a trait of evolution in which species not of similar recent origin acquire similar properties due to natural selection
- **divergent evolution**: the process by which a species with similar traits become groups that are tremendously different from each other over many generations
- **morphology**: the form and structure of an organism

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22.1.5.8: Vestigial Structures

Learning Objectives

- Discuss the connection between evolution and the existence of vestigial structures

What Are Vestigial Structures?

Some organisms possess structures with no apparent function which appear to be residual parts from a past ancestor. For example, some snakes have pelvic bones despite having no legs because they descended from reptiles that did have legs. Another example of a structure with no function is the human vermiform appendix. These unused structures without function are called vestigial structures. Other examples of vestigial structures are wings (which may have other functions) on flightless birds like the ostrich, leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.

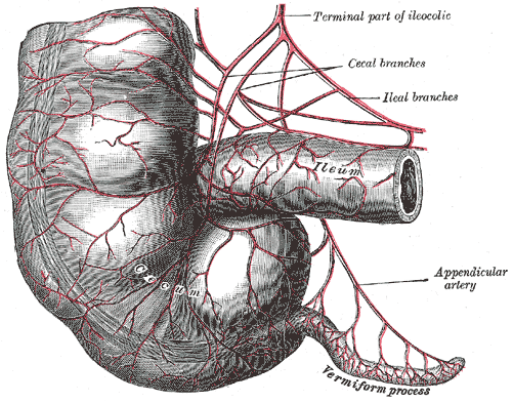


Figure **22.1.5.8.1**: Vestigial appendix: In humans the vermiform appendix is a vestigial structure; it has lost much of its ancestral function.

There are also several reflexes and behaviors that are considered to be vestigial. The formation of goose bumps in humans under stress is a vestigial reflex its function in human ancestors was to raise the body's hair, making the ancestor appear larger and scaring off predators. The arrector pili muscle, which is a band of smooth muscle that connects the hair follicle to connective tissue, contracts and creates the goose bumps on skin.

Vestigial Structures in Evolution

Vestigial structures are often homologous to structures that function normally in other species. Therefore, vestigial structures can be considered evidence for evolution, the process by which beneficial heritable traits arise in populations over an extended period of time. The existence of vestigial traits can be attributed to changes in the environment and behavior patterns of the organism in question. As the function of the trait is no longer beneficial for survival, the likelihood that future offspring will inherit the "normal" form of it decreases. In some cases the structure becomes detrimental to the organism.

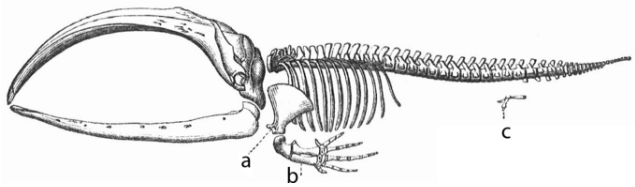


Figure **22.1.5.8.1**: Whale Skeleton: The pelvic bones in whales are also a good example of vestigial evolution (whales evolved from four-legged land mammals and secondarily lost their hind legs). Letter c in the picture indicates the undeveloped hind legs of a baleen whale.

If there are no selection pressures actively lowering the fitness of the individual, the trait will persist in future generations unless the trait is eliminated through genetic drift or other random events.

Although in many cases the vestigial structure is of no direct harm, all structures require extra energy in terms of development, maintenance, and weight and are also a risk in terms of disease (e.g., infection, cancer). This provides some selective pressure for

the removal of parts that do not contribute to an organism's fitness, but a structure that is not directly harmful will take longer to be 'phased out' than one that is. Some vestigial structures persist due to limitations in development, such that complete loss of the structure could not occur without major alterations of the organism's developmental pattern, and such alterations would likely produce numerous negative side-effects.

The vestigial versions of a structure can be compared to the original version of the structure in other species in order to determine the homology of the structure. Homologous structures indicate common ancestry with those organisms that have a functional version of the structure. Vestigial traits can still be considered adaptations because an adaptation is often defined as a trait that has been favored by natural selection. Adaptations, therefore, need not be adaptive, as long as they were at some point.

Key Points

- Structures that have no apparent function and appear to be residual parts from a past ancestor are called vestigial structures.
- Examples of vestigial structures include the human appendix, the pelvic bone of a snake, and the wings of flightless birds.
- Vestigial structures can become detrimental, but in most cases these structures are harmless; however, these structures, like any other structure, require extra energy and are at risk for disease.
- Vestigial structures, especially non-harmful ones, take a long time to be phased out since eliminating them would require major alterations that could result in negative side effects.

Key Terms

- **vestigial structure**: Genetically determined structures or attributes that have lost most or all of their ancestral function in a given species.
- **adaptation**: A modification of something or its parts that makes it more fit for existence under the conditions of its current environment.

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22.1.5.9: Biogeography and the Distribution of Species

Learning Objectives

- Relate biogeography and the distribution of species

Distribution of Species

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors, such as temperature and rainfall, vary based on latitude and elevation, primarily. As these abiotic factors change, the composition of plant and animal communities also changes.

Patterns of Species Distribution

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An endemic species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Since species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia.



Figure **22.1.5.9.1**: Australia: Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal.

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of Proteaceae in Australia, southern Africa, and South America is best explained by the plant family's presence there prior to the southern supercontinent Gondwana breaking up.

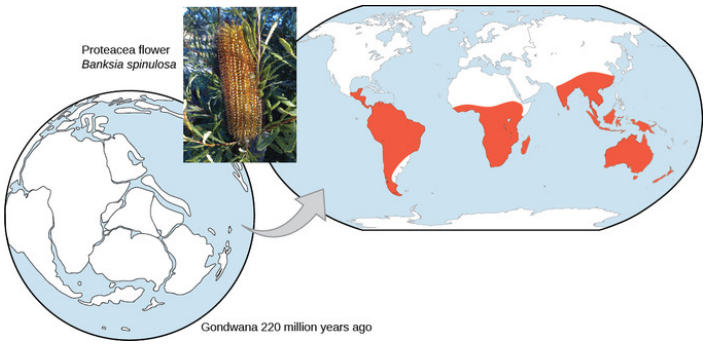


Figure 22.1.5.9.1: Biogeography: The Proteacea family of plants evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in red).

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Key Points

- Biogeography is the study of geological species distribution, which is influenced by both biotic and abiotic factors.
- Some species are endemic and are only found in a particular region, while others are generalists and are distributed worldwide.
- Species that evolved before the breakup of continents are distributed worldwide.
- Species that evolved after the breakup of continents are found in only certain regions of the planet.

Key Terms

- **endemic**: unique to a particular area or region; not found in other places
- **generalist**: species which can thrive in a wide variety of environmental conditions
- **Pangaea**: supercontinent that included all the landmasses of the earth before the Triassic period and that broke up into Laurasia and Gondwana

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22.2: Natural Selection and Reproductive Isolation

One of the best definition os species is that of the evolutionary biologist Ernst Mayr: "A species is an actually or potentially interbreeding population that does not interbreed with other such populations when there is opportunity to do so." However, sometimes breeding may take place (as it can between a horse and a donkey) but if so, the offspring are not so fertile and/or well adapted as the parents (the mule produced is sterile).

Allopatric Speciation: the Role of Isolation in Speciation

The formation of two or more species often (some workers think always!) requires geographical isolation of subpopulations of the species. Only then can natural selection or perhaps genetic drift produce distinctive gene pools. It is no accident that the various **races** (or "**subspecies**") of animals almost never occupy the same territory. Their distribution is **allopatric** ("other country").

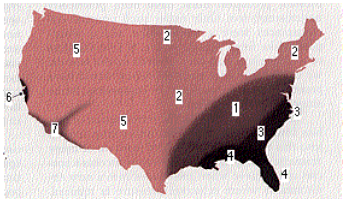


Figure 18.2.1 Yellowthroat

The seven distinct subspecies or races of the yellowthroat ***Geothlypis trichas*** (a warbler) in the continental U.S. would soon merge into a single homogeneous population if they occupied the same territory and bred with one another.

Darwin's Finches

As a young man of 26, Charles Darwin visited the Galapagos Islands off the coast of Ecuador. Among the animals he studied were what appeared to be 13 species* of finches found nowhere else on earth.

- Some have stout beaks for eating seeds of one size or another (#2, #3, #6).
- Others have beaks adapted for eating insects or nectar.
- One (#7) has a beak like a woodpecker's. It uses it to drill holes in wood, but lacking the long tongue of a true woodpecker, it uses a cactus spine held in its beak to dig the insect out.
- One (#12) looks more like a warbler than a finch, but its eggs, nest, and courtship behavior is like that of the other finches.

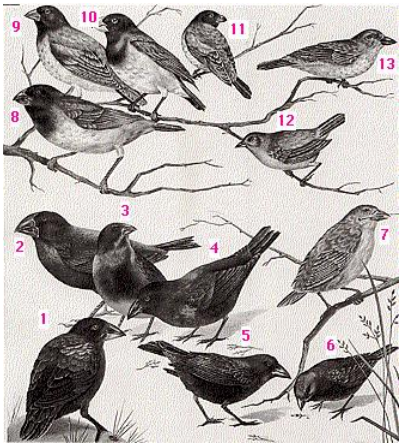


Figure 18.2.2 Darwin's finches

Darwin's finches. The finches numbered 1–7 are ground finches. They seek their food on the ground or in low shrubs. Those numbered 8–13 are tree finches. They live primarily on insects.

1. Large cactus finch (*Geospiza conirostris*)
2. Large ground finch (*Geospiza magnirostris*)
3. Medium ground finch (***Geospiza fortis***)
4. Cactus finch (*Geospiza scandens*)
5. Sharp-beaked ground finch (*Geospiza difficilis*)
6. Small ground finch (*Geospiza fuliginosa*)
7. Woodpecker finch (*Cactospiza pallida*)
8. Vegetarian tree finch (*Platyspiza crassirostris*)
9. Medium tree finch (***Camarhynchus pauper***)
10. Large tree finch (***Camarhynchus psittacula***)
11. Small tree finch (*Camarhynchus parvulus*)
12. Warbler finch (*Certhidia olivacea*)
13. Mangrove finch (*Cactospiza heliobates*)

(From BSCS, Biological Science: Molecules to Man, Houghton Mifflin Co., 1963)

* Genetic analysis provides evidence that:

- There are actually two species of warbler finch — *Certhidia olivacea* now called the green warbler finch and *Certhidia fusca*, the gray warbler finch.
- The various populations of *Geospiza difficilis* found on the different islands belong to one or another of three clades so genetically distinct that they deserve full species status.

Whether the number is 13 or 17, since Darwin's time, these birds have provided a case study of how a single species reaching the Galapagos from Central or South America could - over a few million years - give rise to the various species that live there today. Several factors have been identified that may contribute to speciation.

Ecological opportunity

When the ancestor of Darwin's finches reached the Galapagos, it found **no predators** (There were no mammals and few reptiles on the islands.) and **few, if any, competitors**. There were only a handful of other types of songbirds. In fact, if true warblers or woodpeckers had been present, their efficiency at exploiting their niches would surely have prevented the evolution of warblerlike and woodpeckerlike finches.

Geographical Isolation (allopatry)

The proximity of the various islands has permitted enough migration of Darwin's finches between them to enable distinct island populations to arise. But the distances between the islands is great enough to limit interbreeding between populations on different islands. This has made possible the formation of distinctive **subspecies** (= **races**) on the various islands.

The importance of geographical isolation is illuminated by a single, fourteenth, species of Darwin's finches that lives on **Cocos Island**, some 500 miles (800 km) to the northeast of the Galapagos. The first immigrants there must also have found relaxed selection pressures with few predators or competitors. How different the outcome, though. Where one immigrant species gave rise to at least 13 on the scattered Galapagos Islands, no such divergence has occurred on the single, isolated Cocos Island.

Evolutionary Change

In isolation, changes in the gene pool can occur through some combination of natural selection, genetic drift, and founder effect. These factors may produce distinct subpopulations on the different islands. So long as they remain separate (**allopatric**) we consider them **races** or **subspecies**. In fact, they might not be able to interbreed with other races but so long as we don't know, we assume that they could.

How much genetic change is needed to create a new species? Perhaps not as much as you might think. For example, changes at one or just a few gene loci might do the trick. For example, a single mutation altering flower color or petal shape could immediately prevent cross-pollination between the new and the parental types (a form of prezygotic isolating mechanism).

Reunion

The question of their status - subspecies or true species - is resolved if they ever do come to occupy the same territory again (become **sympatric**). If successful interbreeding occurs, the differences will gradually disappear, and a single population will be formed again. Speciation will not have occurred. If, on the other hand, two subspecies reunite but fail to resume breeding, speciation has occurred and they have become separate species.

An example: The medium tree finch ***Camarhynchus pauper*** is found only on **Floreana Island**. Its close relative, the large tree finch, ***Camarhynchus psittacula***, is found on all the central islands including Floreana. Were it not for its presence on Floreana, both forms would be considered subspecies of the same species. Because they do coexist and maintain their separate identity on Floreana, we know that speciation has occurred.

Isolating Mechanisms

What might keep two subpopulations from interbreeding when reunited geographically? There are several mechanisms.

Prezygotic Isolating Mechanisms act before fertilization occurs. Sexual selection - a failure to elicit mating behavior. On Floreana, *Camarhynchus psittacula* has a longer beak than *Camarhynchus pauper*, and the research teams led by Peter and Rosemary Grant have demonstrated that beak size is an important criterion by which Darwin's finches choose their mates. Two subpopulations may occupy different habitats in the same area and thus fail to meet at breeding time. In plants, a shift in the time of flowering can prevent pollination between the two subpopulations. Structural differences in the sex organs may become an isolating mechanism. The sperm may fail to reach or fuse with the egg.

Postzygotic Isolating Mechanisms act even if fertilization does occur. Even if a zygote is formed, genetic differences may have become so great that the resulting hybrids are less viable or less fertile than the parental types. The sterile mule produced by mating a horse with a donkey is an example. Sterility in the males produced by hybridization is more common than in females. In fact, it is the most common postzygotic isolating mechanism. When ***Drosophila melanogaster*** attempts to mate with its relative ***Drosophila simulans***, no viable males are even produced. Mutations in a single gene (encoding a component of the nuclear pore complex) are responsible.

Reinforcement

When two species that have separated in allopatry become reunited, their prezygotic and postzygotic isolating mechanisms may become more stringent than those between the same species existing apart from each other. This phenomenon is called **reinforcement**. It arises from natural selection working to favor individuals that avoid interspecific matings, which would produce less-fit hybrids, when the two species are first reunited.

Speciation by Hybridization

Hybridization between related angiosperms is sometimes followed by a doubling of the chromosome number. The resulting **polyploids** are now fully fertile with each other although unable to breed with either parental type - a new species has been created. This appears to have been a frequent mechanism of speciation in angiosperms. Even without forming a polyploid, interspecific hybridization can occasionally lead to a new species of angiosperm. Two species of sunflower, the "common sunflower", *Helianthus annuus*, and the "prairie sunflower", *H. petiolaris*, grow widely over the western half of the United States. They can interbreed, but only rarely are fertile offspring produced.

However, Rieseberg and colleagues have found evidence that successful hybridization between them has happened naturally in the past. They have shown that three other species of sunflower (each growing in a habitat too harsh for either parental type) are each the product of an ancient hybridization between *Helianthus annuus* and *H. petiolaris*. Although each of these species has the same **diploid** number of chromosomes as the parents (2**n** = 34), they each have a pattern of chromosome segments that have been derived, by **genetic recombination**, from both the parental genomes. They demonstrated this in several ways, notably by combining RFLP analysis with the polymerase chain reaction (PCR).

They even went on to produce (at a low frequency) *annuus* x *petiolaris* hybrids in the greenhouse that mimicked the phenotypes and genotypes of the natural hybrids. (These monumental studies were described in the 29 August 2003 issue of **Science**.)

Another example. In Pennsylvania, hybrids between a species of fruit fly (not Drosophila) that feeds on blueberries and another species (again, not Drosophila) that feeds on snowberries feed on honeysuckle where they neither encounter competition from their parental species nor have an opportunity to breed with them (no introgression). This study was published in the 28 July 2005 issue of **Nature**. So speciation can occur as a result of hybridization between two related species, if the hybrid

- receives a genome that enables it to breed with other such hybrids but not breed with either parental species,
- can escape to a habitat where it does not have to compete with either parent,
- is adapted to live under those new conditions.

Adaptive Radiation

The processes described in this page can occur over and over. In the case of Darwin's finches, they must have been repeated a number of times forming new species that gradually divided the available habitats between them. From the first arrival have come a variety of ground-feeding and tree-feeding finches as well as the warblerlike finch and the tool-using woodpeckerlike finch. The formation of a number of diverse species from a single ancestral one is called an **adaptive radiation**.

Speciateion in theHouse mice on the island of Madeira

A report in the 13 January 2000 issue of **Nature** describes a study of house mouse populations on the island of Madeira off the Northwest coast of Africa. These workers (Janice Britton-Davidian et al) examined the karyotypes of 143 house mice (***Mus musculus domesticus***) from various locations along the coast of this mountainous island.

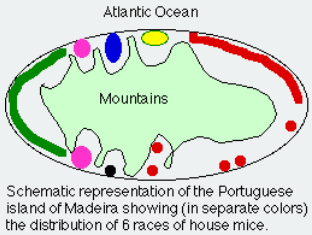


Figure 18.2.3 Madeira mice

Their findings:

- There are 6 distinct populations (shown by different colors)
- Each of these has a distinct karyotype, with a diploid number less than the "normal" (2**n** = 40).
- The reduction in chromosome number has occurred through **Robertsonian fusions**. Mouse chromosomes tend to be **acrocentric**; that is, the centromere connects one long and one very short arm. Acrocentric chromosomes are at risk of translocations that fuse the long arms of two different chromosomes with the loss of the short arms.
- The different populations are **allopatric**; isolated in different valleys leading down to the sea.
- The distinct and uniform karyotype found in each population probably arose from genetic drift rather than natural selection.
- The 6 different populations are technically described as **races** because there is no opportunity for them to attempt interbreeding.
- However, they surely meet the definition of true species. While hybrids would form easily (no prezygotic isolating mechanisms), these would probably be infertile as proper synapsis and segregation of such different chromosomes would be difficult when the hybrids attempted to form gametes by meiosis.

Sympatric Speciation

Sympatric speciation refers to the formation of two or more descendant species from a single ancestral species all occupying the same geographic location. Some evolutionary biologists don't believe that it ever occurs. They feel that interbreeding would soon eliminate any genetic differences that might appear. But there is some compelling (albeit indirect) evidence that sympatric speciation can occur.

Speciation in three-spined sticklebacks

The three-spined sticklebacks, freshwater fishes that have been studied by Dolph Schluter (who received his Ph.D. for his work on Darwin's finches with Peter Grant) and his current colleagues in British Columbia, provide an intriguing example that is best explained by sympatric speciation.

They have found:

- Two different species of three-spined sticklebacks in each of five different lakes.
  - a large benthic species with a large mouth that feeds on large prey in the littoral zone
  - a smaller limnetic species with a smaller mouth that feeds on the small plankton in open water.
- DNA analysis indicates that each lake was colonized independently, presumably by a marine ancestor, after the last ice age.
- DNA analysis also shows that the two species in each lake are more closely related to each other than they are to any of the species in the other lakes.
- Nevertheless, the two species in each lake are reproductively isolated; neither mates with the other.
- However, aquarium tests showed that
  - The benthic species from one lake will spawn with the benthic species from the other lakes and likewise the limnetic species from the different lakes will spawn with each other.
  - These benthic and limnetic species even display their mating preferences when presented with sticklebacks from Japanese lakes; that is, a Canadian benthic prefers a Japanese benthic over its close limnetic cousin from its own lake.
- Their conclusion: in each lake, what began as a single population faced such competition for limited resources that
  - **disruptive selection** — competition favoring fishes at either extreme of body size and mouth size over those nearer the mean — coupled with
  - **assortative mating** — each size preferred mates like it

  favored a divergence into two subpopulations exploiting different food in different parts of the lake.
- The fact that this pattern of speciation occurred the same way on three separate occasions suggests strongly that **ecological factors** in a sympatric population can cause speciation.

Sympatric speciation driven by ecological factors may also account for the extraordinary diversity of crustaceans living in the depths of Siberia's Lake Baikal.

How many genes are needed to start down the path to sympatric speciation?

Perhaps not very many. The European corn borer, *Ostrinia nubilalis*, (which despite its common name is a major pest in the U.S. as well) exists as two distinct races designated **Z** and **E**. Both can be found in the same area; that is, they are sympatric. But in the field, they practice assortative mating - only breeding with mates of their own race.

The females of both races synthesize and release a pheromone that is a sex attractant for the males. Both races use the same substance but different isomers of it. Which isomer is produced is under the control of a single enzyme-encoding gene locus. The ability of the males to respond to one isomer or the other is controlled by 2 loci.

The Problem of Clines

There is another possible way for new species to arise in the absence of geographical barriers. If a population ranges over a large area and if the individuals in that population can disperse over only a small portion of this range, then gene flow across these great distances would be reduced. The occurrence of gradual phenotypic (and genotypic) differences in a population across a large geographical area is called a **cline**. Successful interbreeding occurs freely at every point along the cline, but individuals at the ends of the cline may not be able to interbreed. This can be tested in the laboratory.

And, on occasions, it is tested in nature. If a cline bends around so that the ends meet, and the populations reunited at the junction cannot interbreed, then the definition of separate species has been met. Such species are called **ring species** and this type of speciation is called **parapatric speciation**.

Two examples:

1. The Caribbean slipper spurge *Euphorbia tithymaloides*.
Genetic analysis shows that this wildflower originated in Central America where Mexico and Guatemala share a common boundary. From there it spread in two directions

- northeast through the Yucatan peninsula and then island-hopped through Jamaica, the Dominican Republic, Puerto Rico and into the Virgin Islands;
- south through Central America, on through Venezuela, and then north through Barbados and the other islands of the Lesser Antilles finally also reaching the Virgin Islands.

Reunited in the Virgin Islands, the two populations have diverged sufficiently that they retain their distinctive genotypic and phenotypic traits. Ongoing studies will determine to what degree they may be reproductively isolated.

2. The large-blotched salamander *Ensatina eschscholtzii*.

This animal is found in California where it occurs in a number of different subspecies or races. A single subspecies is found in Northern California, and it is thought to be the founder of all the others. Over time that original population spread southward in two directions:

- down the Sierra Nevada mountains east of the great central San Joaquin Valley and
- down the coast range of mountains west of the valley.

South of the valley, the eastern group has moved west and now meets the western group, closing the ring. Here the two populations fail to interbreed successfully, maintaining their distinct identities. But each subspecies interbreeds in an unbroken chain up the two paths their ancestors took.

Ring species present a difficult problem in assigning species designations. It is easy to say that the populations at the ends of the cline represent separate species, but where did one give rise to the other? At every point along the cline, interbreeding goes on successfully.

The same problem faces paleontologists examining the gradual phenotypic changes seen in an unbroken line of ever-younger fossils from what one presumes to be a single line of descent. If one could resurrect the ancestral species (A) and the descendant species (B) and they could not interbreed, then they meet the definition of separate species. But there was no moment in time when one could say that A became B. So the clines of today are a model in **space** of Darwin's descent with modification occurring over **time**.

Although clines present a problem for classifiers, they are a beautiful demonstration of Darwin's conviction that the accumulation of small inherited differences can lead to the formation of new species.

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SECTION OVERVIEW

22.3: The Role of Genetic Drift and Natural Selection in Speciation

Learning Objectives

- Give examples of allopatric speciation

Allopatric Speciation

A geographically-continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous, that free-flow of alleles is prevented. When that separation continues for a period of time, the two populations are able to evolve along different trajectories. This is known as allopatric speciation. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ causing natural selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion forming a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are individuals from each population would fly back and forth, continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be improbable; therefore, speciation would be probably occur.

Biologists group allopatric processes into two categories: dispersal and vicariance. Dispersal occurs when a few members of a species move to a new geographical area, while vicariance occurs when a natural situation arises to physically divide organisms.

Scientists have documented numerous cases of allopatric speciation. For example, along the west coast of the United States, two separate sub-species of spotted owls exist. The northern spotted owl has genetic and phenotypic differences from its close relative, the Mexican spotted owl, which lives in the south.



Figure **22.3.1**: Allopatric speciation due to geographic separation: The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation.

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more probable it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would generally have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler

than in the south causing the types of organisms in each ecosystem differ, as do their behaviors and habits. Also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, resulting in speciation.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area with each finding a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. This is called adaptive radiation because many adaptations evolve from a single point of origin, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved.

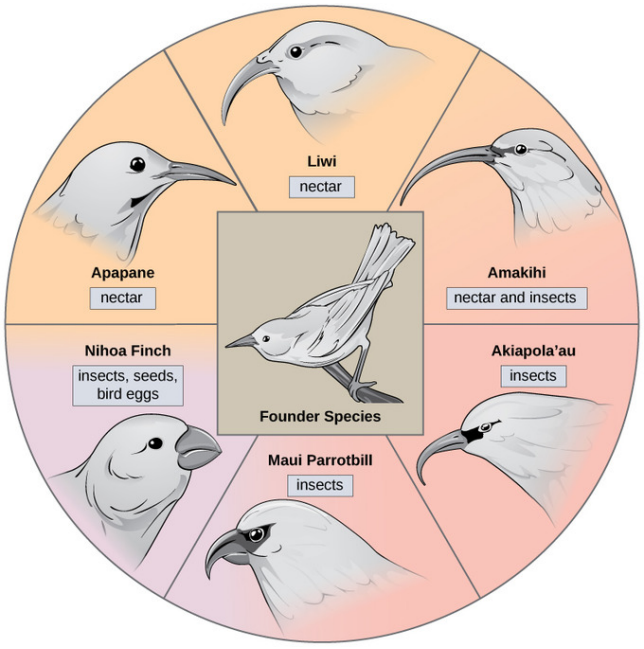


Figure **22.3.1**: Adaptive Radiation: The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

In Hawaiian honeycreepers, the response to natural selection based on specific food sources in each new habitat led to the evolution of a different beak suited to the specific food source. The seed-eating birds have a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects.

Key Points

- When a population is geographically continuous, the allele frequencies among its members are similar; however, when a population becomes separated, the allele frequencies between the two groups can begin to vary.
- If the separation between groups continues for a long period of time, the differences between their alleles can become more and more pronounced due to differences in climate, predation, food sources, and other factors, eventually leading to the formation of a new species.
- Geographic separation between populations can occur in many ways; the severity of the separation depends on the travel capabilities of the species.
- Allopatric speciation events can occur either by dispersal, when a few members of a species move to a new geographical area, or by vicariance, when a natural situation, such as the formation of a river or valley, physically divide organisms.
- When a population disperses throughout an area, into new, different and often isolated habitats, multiple speciation events can occur in which the single original species gives rise to many new species; this phenomenon is called adaptive radiation.

Key Terms

- **vicariance**: the separation of a group of organisms by a geographic barrier, resulting in differentiation of the original group into new varieties or species
- **adaptive radiation**: the diversification of species into separate forms that each adapt to occupy a specific environmental niche
- **dispersal**: the movement of a few members of a species to a new geographical area, resulting in differentiation of the original group into new varieties or species

22.3.1: Gene Duplications and Divergence

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22.3.1: Gene Duplications and Divergence

Learning Objectives

- Explain the mechanisms of gene duplication and divergence

Gene Duplication

Gene duplication is the process by which a region of DNA coding for a gene is copied. Gene duplication can occur as the result of an error in recombination or through a retrotransposition event. Duplicate genes are often immune to the selective pressure under which genes normally exist. This can result in a large number of mutations accumulating in the duplicate gene code. This may render the gene non-functional or in some cases confer some benefit to the organism. There are multiple mechanisms by which gene duplication can occur.

Ectopic Recombination

Duplications can arise from unequal crossing-over that occurs during meiosis between misaligned homologous chromosomes. The product of this recombination is a duplication at the site of the exchange and a reciprocal deletion. Ectopic recombination is typically mediated by sequence similarity at the duplicate breakpoints, which form direct repeats. Repetitive genetic elements, such as transposable elements, offer one source of repetitive DNA that can facilitate recombination, and they are often found at duplication breakpoints in plants and mammals.

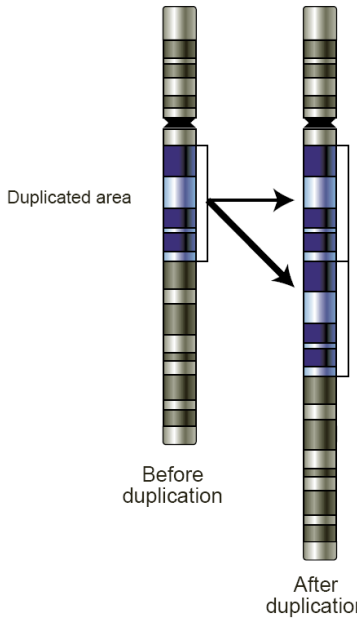


Figure **22.3.1.1**: Gene Duplication: This figure indicates a schematic of a region of a chromosome before and after a duplication event. Ectopic recombination is typically mediated by sequence similarity at the duplicate breakpoints, which form direct repeats.

Replication Slippage

Replication slippage is an error in DNA replication, which can produce duplications of short genetic sequences. During replication, DNA polymerase begins to copy the DNA, and at some point during the replication process, the polymerase dissociates from the DNA and replication stalls. When the polymerase reattaches to the DNA strand, it aligns the replicating strand to an incorrect position and incidentally copies the same section more than once. Replication slippage is also often facilitated by repetitive sequence but requires only a few bases of similarity.

Retrotransposition

During cellular invasion by a replicating retroelement or retrovirus, viral proteins copy their genome by reverse transcribing RNA to DNA. If viral proteins attach irregularly to cellular mRNA, they can reverse-transcribe copies of genes to create retrogenes. Retrogenes usually lack intronic sequence and often contain poly A sequences that are also integrated into the genome. Many retrogenes display changes in gene regulation in comparison to their parental gene sequences, which sometimes results in novel functions.

Aneuploidy

Aneuploidy occurs when nondisjunction at a single chromosome results in an abnormal number of chromosomes. Aneuploidy is often harmful and in mammals regularly leads to spontaneous abortions. Some aneuploid individuals are viable. For example, trisomy 21 in humans leads to Down syndrome, but it is not fatal. Aneuploidy often alters gene dosage in ways that are detrimental to the organism and therefore, will not likely spread through populations.

Gene duplication as an evolutionary event

Gene duplications are an essential source of genetic novelty that can lead to evolutionary innovation. Duplication creates genetic redundancy and if one copy of a gene experiences a mutation that affects its original function, the second copy can serve as a ‘spare part’ and continue to function correctly. Thus, duplicate genes accumulate mutations faster than a functional single-copy gene, over generations of organisms, and it is possible for one of the two copies to develop a new and different function. This is an examples of neofunctionalization.

Gene duplication is believed to play a major role in evolution; this stance has been held by members of the scientific community for over 100 years. It has been argued that gene duplication is the most important evolutionary force since the emergence of the universal common ancestor.

Another possible fate for duplicate genes is that both copies are equally free to accumulate degenerative mutations, so long as any defects are complemented by the other copy. This leads to a neutral “subfunctionalization” model, in which the functionality of the original gene is distributed among the two copies. Neither gene can be lost, as both now perform important non-redundant functions, but ultimately neither is able to achieve novel functionality. Subfunctionalization can occur through neutral processes in which mutations accumulate with no detrimental or beneficial effects. However, in some cases subfunctionalization can occur with clear adaptive benefits. If an ancestral gene is pleiotropic and performs two functions, often times neither one of these two functions can be changed without affecting the other function. In this way, partitioning the ancestral functions into two separate genes can allow for adaptive specialization of subfunctions, thereby providing an adaptive benefit.

Divergence

Genetic divergence is the process in which two or more populations of an ancestral species accumulate independent genetic changes through time, often after the populations have become reproductively isolated for some period of time. In some cases, subpopulations living in ecologically distinct peripheral environments can exhibit genetic divergence from the remainder of a population, especially where the range of a population is very large. The genetic differences among divergent populations can involve silent mutations (that have no effect on the phenotype) or give rise to significant morphological and/or physiological changes. Genetic divergence will always accompany reproductive isolation, either due to novel adaptations via selection and/or due to genetic drift, and is the principal mechanism underlying speciation.

Genetic drift or allelic drift is the change in the frequency of a gene variant (allele) in a population due to random sampling. The alleles in the offspring are a sample of those in the parents, and chance has a role in determining whether a given individual survives and reproduces. A population’s allele frequency is the fraction of the copies of one gene that share a particular form. Genetic drift may cause gene variants to disappear completely and thereby reduce genetic variation. When there are few copies of an allele, the effect of genetic drift is larger, and when there are many copies the effect is smaller. These changes in gene frequency can contribute to divergence.

Divergent evolution is usually a result of diffusion of the same species to different and isolated environments, which blocks the gene flow among the distinct populations allowing differentiated fixation of characteristics through genetic drift and natural selection.Divergent evolution can also be applied to molecular biology characteristics. This could apply to a pathway in two or

more organisms or cell types. This can apply to genes and proteins, such as nucleotide sequences or protein sequences that are derived from two or more homologous genes. Both orthologous genes (resulting from a speciation event) and paralogous genes (resulting from gene duplication within a population) can be said to display divergent evolution.

Key Points

- Ectopic recombination occurs when there is an unequal crossing-over and the product of this recombination are a duplication at the site of the exchange and a reciprocal deletion.
- Gene duplications do not always result in detrimental mutations; they can contribute to divergent evolution, which causes genetic differences between groups to develop and eventually form new species.
- Replication slippage can occur when there is an error during DNA replication and duplications of short genetic sequences are produced.
- Retrotranspositions occur when a retrovirus copies their genome by reverse transcribing RNA to DNA and aberrantly attach to cellular mRNA and reverse transcribe copies of genes to create retrogenes.
- Aneuploidy can occur when there is a nondisjunction even at a single chromosome thus, the result is an abnormal number of chromosomes.
- Genetic divergence can occur by mechanisms such as genetic drift which contibute to the accumulation of independent genetic changes of two or more populations derived from a common ancestor.

Key Terms

- **paralogous**: having a similar structure indicating divergence from a common ancestral gene
- **nondisjunction**: the failure of chromosome pairs to separate properly during meiosis
- **retrogene**: a DNA gene copied back from RNA by reverse transcription
- **genetic drift**: an overall shift of allele distribution in an isolated population, due to random fluctuations in the frequencies of individual alleles of the genes

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22.4: The Geography of Speciation

One of the best definition os species is that of the evolutionary biologist Ernst Mayr: "A species is an actually or potentially interbreeding population that does not interbreed with other such populations when there is opportunity to do so." However, sometimes breeding may take place (as it can between a horse and a donkey) but if so, the offspring are not so fertile and/or well adapted as the parents (the mule produced is sterile).

Allopatric Speciation: the Role of Isolation in Speciation

The formation of two or more species often (some workers think always!) requires geographical isolation of subpopulations of the species. Only then can natural selection or perhaps genetic drift produce distinctive gene pools. It is no accident that the various **races** (or "**subspecies**") of animals almost never occupy the same territory. Their distribution is **allopatric** ("other country").

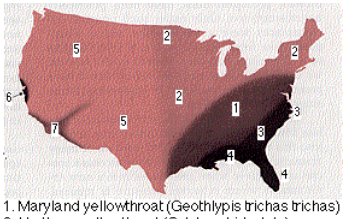


Figure 18.2.1 Yellowthroat

The seven distinct subspecies or races of the yellowthroat ***Geothlypis trichas*** (a warbler) in the continental U.S. would soon merge into a single homogeneous population if they occupied the same territory and bred with one another.

Darwin's Finches

As a young man of 26, Charles Darwin visited the Galapagos Islands off the coast of Ecuador. Among the animals he studied were what appeared to be 13 species* of finches found nowhere else on earth.

- Some have stout beaks for eating seeds of one size or another (#2, #3, #6).
- Others have beaks adapted for eating insects or nectar.
- One (#7) has a beak like a woodpecker's. It uses it to drill holes in wood, but lacking the long tongue of a true woodpecker, it uses a cactus spine held in its beak to dig the insect out.
- One (#12) looks more like a warbler than a finch, but its eggs, nest, and courtship behavior is like that of the other finches.

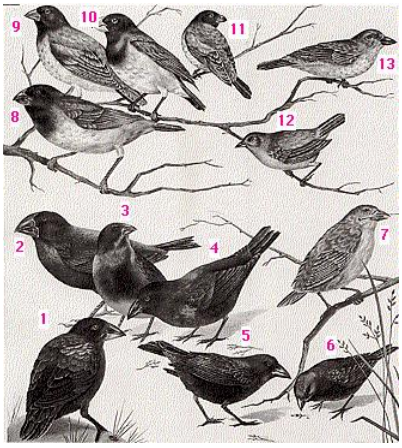


Figure 18.2.2 Darwin's finches

Darwin's finches. The finches numbered 1–7 are ground finches. They seek their food on the ground or in low shrubs. Those numbered 8–13 are tree finches. They live primarily on insects.

1. Large cactus finch (*Geospiza conirostris*)
2. Large ground finch (*Geospiza magnirostris*)
3. Medium ground finch (***Geospiza fortis***)
4. Cactus finch (*Geospiza scandens*)
5. Sharp-beaked ground finch (*Geospiza difficilis*)
6. Small ground finch (*Geospiza fuliginosa*)
7. Woodpecker finch (*Cactospiza pallida*)
8. Vegetarian tree finch (*Platyspiza crassirostris*)
9. Medium tree finch (***Camarhynchus pauper***)
10. Large tree finch (***Camarhynchus psittacula***)
11. Small tree finch (*Camarhynchus parvulus*)
12. Warbler finch (*Certhidia olivacea*)
13. Mangrove finch (*Cactospiza heliobates*)

(From BSCS, Biological Science: Molecules to Man, Houghton Mifflin Co., 1963)

* Genetic analysis provides evidence that:

- There are actually two species of warbler finch — *Certhidia olivacea* now called the green warbler finch and *Certhidia fusca*, the gray warbler finch.
- The various populations of *Geospiza difficilis* found on the different islands belong to one or another of three clades so genetically distinct that they deserve full species status.

Whether the number is 13 or 17, since Darwin's time, these birds have provided a case study of how a single species reaching the Galapagos from Central or South America could - over a few million years - give rise to the various species that live there today. Several factors have been identified that may contribute to speciation.

Ecological opportunity

When the ancestor of Darwin's finches reached the Galapagos, it found **no predators** (There were no mammals and few reptiles on the islands.) and **few, if any, competitors**. There were only a handful of other types of songbirds. In fact, if true warblers or woodpeckers had been present, their efficiency at exploiting their niches would surely have prevented the evolution of warblerlike and woodpeckerlike finches.

Geographical Isolation (allopatry)

The proximity of the various islands has permitted enough migration of Darwin's finches between them to enable distinct island populations to arise. But the distances between the islands is great enough to limit interbreeding between populations on different islands. This has made possible the formation of distinctive **subspecies** (= **races**) on the various islands.

The importance of geographical isolation is illuminated by a single, fourteenth, species of Darwin's finches that lives on **Cocos Island**, some 500 miles (800 km) to the northeast of the Galapagos. The first immigrants there must also have found relaxed selection pressures with few predators or competitors. How different the outcome, though. Where one immigrant species gave rise to at least 13 on the scattered Galapagos Islands, no such divergence has occurred on the single, isolated Cocos Island.

Evolutionary Change

In isolation, changes in the gene pool can occur through some combination of natural selection, genetic drift, and founder effect. These factors may produce distinct subpopulations on the different islands. So long as they remain separate (**allopatric**) we consider them **races** or **subspecies**. In fact, they might not be able to interbreed with other races but so long as we don't know, we assume that they could.

How much genetic change is needed to create a new species? Perhaps not as much as you might think. For example, changes at one or just a few gene loci might do the trick. For example, a single mutation altering flower color or petal shape could immediately prevent cross-pollination between the new and the parental types (a form of prezygotic isolating mechanism).

Reunion

The question of their status - subspecies or true species - is resolved if they ever do come to occupy the same territory again (become **sympatric**). If successful interbreeding occurs, the differences will gradually disappear, and a single population will be formed again. Speciation will not have occurred. If, on the other hand, two subspecies reunite but fail to resume breeding, speciation has occurred and they have become separate species.

An example: The medium tree finch ***Camarhynchus pauper*** is found only on **Floreana Island**. Its close relative, the large tree finch, ***Camarhynchus psittacula***, is found on all the central islands including Floreana. Were it not for its presence on Floreana, both forms would be considered subspecies of the same species. Because they do coexist and maintain their separate identity on Floreana, we know that speciation has occurred.

Isolating Mechanisms

What might keep two subpopulations from interbreeding when reunited geographically? There are several mechanisms.

Prezygotic Isolating Mechanisms act before fertilization occurs. Sexual selection - a failure to elicit mating behavior. On Floreana, *Camarhynchus psittacula* has a longer beak than *Camarhynchus pauper*, and the research teams led by Peter and Rosemary Grant have demonstrated that beak size is an important criterion by which Darwin's finches choose their mates. Two subpopulations may occupy different habitats in the same area and thus fail to meet at breeding time. In plants, a shift in the time of flowering can prevent pollination between the two subpopulations. Structural differences in the sex organs may become an isolating mechanism. The sperm may fail to reach or fuse with the egg.

Postzygotic Isolating Mechanisms act even if fertilization does occur. Even if a zygote is formed, genetic differences may have become so great that the resulting hybrids are less viable or less fertile than the parental types. The sterile mule produced by mating a horse with a donkey is an example. Sterility in the males produced by hybridization is more common than in females. In fact, it is the most common postzygotic isolating mechanism. When ***Drosophila melanogaster*** attempts to mate with its relative ***Drosophila simulans***, no viable males are even produced. Mutations in a single gene (encoding a component of the nuclear pore complex) are responsible.

Reinforcement

When two species that have separated in allopatry become reunited, their prezygotic and postzygotic isolating mechanisms may become more stringent than those between the same species existing apart from each other. This phenomenon is called **reinforcement**. It arises from natural selection working to favor individuals that avoid interspecific matings, which would produce less-fit hybrids, when the two species are first reunited.

Speciation by Hybridization

Hybridization between related angiosperms is sometimes followed by a doubling of the chromosome number. The resulting **polyploids** are now fully fertile with each other although unable to breed with either parental type - a new species has been created. This appears to have been a frequent mechanism of speciation in angiosperms. Even without forming a polyploid, interspecific hybridization can occasionally lead to a new species of angiosperm. Two species of sunflower, the "common sunflower", *Helianthus annuus*, and the "prairie sunflower", *H. petiolaris*, grow widely over the western half of the United States. They can interbreed, but only rarely are fertile offspring produced.

However, Rieseberg and colleagues have found evidence that successful hybridization between them has happened naturally in the past. They have shown that three other species of sunflower (each growing in a habitat too harsh for either parental type) are each the product of an ancient hybridization between *Helianthus annuus* and *H. petiolaris*. Although each of these species has the same **diploid** number of chromosomes as the parents (2**n** = 34), they each have a pattern of chromosome segments that have been derived, by **genetic recombination**, from both the parental genomes. They demonstrated this in several ways, notably by combining RFLP analysis with the polymerase chain reaction (PCR).

They even went on to produce (at a low frequency) *annuus* x *petiolaris* hybrids in the greenhouse that mimicked the phenotypes and genotypes of the natural hybrids. (These monumental studies were described in the 29 August 2003 issue of **Science**.)

Another example. In Pennsylvania, hybrids between a species of fruit fly (not Drosophila) that feeds on blueberries and another species (again, not Drosophila) that feeds on snowberries feed on honeysuckle where they neither encounter competition from their parental species nor have an opportunity to breed with them (no introgression). This study was published in the 28 July 2005 issue of **Nature**. So speciation can occur as a result of hybridization between two related species, if the hybrid

- receives a genome that enables it to breed with other such hybrids but not breed with either parental species,
- can escape to a habitat where it does not have to compete with either parent,
- is adapted to live under those new conditions.

Adaptive Radiation

The processes described in this page can occur over and over. In the case of Darwin's finches, they must have been repeated a number of times forming new species that gradually divided the available habitats between them. From the first arrival have come a variety of ground-feeding and tree-feeding finches as well as the warblerlike finch and the tool-using woodpeckerlike finch. The formation of a number of diverse species from a single ancestral one is called an **adaptive radiation**.

Speciateion in theHouse mice on the island of Madeira

A report in the 13 January 2000 issue of **Nature** describes a study of house mouse populations on the island of Madeira off the Northwest coast of Africa. These workers (Janice Britton-Davidian et al) examined the karyotypes of 143 house mice (***Mus musculus domesticus***) from various locations along the coast of this mountainous island.

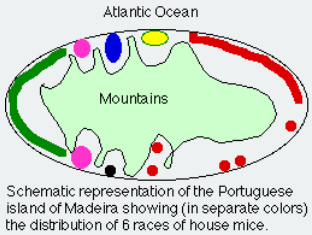


Figure 18.2.3 Madeira mice

Their findings:

- There are 6 distinct populations (shown by different colors)
- Each of these has a distinct karyotype, with a diploid number less than the "normal" (2**n** = 40).
- The reduction in chromosome number has occurred through **Robertsonian fusions**. Mouse chromosomes tend to be **acrocentric**; that is, the centromere connects one long and one very short arm. Acrocentric chromosomes are at risk of translocations that fuse the long arms of two different chromosomes with the loss of the short arms.
- The different populations are **allopatric**; isolated in different valleys leading down to the sea.
- The distinct and uniform karyotype found in each population probably arose from genetic drift rather than natural selection.
- The 6 different populations are technically described as **races** because there is no opportunity for them to attempt interbreeding.
- However, they surely meet the definition of true species. While hybrids would form easily (no prezygotic isolating mechanisms), these would probably be infertile as proper synapsis and segregation of such different chromosomes would be difficult when the hybrids attempted to form gametes by meiosis.

Sympatric Speciation

Sympatric speciation refers to the formation of two or more descendant species from a single ancestral species all occupying the same geographic location. Some evolutionary biologists don't believe that it ever occurs. They feel that interbreeding would soon eliminate any genetic differences that might appear. But there is some compelling (albeit indirect) evidence that sympatric speciation can occur.

Speciation in three-spined sticklebacks

The three-spined sticklebacks, freshwater fishes that have been studied by Dolph Schluter (who received his Ph.D. for his work on Darwin's finches with Peter Grant) and his current colleagues in British Columbia, provide an intriguing example that is best explained by sympatric speciation.

They have found:

- Two different species of three-spined sticklebacks in each of five different lakes.
  - a large benthic species with a large mouth that feeds on large prey in the littoral zone
  - a smaller limnetic species with a smaller mouth that feeds on the small plankton in open water.
- DNA analysis indicates that each lake was colonized independently, presumably by a marine ancestor, after the last ice age.
- DNA analysis also shows that the two species in each lake are more closely related to each other than they are to any of the species in the other lakes.
- Nevertheless, the two species in each lake are reproductively isolated; neither mates with the other.
- However, aquarium tests showed that
  - The benthic species from one lake will spawn with the benthic species from the other lakes and likewise the limnetic species from the different lakes will spawn with each other.
  - These benthic and limnetic species even display their mating preferences when presented with sticklebacks from Japanese lakes; that is, a Canadian benthic prefers a Japanese benthic over its close limnetic cousin from its own lake.
- Their conclusion: in each lake, what began as a single population faced such competition for limited resources that
  - **disruptive selection** — competition favoring fishes at either extreme of body size and mouth size over those nearer the mean — coupled with
  - **assortative mating** — each size preferred mates like it

  favored a divergence into two subpopulations exploiting different food in different parts of the lake.
- The fact that this pattern of speciation occurred the same way on three separate occasions suggests strongly that **ecological factors** in a sympatric population can cause speciation.

Sympatric speciation driven by ecological factors may also account for the extraordinary diversity of crustaceans living in the depths of Siberia's Lake Baikal.

How many genes are needed to start down the path to sympatric speciation?

Perhaps not very many. The European corn borer, *Ostrinia nubilalis*, (which despite its common name is a major pest in the U.S. as well) exists as two distinct races designated **Z** and **E**. Both can be found in the same area; that is, they are sympatric. But in the field, they practice assortative mating - only breeding with mates of their own race.

The females of both races synthesize and release a pheromone that is a sex attractant for the males. Both races use the same substance but different isomers of it. Which isomer is produced is under the control of a single enzyme-encoding gene locus. The ability of the males to respond to one isomer or the other is controlled by 2 loci.

The Problem of Clines

There is another possible way for new species to arise in the absence of geographical barriers. If a population ranges over a large area and if the individuals in that population can disperse over only a small portion of this range, then gene flow across these great distances would be reduced. The occurrence of gradual phenotypic (and genotypic) differences in a population across a large geographical area is called a **cline**. Successful interbreeding occurs freely at every point along the cline, but individuals at the ends of the cline may not be able to interbreed. This can be tested in the laboratory.

And, on occasions, it is tested in nature. If a cline bends around so that the ends meet, and the populations reunited at the junction cannot interbreed, then the definition of separate species has been met. Such species are called **ring species** and this type of speciation is called **parapatric speciation**.

Two examples:

1. The Caribbean slipper spurge *Euphorbia tithymaloides*.
Genetic analysis shows that this wildflower originated in Central America where Mexico and Guatemala share a common boundary. From there it spread in two directions

- northeast through the Yucatan peninsula and then island-hopped through Jamaica, the Dominican Republic, Puerto Rico and into the Virgin Islands;
- south through Central America, on through Venezuela, and then north through Barbados and the other islands of the Lesser Antilles finally also reaching the Virgin Islands.

Reunited in the Virgin Islands, the two populations have diverged sufficiently that they retain their distinctive genotypic and phenotypic traits. Ongoing studies will determine to what degree they may be reproductively isolated.

2. The large-blotched salamander *Ensatina eschscholtzii*.

This animal is found in California where it occurs in a number of different subspecies or races. A single subspecies is found in Northern California, and it is thought to be the founder of all the others. Over time that original population spread southward in two directions:

- down the Sierra Nevada mountains east of the great central San Joaquin Valley and
- down the coast range of mountains west of the valley.

South of the valley, the eastern group has moved west and now meets the western group, closing the ring. Here the two populations fail to interbreed successfully, maintaining their distinct identities. But each subspecies interbreeds in an unbroken chain up the two paths their ancestors took.

Ring species present a difficult problem in assigning species designations. It is easy to say that the populations at the ends of the cline represent separate species, but where did one give rise to the other? At every point along the cline, interbreeding goes on successfully.

The same problem faces paleontologists examining the gradual phenotypic changes seen in an unbroken line of ever-younger fossils from what one presumes to be a single line of descent. If one could resurrect the ancestral species (A) and the descendant species (B) and they could not interbreed, then they meet the definition of separate species. But there was no moment in time when one could say that A became B. So the clines of today are a model in **space** of Darwin's descent with modification occurring over **time**.

Although clines present a problem for classifiers, they are a beautiful demonstration of Darwin's conviction that the accumulation of small inherited differences can lead to the formation of new species.

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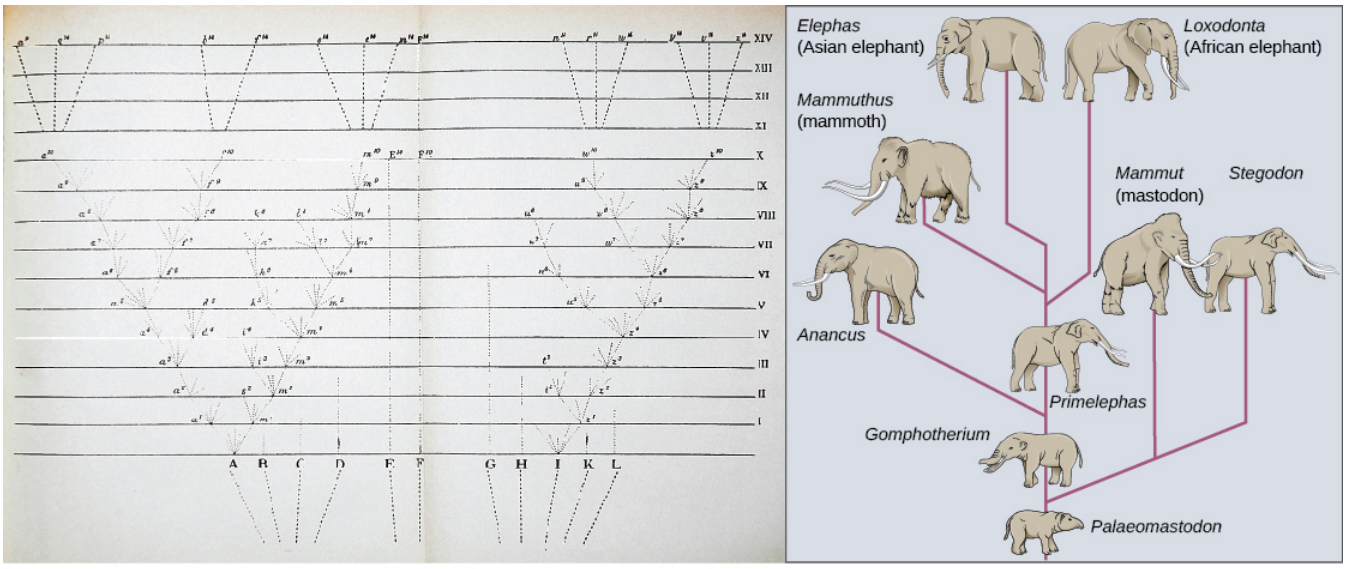
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22.5: Adaptive Radiation and Biological Diversity

The biological definition of species, which works for sexually reproducing organisms, is a group of actually or potentially interbreeding individuals. According to this definition, one species is distinguished from another by the possibility of matings between individuals from each species to produce fertile offspring. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. In fact, the presence of hybrids between similar species suggests that they may have descended from a single interbreeding species and that the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for speciation: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species* (Figure **22.5.1a**). For speciation to occur, two new populations must be formed from one original population, and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. Allopatric speciation, meaning speciation in "other homelands," involves a geographic separation of populations from a parent species and subsequent evolution. Sympatric speciation, meaning speciation in the "same homeland," involves speciation occurring within a parent species while remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely and such multiple events can also be conceptualized as single splits occurring close in time.



(a) (b)

Figure 22.5.1: The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the Palaeomastodon, a species that lived in Egypt 35–50 million years ago.

Speciation through Geographic Separation

A geographically continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous that free-flow of alleles is prevented. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors, for the two populations will differ causing natural

selection to favor divergent adaptations in each group. Different histories of genetic drift, enhanced because the populations are smaller than the parent population, will also lead to divergence.

Given enough time, the genetic and phenotypic divergence between populations will likely affect characters that influence reproduction enough that were individuals of the two populations brought together, mating would be less likely, or if a mating occurred, offspring would be non-viable or infertile. Many types of diverging characters may affect the reproductive isolation (inability to interbreed) of the two populations. These mechanisms of reproductive isolation can be divided into prezygotic mechanisms (those that operate before fertilization) and postzygotic mechanisms (those that operate after fertilization). Prezygotic mechanisms include traits that allow the individuals to find each other, such as the timing of mating, sensitivity to pheromones, or choice of mating sites. If individuals are able to encounter each other, character divergence may prevent courtship rituals from leading to a mating either because female preferences have changed or male behaviors have changed. Physiological changes may interfere with successful fertilization if mating is able to occur. Postzygotic mechanisms include genetic incompatibilities that prevent proper development of the offspring, or if the offspring live, they may be unable to produce viable gametes themselves as in the example of the mule, the infertile offspring of a female horse and a male donkey.

If the two isolated populations are brought back together and the hybrid offspring that formed from matings between individuals of the two populations have lower survivorship or reduced fertility, then selection will favor individuals that are able to discriminate between potential mates of their own population and the other population. This selection will enhance the reproductive isolation.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: from a river forming a new branch, erosion forming a new valley, or a group of organisms traveling to a new location without the ability to return, such as seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are that individuals from each population would fly back and forth, continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories. If a few members of a species move to a new geographical area, this is called dispersal. If a natural situation arises to physically divide organisms, this is called vicariance.

Scientists have documented numerous cases of allopatric speciation taking place. For example, along the west coast of the United States, two separate subspecies of spotted owls exist. The northern spotted owl has genetic and phenotypic differences from its close relative, the Mexican spotted owl, which lives in the south (Figure **22.5.2**). The cause of their initial separation is not clear, but it may have been caused by the glaciers of the ice age dividing an initial population into two.[1]

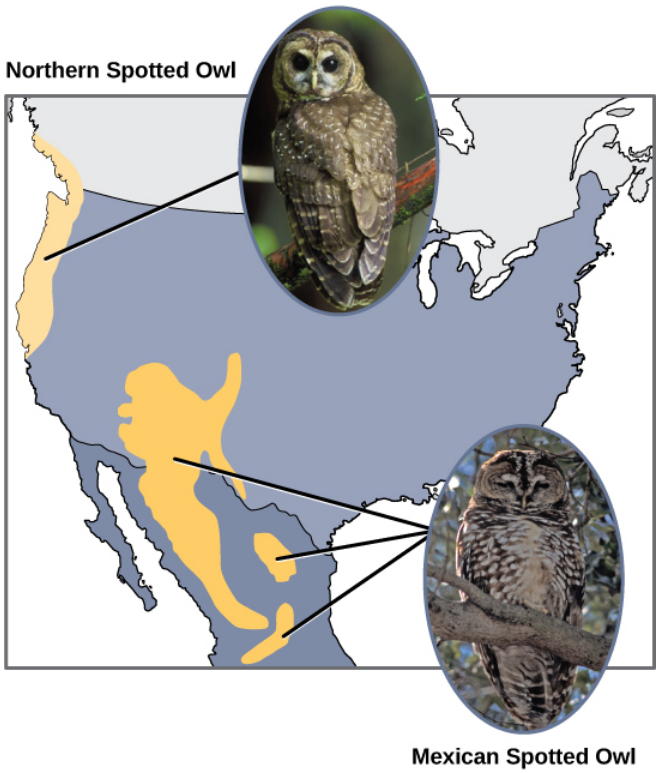


Figure 22.5.2: The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of incipient speciation. (credit "northern spotted owl": modification of work by John and Karen Hollingsworth, USFWS; credit "Mexican spotted owl": modification of work by Bill Radke, USFWS)

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely for speciation to take place. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls; in the north, the climate is cooler than in the south; the other types of organisms in each ecosystem differ, as do their behaviors and habits; also, the hunting habits and prey choices of the owls in the south vary from the northern ones. These variances can lead to evolved differences in the owls, and over time speciation will likely occur unless gene flow between the populations is restored.

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species, which is called adaptive radiation. From one point of origin, many adaptations evolve causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island, which leads to geographical isolation for many organisms (Figure **22.5.3**). The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved, including the eight shown in Figure **22.5.3**.

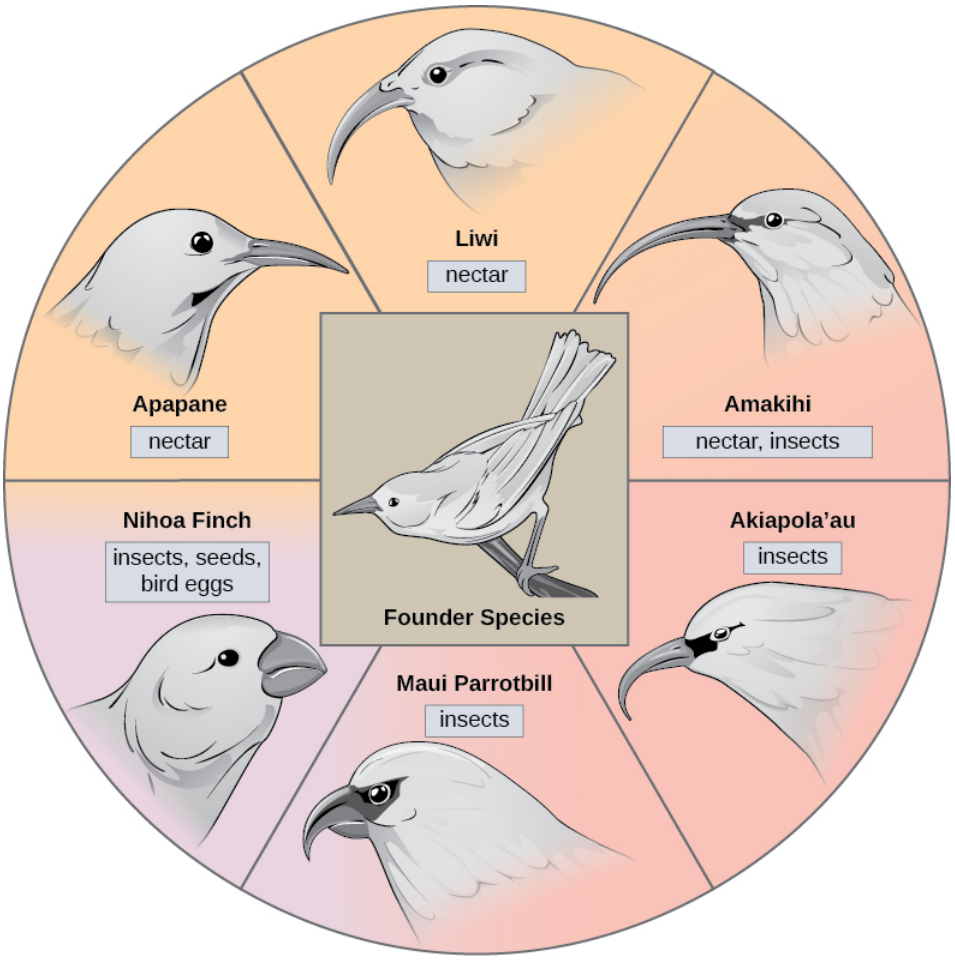


Figure 22.5.3: The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Notice the differences in the species' beaks in Figure **22.5.3**. Change in the genetic variation for beaks in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The fruit and seed-eating birds have thicker, stronger beaks which are suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach their nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another well-studied example of adaptive radiation in an archipelago.

Speciation without Geographic Separation

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a chromosomal error during meiosis or the formation of a hybrid individual with too many chromosomes. Polyploidy is a condition in which a cell, or organism, has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploid state. In some cases a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called autopolyploidy (Figure **22.5.4**). The prefix "auto" means self, so the term means multiple chromosomes from one's own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.

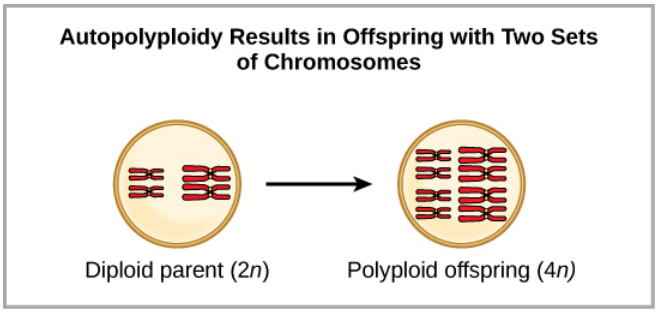


Figure 22.5.4: Autopolyploidy results when mitosis is not followed by cytokinesis.

For example, if a plant species with $2n = 6$ produces autopolyploid gametes that are also diploid ($2n = 6$, when they should be $n = 3$), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes produced by this plant species. But they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with $4n$ called a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species. The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an allopolyploid. The prefix "allo" means "other" (recall from allopatric); therefore, an allopolyploid occurs when gametes from two different species combine. Figure 22.5.5 illustrates one possible way an allopolyploidy can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

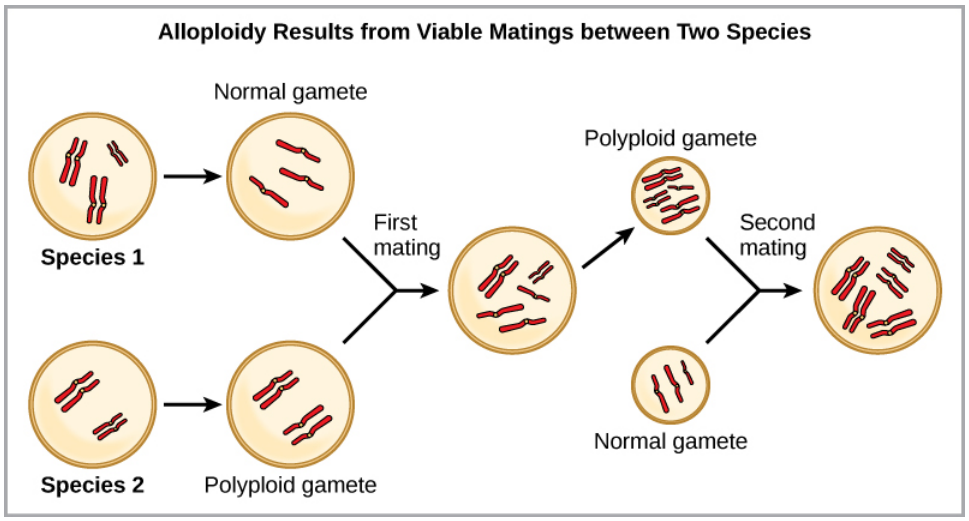


Figure 22.5.5: Alloploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploid gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, most chromosomal abnormalities in animals are lethal; it takes place most commonly in plants. Scientists have discovered more than 1/2 of all plant species studied relate back to a species evolved through polyploidy.

Sympatric speciation may also take place in ways other than polyploidy. For example, imagine a species of fish that lived in a lake. As the population grew, competition for food also grew. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that was unused by the other fish. What if this new food source was found at a different depth of the lake? Over time, those feeding on the second food source would interact more with each other than the other fish; therefore they would breed together as well. Offspring of these fish would likely behave as their parents and feed and live in the same area, keeping them separate from the original population. If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. Figure 22.5.6 shows this type of speciation

among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location; however, they have come to have different morphologies that allow them to eat various food sources.

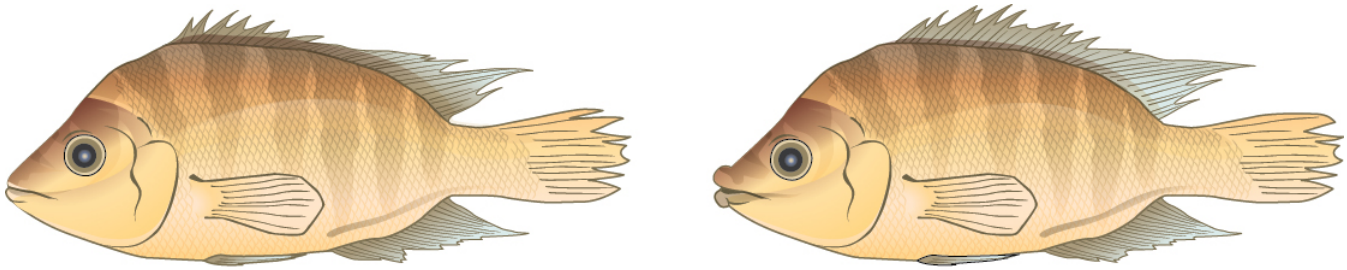


Figure 22.5.6: Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that the lake was populated only 100 years ago by a single population of cichlid fish. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

Finally, a well-documented example of ongoing sympatric speciation occurred in the apple maggot fly, *Rhagoletis pomonella*, which arose as an isolated population sometime after the introduction of the apple into North America. The native population of flies fed on hawthorn species and is host-specific: it only infests hawthorn trees. Importantly, it also uses the trees as a location to meet for mating. It is hypothesized that either through mutation or a behavioral mistake, flies jumped hosts and met and mated in apple trees, subsequently laying their eggs in apple fruit. The offspring matured and kept their preference for the apple trees effectively dividing the original population into two new populations separated by host species, not by geography. The host jump took place in the nineteenth century, but there are now measureable differences between the two populations of fly. It seems likely that host specificity of parasites in general is a common cause of sympatric speciation.

Section Summary

Speciation occurs along two main pathways: geographic separation (allopatric speciation) and through mechanisms that occur within a shared habitat (sympatric speciation). Both pathways force reproductive isolation between populations. Sympatric speciation can occur through errors in meiosis that form gametes with extra chromosomes, called polyploidy. Autopolyploidy occurs within a single species, whereas allopolyploidy occurs because of a mating between closely related species. Once the populations are isolated, evolutionary divergence can take place leading to the evolution of reproductive isolating traits that prevent interbreeding should the two populations come together again. The reduced viability of hybrid offspring after a period of isolation is expected to select for stronger inherent isolating mechanisms.

Footnotes

1. 1 Courtney, S.P., et al, “Scientific Evaluation of the Status of the Northern Spotted Owl,” Sustainable Ecosystems Institute (2004), Portland, OR.

Glossary

adaptive radiation

a speciation when one species radiates out to form several other species

allopatric speciation

a speciation that occurs via a geographic separation

dispersal

an allopatric speciation that occurs when a few members of a species move to a new geographical area

speciation

a formation of a new species

sympatric speciation

a speciation that occurs in the same geographic space

vicariance

an allopatric speciation that occurs when something in the environment separates organisms of the same species into separate groups

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22.6: The Pace of Evolution

Learning Objectives

- Explain how the interaction of an organism's population size in association with environmental changes can lead to different rates of speciation

Varying Rates of Speciation

Scientists around the world study speciation, documenting observations both of living organisms and those found in the fossil record. As their ideas take shape and as research reveals new details about how life evolves, they develop models to help explain rates of speciation. In terms of how quickly speciation occurs, two patterns are currently observed: the gradual speciation model and the punctuated equilibrium model.

In the gradual speciation model, species diverge gradually over time in small steps. In the punctuated equilibrium model, a new species changes quickly from the parent species and then remains largely unchanged for long periods of time afterward. This early change model is called punctuated equilibrium, because it begins with a punctuated or periodic change and then remains in balance afterward. While punctuated equilibrium suggests a faster tempo, it does not necessarily exclude gradualism.

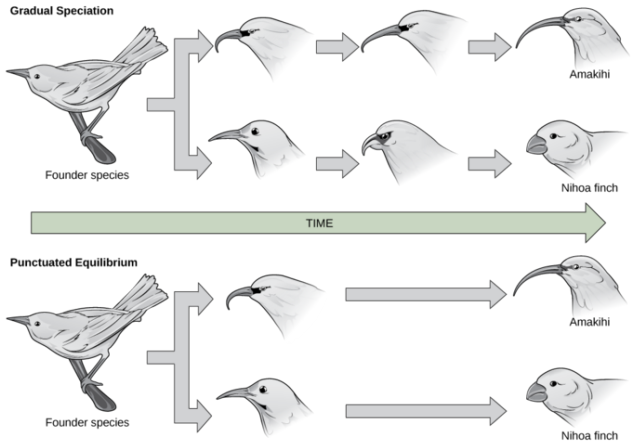


Figure **22.6.1**: Graduated Speciation vs Punctuated Equilibrium: In (a) gradual speciation, species diverge at a slow, steady pace as traits change incrementally. In (b) punctuated equilibrium, species diverge quickly and then remain unchanged for long periods of time.

The primary influencing factor on changes in speciation rate is environmental conditions. Under some conditions, selection occurs quickly or radically. Consider a species of snails that had been living with the same basic form for many thousands of years. Layers of their fossils would appear similar for a long time. When a change in the environment takes place, such as a drop in the water level, a small number of organisms are separated from the rest in a brief period of time, essentially forming one large and one tiny population. The tiny population faces new environmental conditions. Because its gene pool quickly became so small, any variation that surfaces and that aids in surviving the new conditions becomes the predominant form.

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Key Points

- In the gradual speciation model, species diverge slowly over time in small steps while in the punctuated equilibrium model, a new species diverges rapidly from the parent species.
- The two key influencing factors on the change in speciation rate are the environmental conditions and the population size.
- Gradual speciation is most likely to occur in large populations that live in a stable environment, while the punctuation equilibrium model is more likely to occur in a small population with rapid environmental change.

Key Terms

- **punctuated equilibrium**: a theory of evolution holding that evolutionary change tends to be characterized by long periods of stability, with infrequent episodes of very fast development
- **gradualism**: in evolutionary biology, belief that evolution proceeds at a steady pace, without the sudden development of new species or biological features from one generation to the next

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22.7: Speciation and Extinction Through Time

History of life as revealed by the fossil record

With help from molecular phylogenies:

https://bio.libretexts.org/@go/page/74230

Eras	Periods	Epochs	Aquatic Life	Terrestrial Life
With approximate starting dates in millions of years ago in parentheses. Geologic features in green				
Cenozoic (66) The "Age of Mammals"	Quaternary (2.6)	Holocene		Humans in the new world
		Pleistocene	Periodic glaciation	First humans
			Continental drift continues	
	Neogene (23)	Pliocene	Atmospheric oxygen reaches today's level (21%)	Hominids
		Miocene		Adaptive radiation of birds, continued radiation of mammals
	Paleogene (66)	Oligocene	All modern groups present	
		Eocene		
		Paleocene		
Mesozoic (251) The "Age of Reptiles"	Cretaceous (146)	Still attached: N. America & N. Europe; Australia & Antarctica; Mass extinction of both aquatic and terrestrial life at the end		
			Modern bony fishes	Extinction of dinosaurs and pterosaurs; first snakes
			Extinction of ammonites, plesiosaurs, ichthyosaurs	Rise of angiosperms
		Africa & S. America begin to drift apart		
	Jurassic (200)		Plesiosaurs, ichthyosaurs abundant; first diatoms	*Archaeopteryx*; dinosaurs dominant but mammals (Eutheria) begin to diversify
			Ammonites again abundant	First lizards
			Skates, rays, and bony fishes abundant	Adaptive radiation of dinosaurs
			Pangaea splits into Laurasia and Gondwana;	

Eras	Periods	Epochs	Aquatic Life	Terrestrial Life			
			atmospheric oxygen drops to ~13%				
	Triassic (251)		Mass extinctions at the end.	Mass extinctions at the end. First mammals Adaptive radiation of reptiles: thecodonts, therapsids, turtles, crocodiles, first dinosaurs			
			Ammonites abundant at first				
			Rise of bony fishes				
	Paleozoic (542)		Periodic glaciation and arid climate; atmospheric oxygen reaches ~30%. Volcanic eruptions killed off 90% of marine species at end.				
		Permian (299)	Extinction of trilobites	Reptiles abundant. Cycads, conifers, ginkgos			
Pennsylvanian (320)		Warm, humid climate Together the Pennsylvanian and Mississippian make up the "Carboniferous"; also called the "Age of Amphibians"	Ammonites, bony fishes	First reptiles Coal swamps			
Mississippian (359)			Adaptive radiation of sharks	Forests of lycopsids, sphenopsids, and seed ferns Amphibians abundant Adaptive radiation of the insects (Hexapoda)			
			Atmospheric oxygen begins to rise as organic matter is buried, not respired				
Devonian (416) The "Age of Fishes"		Extensive inland seas	Cartilaginous and bony fishes abundant. Ammonites, nautiloids, ostracoderms, eurypterids	Ferns, lycopsids, and sphenopsids First gymnosperms First amphibians			
					Silurian (443)	Mild climate; inland seas	First bony fishes	First myriapods and chelicerates
Ordovician (485)		Mild climate, inland seas	Trilobites abundant	Fungi present First plants			

Eras	Periods	Epochs	Aquatic Life	Terrestrial Life
				(liverworts?) First insects
Cambrian (541)			First vertebrates (jawless fishes). Eurypterids, crustaceans mollusks, echinoderms, sponges, cnidarians, annelids, and tunicates present. Trilobites dominant.	No fossils of terrestrial eukaryotes, but phylogenetic trees suggest that lichens, mosses, perhaps even vascular plants were present.
		Periodic glaciation		
Proterozoic (2500)		Ediacaran (635)		Fossil evidence of multicellular algae, fungi, and bilaterian invertebrates
				Evidence of eukaryotes ~1.8 x10^9 years ago
Archaean (3600)			Evidence of archaea and bacteria ~3.5 x10^9 years ago	

The Geologic and Evolutionary Record

A remarkable feature of the table above is how often evolutionary changes coincided with geologic changes on the earth. But consider that changes in geology (e.g., mountain formation or lowering of the sea level) cause changes in climate, and together these alter the habitats available for life. Two types of geologic change seem to have had especially dramatic effects on life: **continental drift** and the **impact of asteroids**

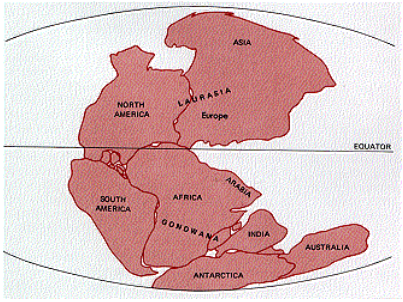


Figure 18.12.1 Pangaea

A body of evidence, both geological and biological, supports the conclusion that 200 million years ago, at the start of the **Mesozoic era**, all the continents were attached to one another in a single land mass, which has been named **Pangaea**. This drawing of Pangaea (adapted from data of R. S. Dietz and J. C. Holden) is based on a computer-generated fit of the continents as they would look if the sea level were lowered by 6000 feet (~1800 meters). During the **Triassic**, Pangaea began to break up, first into two major land masses:

- **Laurasia** in the Northern Hemisphere
- **Gondwana** in the Southern Hemisphere.

The present continents separated at intervals throughout the remainder of the Mesozoic and through the Cenozoic, eventually reaching the positions they have today. Let us examine some of the evidence.

Shape of the Continents

The east coast of South America and the west coast of Africa and are strikingly complementary. This is even more dramatic when one tries to fit the continents together using the boundaries of the continental slopes, e.g., 6000 feet (~1800 meters) down, rather than the shorelines.

Geology

- In both mineral content and age, the rocks in a region on the east coast of Brazil match precisely those found in Ghana on the west coast of Africa.
- The low mountain ranges and rock types in New England and eastern Canada appear to be continued in parts of Great Britain, France, and Scandinavia.
- India and the southern part of Africa both show evidence of periodic glaciation during Paleozoic times (even though both are now close to the equator). The pattern of glacial deposits in the two regions not only match each other but also glacial deposits found in South America, Australia, and Antarctica.

Fossils

- Fossil reptiles found in South Africa are also found in Brazil and Argentina.
- Fossil amphibians and reptiles found in Antarctica are also found in South Africa, India, and China.
- Most of the marsupials alive today are confined to South America and Australia. But if these two continents were connected by Antarctica in the Mesozoic, one might expect to find fossil marsupials there. In March 1982, this prediction was fulfilled with the discovery in Antarctica of the remains of **Polydolops**, a 9-ft (2.7 m) marsupial.

The Impact Hypothesis

The Cretaceous period, the last period of the Mesozoic, marked the end of the Age of Reptiles. It was followed by the Cenozoic era, the Age of Mammals. Although extinctions have occurred throughout the history of life, an extraordinary number of them occurred in a relatively brief period at the end of the Cretaceous. Why?

The Alvarez Theory

Louis Alvarez, his son Walter, and their colleagues proposed that a giant asteroid or comet striking the earth some 66 million years ago caused the massive die-off at the end of the Cretaceous. Presumably, the impact generated so much dust and gases that skies

were darkened all over the earth, photosynthesis declined, and worldwide temperatures dropped. The outcome was that as many as 75% of all species — including all dinosaurs — became extinct.

The key piece of evidence for the Alvarez hypothesis was the finding of thin deposits of clay containing the element iridium at the interface between the rocks of the Cretaceous and those of the Paleogene period (called the K-Pg boundary after the German word for Cretaceous). Iridium is a rare element on earth (although often discharged from volcanoes), but occurs in certain meteorites at concentrations thousands of times greater than in the earth's crust.

After languishing for many years, the Alvarez theory gained strong support from the discovery in the 1990s of the remains of a huge (180 km in diameter) crater in the Yucatan Peninsula that dated to 65 million years ago.

The abundance of sulfate-containing rock in the region suggests that the impact generated enormous amounts of sulfur dioxide (SO_2), which later returned to earth as a bath of acid rain. A smaller crater in Iowa, formed at the same time, many have contributed to the devastation. Perhaps during this period the earth passed through a swarm of asteroids or a comet and the repeated impacts made the earth uninhabitable for so many creatures of the Mesozoic.

Other Impacts

A mass extinction of non-dinosaur reptiles occurred earlier, at the end of the **Triassic**. It was followed by a great expansion in the diversity of dinosaurs. The recent discovery of a layer enriched in iridium in rocks formed at the boundary between the Triassic and Jurassic suggests that impact from an asteroid or comet may have been responsible then just as it was at the K-Pg boundary.

The largest extinction of all time occurred still earlier at the end of the Permian period. There is evidence off the coast of Australia that a huge impact there may have contributed to the extinctions at the Permian-Triassic (P-T) boundary.

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CHAPTER OVERVIEW

23: Systematics, Phylogeny and Comparative Biology

23.1: Systematics

23.2: Cladistics

23.3: Systematics and Classification

23.4: Phylogenetics and Comparative Biology

23.5: Phylogenetics and Disease Evolution

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23.1: Systematics

Learning Objecctives

- Describe how microorganisms are classified and distinguished as unique species
- Compare historical and current systems of taxonomy used to classify microorganisms

Once microbes became visible to humans with the help of microscopes, scientists began to realize their enormous diversity. Microorganisms vary in all sorts of ways, including their size, their appearance, and their rates of reproduction. To study this incredibly diverse new array of organisms, researchers needed a way to systematically organize them.

The Science of Taxonomy

Taxonomy is the classification, description, identification, and naming of living organisms. Classification is the practice of organizing organisms into different groups based on their shared characteristics. The most famous early taxonomist was a Swedish botanist, zoologist, and physician named Carolus Linnaeus (1701–1778). In 1735, Linnaeus published *Systema Naturae*, an 11-page booklet in which he proposed the Linnaean taxonomy, a system of categorizing and naming organisms using a standard format so scientists could discuss organisms using consistent terminology. He continued to revise and add to the book, which grew into multiple volumes (Figure **23.1.1**).



Figure **23.1.1**: Swedish botanist, zoologist, and physician Carolus Linnaeus developed a new system for categorizing plants and animals. In this 1853 portrait by Hendrik Hollander, Linnaeus is holding a twinflower, named *Linnaea borealis* in his honor.

In his taxonomy, Linnaeus divided the natural world into three kingdoms: animal, plant, and mineral (the mineral kingdom was later abandoned). Within the animal and plant kingdoms, he grouped organisms using a hierarchy of increasingly specific levels and sublevels based on their similarities. The names of the levels in Linnaeus's original taxonomy were kingdom, class, order, family, genus (plural: genera), and species. Species was, and continues to be, the most specific and basic taxonomic unit.

Evolving Trees of Life (Phylogenies)

With advances in technology, other scientists gradually made refinements to the Linnaean system and eventually created new systems for classifying organisms. In the 1800s, there was a growing interest in developing taxonomies that took into account the evolutionary relationships, or phylogenies, of all different species of organisms on earth. One way to depict these relationships is via a diagram called a phylogenetic tree (or tree of life). In these diagrams, groups of organisms are arranged by how closely related they are thought to be. In early phylogenetic trees, the relatedness of organisms was inferred by their visible similarities, such as the presence or absence of hair or the number of limbs. Now, the analysis is more complicated. Today, phylogenic analyses include genetic, biochemical, and embryological comparisons, as will be discussed later in this chapter.

Linnaeus's tree of life contained just two main branches for all living things: the animal and plant kingdoms. In 1866, Ernst Haeckel, a German biologist, philosopher, and physician, proposed another kingdom, Protista, for unicellular organisms (Figure **23.1.2**). He later proposed a fourth kingdom, Monera, for unicellular organisms whose cells lack nuclei, like bacteria.

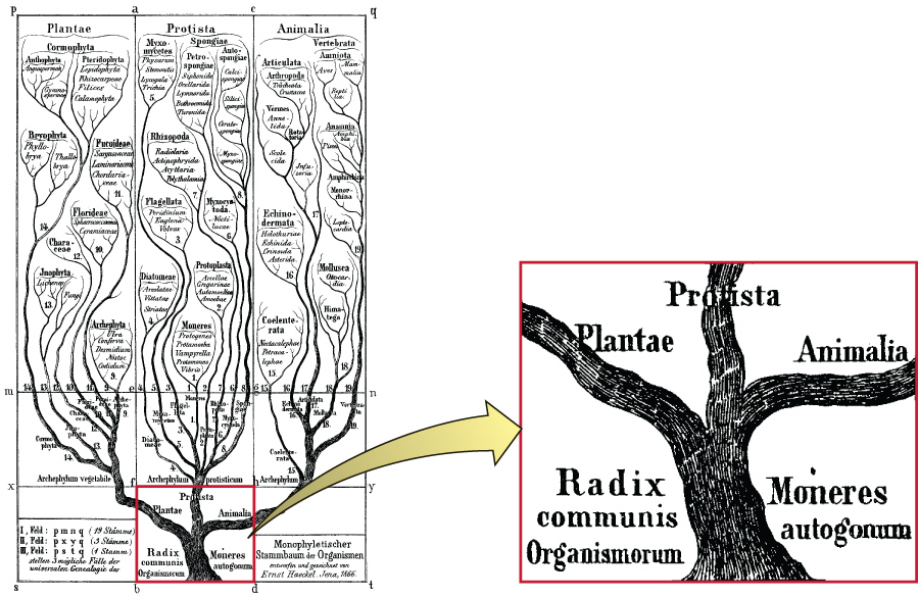


Figure **23.1.2**: Ernst Haeckel's rendering of the tree of life, from his 1866 book *General Morphology of Organisms*, contained three kingdoms: Plantae, Protista, and Animalia. He later added a fourth kingdom, Monera, for unicellular organisms lacking a nucleus.

Nearly 100 years later, in 1969, American ecologist Robert Whittaker (1920–1980) proposed adding another kingdom—Fungi—in his tree of life. Whittaker's tree also contained a level of categorization above the kingdom level—the empire or superkingdom level—to distinguish between organisms that have membrane-bound nuclei in their cells (eukaryotes) and those that do not (prokaryotes). Empire Prokaryota contained just the Kingdom Monera. The Empire Eukaryota contained the other four kingdoms: Fungi, Protista, Plantae, and Animalia. Whittaker's five-kingdom tree was considered the standard phylogeny for many years.

Figure **23.1.3** shows how the tree of life has changed over time. Note that viruses are not found in any of these trees. That is because they are not made up of cells and thus it is difficult to determine where they would fit into a tree of life.

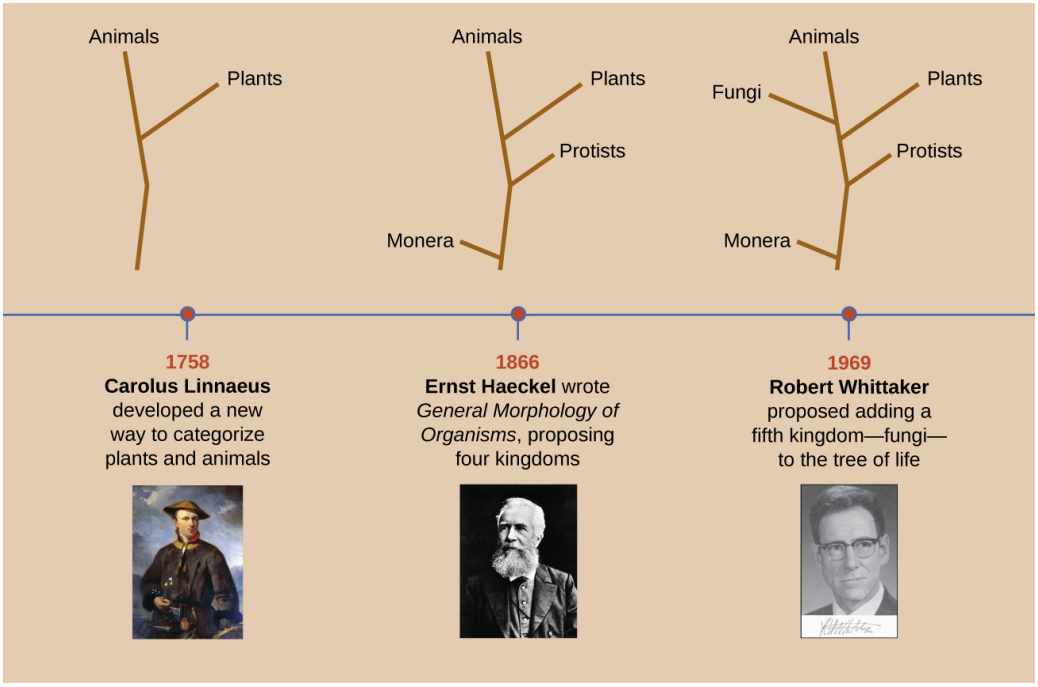


Figure **23.1.3**: This timeline shows how the shape of the tree of life has changed over the centuries. Even today, the taxonomy of living organisms is continually being reevaluated and refined with advances in technology.

Exercise 23.1.1

Briefly summarize how our evolving understanding of microorganisms has contributed to changes in the way that organisms are classified.

Clinical Focus: Part 2

Antibiotic drugs are specifically designed to kill or inhibit the growth of bacteria. But after a couple of days on antibiotics, Cora shows no signs of improvement. Also, her CSF cultures came back from the lab negative. Since bacteria or fungi were not isolated from Cora's CSF sample, her doctor rules out bacterial and fungal meningitis. Viral meningitis is still a possibility.

However, Cora now reports some troubling new symptoms. She is starting to have difficulty walking. Her muscle stiffness has spread from her neck to the rest of her body, and her limbs sometimes jerk involuntarily. In addition, Cora's cognitive symptoms are worsening. At this point, Cora's doctor becomes very concerned and orders more tests on the CSF samples.

Exercise 23.1.2

What types of microorganisms could be causing Cora's symptoms?

The Role of Genetics in Modern Taxonomy

Haeckel's and Whittaker's trees presented hypotheses about the phylogeny of different organisms based on readily observable characteristics. But the advent of molecular genetics in the late 20th century revealed other ways to organize phylogenetic trees. Genetic methods allow for a standardized way to compare all living organisms without relying on observable characteristics that can often be subjective. Modern taxonomy relies heavily on comparing the nucleic acids (deoxyribonucleic acid [DNA] or ribonucleic acid [RNA]) or proteins from different organisms. The more similar the nucleic acids and proteins are between two organisms, the more closely related they are considered to be.

In the 1970s, American microbiologist Carl Woese discovered what appeared to be a "living record" of the evolution of organisms. He and his collaborator George Fox created a genetics-based tree of life based on similarities and differences they observed in the small subunit ribosomal RNA (rRNA) of different organisms. In the process, they discovered that a certain type of bacteria, called archaebacteria (now known simply as archaea), were significantly different from other bacteria and eukaryotes in terms of the sequence of small subunit rRNA. To accommodate this difference, they created a tree with three Domains above the level of Kingdom: Archaea, Bacteria, and Eukarya (Figure 23.1.4). Genetic analysis of the small subunit rRNA suggests archaea, bacteria, and eukaryotes all evolved from a common ancestral cell type. The tree is skewed to show a closer evolutionary relationship between Archaea and Eukarya than they have to Bacteria.

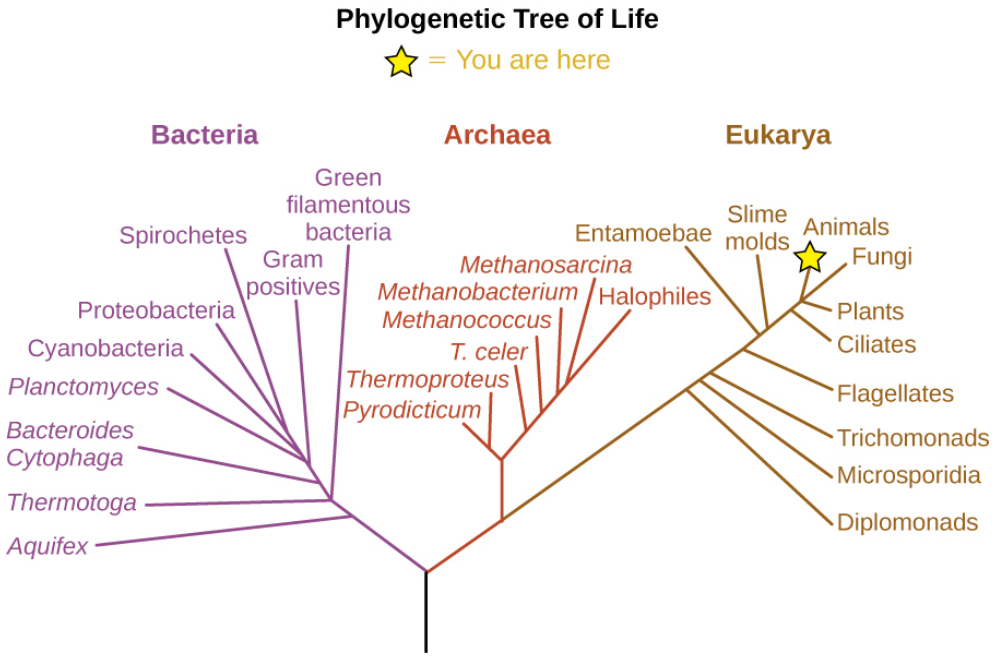


Figure **23.1.4**: Scientists continue to use analysis of RNA, DNA, and proteins to determine how organisms are related. One interesting, and complicating, discovery is that of horizontal gene transfer—when a gene of one species is absorbed into another organism's genome. Horizontal gene transfer is especially common in microorganisms and can make it difficult to determine how organisms are evolutionarily related. Consequently, some scientists now think in terms of "webs of life" rather than "trees of life."

? Exercise 23.1.3

1. In modern taxonomy, how do scientists determine how closely two organisms are related?
2. Explain why the branches on the "tree of life" all originate from a single "trunk."

Naming Microbes

In developing his taxonomy, Linnaeus used a system of binomial nomenclature, a two-word naming system for identifying organisms by genus and species. For example, modern humans are in the genus *Homo* and have the species name *sapiens*, so their scientific name in binomial nomenclature is *Homo sapiens*. In binomial nomenclature, the genus part of the name is always capitalized; it is followed by the species name, which is not capitalized. Both names are italicized.

Taxonomic names in the 18th through 20th centuries were typically derived from Latin, since that was the common language used by scientists when taxonomic systems were first created. Today, newly discovered organisms can be given names derived from Latin, Greek, or English. Sometimes these names reflect some distinctive trait of the organism; in other cases, microorganisms are named after the scientists who discovered them. The archaeon *Haloquadratum walsbyi* is an example of both of these naming schemes. The genus, *Haloquadratum*, describes the microorganism's saltwater habitat (*halo* is derived from the Greek word for "salt") as well as the arrangement of its square cells, which are arranged in square clusters of four cells (*quadratum* is Latin for "foursquare"). The species, *walsbyi*, is named after Anthony Edward Walsby, the microbiologist who discovered *Haloquadratum walsbyi* in in 1980. While it might seem easier to give an organism a common descriptive name—like a red-headed woodpecker—we can imagine how that could become problematic. What happens when another species of woodpecker with red head coloring is discovered? The systematic nomenclature scientists use eliminates this potential problem by assigning each organism a single, unique two-word name that is recognized by scientists all over the world.

In this text, we will typically abbreviate an organism's genus and species after its first mention. The abbreviated form is simply the first initial of the genus, followed by a period and the full name of the species. For example, the bacterium *Escherichia coli* is shortened to *E. coli* in its abbreviated form. You will encounter this same convention in other scientific texts as well.

Bergey's Manuals

Whether in a tree or a web, microbes can be difficult to identify and classify. Without easily observable macroscopic features like feathers, feet, or fur, scientists must capture, grow, and devise ways to study their biochemical properties to differentiate and classify microbes. Despite these hurdles, a group of microbiologists created and updated a set of manuals for identifying and classifying microorganisms. First published in 1923 and since updated many times, *Bergey's Manual of Determinative Bacteriology* and *Bergey's Manual of Systematic Bacteriology* are the standard references for identifying and classifying different prokaryotes. (Appendix D of this textbook is partly based on Bergey's manuals; it shows how the organisms that appear in this textbook are classified.) Because so many bacteria look identical, methods based on nonvisual characteristics must be used to identify them. For example, biochemical tests can be used to identify chemicals unique to certain species. Likewise, serological tests can be used to identify specific antibodies that will react against the proteins found in certain species. Ultimately, DNA and rRNA sequencing can be used both for identifying a particular bacterial species and for classifying newly discovered species.

? Exercise 23.1.4

- What is binomial nomenclature and why is it a useful tool for naming organisms?
- Explain why a resource like one of Bergey's manuals would be helpful in identifying a microorganism in a sample.

Same Name, Different Strain

Within one species of microorganism, there can be several subtypes called strains. While different strains may be nearly identical genetically, they can have very different attributes. The bacterium*Escherichia coli* is infamous for causing food poisoning and traveler's diarrhea. However, there are actually many different strains of *E. coli*, and they vary in their ability to cause disease.

One pathogenic (disease-causing) *E. coli* strain that you may have heard of is *E. coli* O157:H7. In humans, infection from *E. coli* O157:H7 can cause abdominal cramps and diarrhea. Infection usually originates from contaminated water or food, particularly raw vegetables and undercooked meat. In the 1990s, there were several large outbreaks of *E. coli* O157:H7 thought to have originated in undercooked hamburgers.

While *E. coli* O157:H7 and some other strains have given *E. coli* a bad name, most *E. coli* strains do not cause disease. In fact, some can be helpful. Different strains of *E. coli* found naturally in our gut help us digest our food, provide us with some needed chemicals, and fight against pathogenic microbes.

Summary

- Carolus Linnaeus developed a taxonomic system for categorizing organisms into related groups.
- Binomial nomenclature assigns organisms Latinized scientific names with a genus and species designation.
- A phylogenetic tree is a way of showing how different organisms are thought to be related to one another from an evolutionary standpoint.
- The first phylogenetic tree contained kingdoms for plants and animals; Ernst Haeckel proposed adding a kingdom for protists.
- Robert Whittaker's tree contained five kingdoms: Animalia, Plantae, Protista, Fungi, and Monera.
- Carl Woese used small subunit ribosomal RNA to create a phylogenetic tree that groups organisms into three domains based on their genetic similarity.
- Bergey's manuals of determinative and systemic bacteriology are the standard references for identifying and classifying bacteria, respectively.
- Bacteria can be identified through biochemical tests, DNA/RNA analysis, and serological testing methods.

Glossary

binomial nomenclature

a universal convention for the scientific naming of organisms using Latinized names for genus and species

eukaryote

an organism made up of one or more cells that contain a membrane-bound nucleus and organelles

phylogeny
the evolutionary history of a group of organisms

prokaryote
an organism whose cell structure does not include a membrane-bound nucleus

taxonomy
the classification, description, identification, and naming of living organisms

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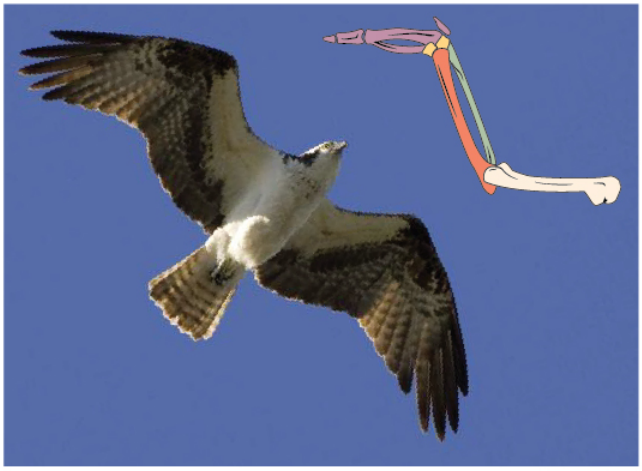
23.2: Cladistics

Scientists collect information that allows them to make evolutionary connections between organisms. Similar to detective work, scientists must use evidence to uncover the facts. In the case of phylogeny, evolutionary investigations focus on two types of evidence: morphologic (form and function) and genetic.

Two Measures of Similarity

Organisms that share similar physical features *and* genetic sequences tend to be more closely related than those that do not. Features that overlap both morphologically and genetically are referred to as homologous structures; the similarities stem from common evolutionary paths. For example, as shown in Figure **23.2.1**, the bones in the wings of bats and birds, the arms of humans, and the foreleg of a horse are homologous structures. Notice the structure is not simply a single bone, but rather a grouping of several bones arranged in a similar way in each organism even though the elements of the structure may have changed shape and size.

Homologous Structures



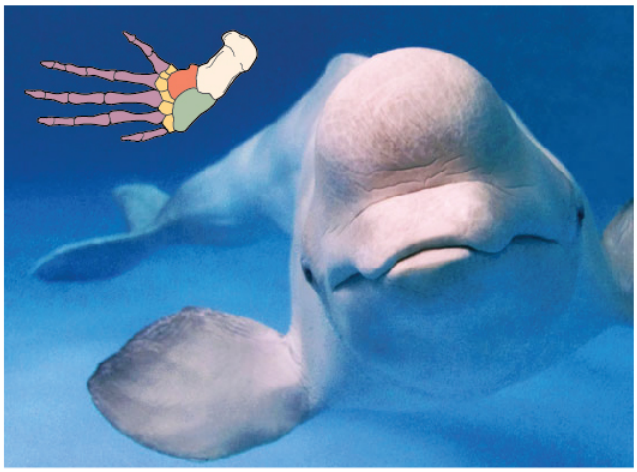
(a) Bird wing



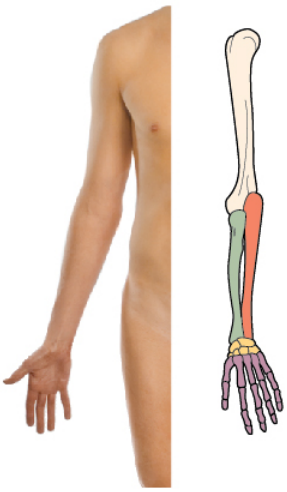
(b) Bat wing



(c) Horse leg



(d) Whale flipper



(e) Human arm

https://bio.libretexts.org/@go/page/74232

Figure 23.2.1: Bat and bird wings, the foreleg of a horse, the flipper of a whale, and the arm of a human are homologous structures, indicating that bats, birds, horses, whales, and humans share a common evolutionary past. (credit a photo: modification of work by Steve Hillebrand, USFWS; credit b photo: modification of work by U.S. BLM; credit c photo: modification of work by Virendra Kankariya; credit d photo: modification of work by Russian Gov./Wikimedia Commons)

Misleading Appearances

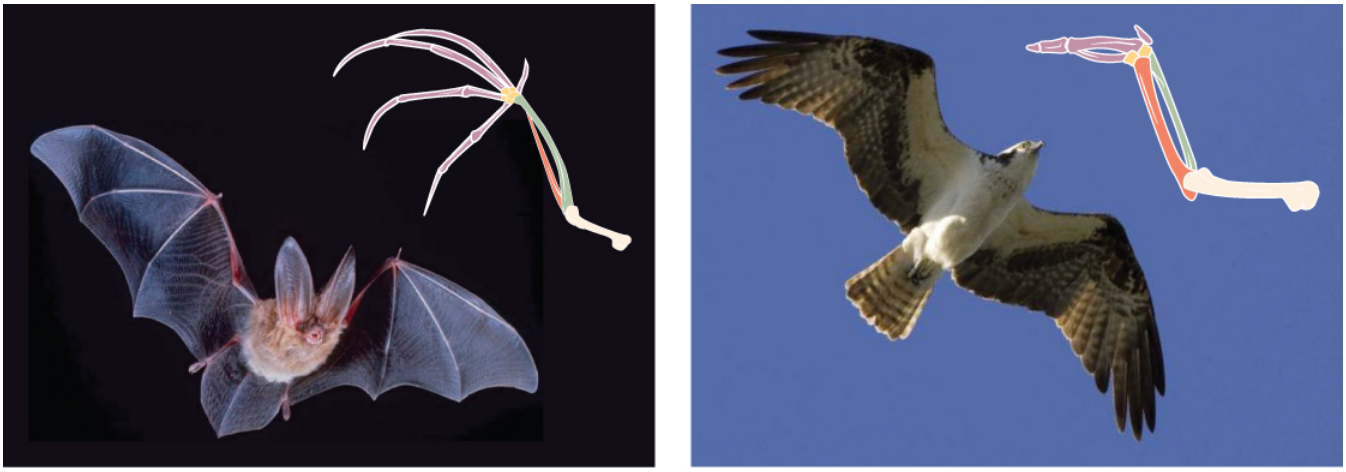
Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. For example, chimpanzees and humans, the skulls of which are shown in Figure **23.2.2** are very similar genetically, sharing 99 percent[1] of their genes. However, chimpanzees and humans show considerable anatomical differences, including the degree to which the jaw protrudes in the adult and the relative lengths of our arms and legs.



Figure 23.2.2: (a) The chimpanzee jaw protrudes to a much greater degree than (b) the human jaw. (credit a: modification of work by "Pastorius"/Wikimedia Commons)

However, unrelated organisms may be distantly related yet appear very much alike, usually because common adaptations to similar environmental conditions evolved in both. An example is the streamlined body shapes, the shapes of fins and appendages, and the shape of the tails in fishes and whales, which are mammals. These structures bear superficial similarity because they are adaptations to moving and maneuvering in the same environment—water. When a characteristic that is similar occurs by adaptive convergence (convergent evolution), and not because of a close evolutionary relationship, it is called an analogous structure. In another example, insects use wings to fly like bats and birds. We call them both wings because they perform the same function and have a superficially similar form, but the embryonic origin of the two wings is completely different. The difference in the development, or embryogenesis, of the wings in each case is a signal that insects and bats or birds do not share a common ancestor that had a wing. The wing structures, shown in Figure **23.2.3** evolved independently in the two lineages.

Similar traits can be either homologous or analogous. Homologous traits share an evolutionary path that led to the development of that trait, and analogous traits do not. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.



(a) Bat wing

(b) Bird wing



(c) Insect wing

Figure 23.2.3: The wing of a honey bee is similar in shape to a bird wing and a bat wing and serves the same function (flight). The bird and bat wings are homologous structures. However, the honey bee wing has a different structure (it is made of a chitinous exoskeleton, not a boney endoskeleton) and embryonic origin. The bee and bird or bat wing types illustrate an analogy—similar structures that do not share an evolutionary history. (credit a photo: modification of work by U.S. BLM; credit b: modification of work by Steve Hillebrand, USFWS; credit c: modification of work by Jon Sullivan)

Molecular Comparisons

With the advancement of DNA technology, the area of molecular systematics, which describes the use of information on the molecular level including DNA sequencing, has blossomed. New analysis of molecular characters not only confirms many earlier classifications, but also uncovers previously made errors. Molecular characters can include differences in the amino-acid sequence of a protein, differences in the individual nucleotide sequence of a gene, or differences in the arrangements of genes. Phylogenies based on molecular characters assume that the more similar the sequences are in two organisms, the more closely related they are. Different genes change evolutionarily at different rates and this affects the level at which they are useful at identifying relationships. Rapidly evolving sequences are useful for determining the relationships among closely related species. More slowly evolving sequences are useful for determining the relationships between distantly related species. To determine the relationships between very different species such as Eukarya and Archaea, the genes used must be very ancient, slowly evolving genes that are present in both groups, such as the genes for ribosomal RNA. Comparing phylogenetic trees using different sequences and finding them similar helps to build confidence in the inferred relationships.

Sometimes two segments of DNA in distantly related organisms randomly share a high percentage of bases in the same locations, causing these organisms to appear closely related when they are not. For example, the fruit fly shares 60 percent of its DNA with

humans.[2] In this situation, computer-based statistical algorithms have been developed to help identify the actual relationships, and ultimately, the coupled use of both morphologic and molecular information is more effective in determining phylogeny.

EVOLUTION IN ACTION: Why Does Phylogeny Matter?

In addition to enhancing our understanding of the evolutionary history of species, our own included, phylogenetic analysis has numerous practical applications. Two of those applications include understanding the evolution and transmission of disease and making decisions about conservation efforts. A 2010 study[3] of MRSA (methicillin-resistant *Staphylococcus aureus*), an antibiotic resistant pathogenic bacterium, traced the origin and spread of the strain throughout the past 40 years. The study uncovered the timing and patterns in which the resistant strain moved from its point of origin in Europe to centers of infection and evolution in South America, Asia, North America, and Australasia. The study suggested that introductions of the bacteria to new populations occurred very few times, perhaps only once, and then spread from that limited number of individuals. This is in contrast to the possibility that many individuals had carried the bacteria from one place to another. This result suggests that public health officials should concentrate on quickly identifying the contacts of individuals infected with a new strain of bacteria to control its spread.

A second area of usefulness for phylogenetic analysis is in conservation. Biologists have argued that it is important to protect species throughout a phylogenetic tree rather than just those from one branch of the tree. Doing this will preserve more of the variation produced by evolution. For example, conservation efforts should focus on a single species without sister species rather than another species that has a cluster of close sister species that recently evolved. If the single evolutionarily distinct species goes extinct a disproportionate amount of variation from the tree will be lost compared to one species in the cluster of closely related species. A study published in 2007[4] made recommendations for conservation of mammal species worldwide based on how evolutionarily distinct and at risk of extinction they are. The study found that their recommendations differed from priorities based on simply the level of extinction threat to the species. The study recommended protecting some threatened and valued large mammals such as the orangutans, the giant and lesser pandas, and the African and Asian elephants. But they also found that some much lesser known species should be protected based on how evolutionary distinct they are. These include a number of rodents, bats, shrews and hedgehogs. In addition there are some critically endangered species that did not rate as very important in evolutionary distinctiveness including species of deer mice and gerbils. While many criteria affect conservation decisions, preserving phylogenetic diversity provides an objective way to protect the full range of diversity generated by evolution.

Building Phylogenetic Trees

How do scientists construct phylogenetic trees? Presently, the most accepted method for constructing phylogenetic trees is a method called cladistics. This method sorts organisms into clades, groups of organisms that are most closely related to each other and the ancestor from which they descended. For example, in Figure **23.2.4**, all of the organisms in the shaded region evolved from a single ancestor that had amniotic eggs. Consequently, all of these organisms also have amniotic eggs and make a single clade, also called a monophyletic group. Clades must include the ancestral species and all of the descendants from a branch point.

ART CONNECTION

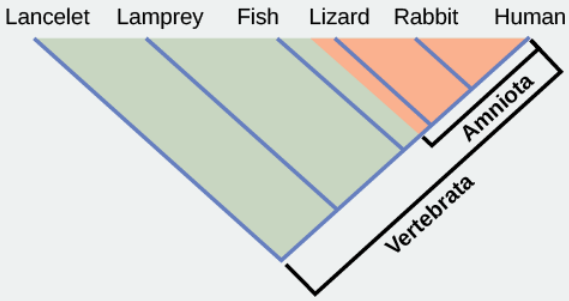


Figure 23.2.4: Lizards, rabbits, and humans all descend from a common ancestor in which the amniotic egg evolved. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

Which animals in this figure belong to a clade that includes animals with hair? Which evolved first: hair or the amniotic egg?

Clades can vary in size depending on which branch point is being referenced. The important factor is that all of the organisms in the clade or monophyletic group stem from a single point on the tree. This can be remembered because monophyletic breaks down into “mono,” meaning one, and “phyletic,” meaning evolutionary relationship.

Shared Characteristics

Cladistics rests on three assumptions. The first is that living things are related by descent from a common ancestor, which is a general assumption of evolution. The second is that speciation occurs by splits of one species into two, never more than two at a time, and essentially at one point in time. This is somewhat controversial, but is acceptable to most biologists as a simplification. The third assumption is that traits change enough over time to be considered to be in a different state .It is also assumed that one can identify the actual direction of change for a state. In other words, we assume that an amniotic egg is a later character state than non-amniotic eggs. This is called the polarity of the character change. We know this by reference to a group outside the clade: for example, insects have non-amniotic eggs; therefore, this is the older or ancestral character state. Cladistics compares ingroups and outgroups. An ingroup (lizard, rabbit and human in our example) is the group of taxa being analyzed. An outgroup (lancelet, lamprey and fish in our example) is a species or group of species that diverged before the lineage containing the group(s) of interest. By comparing ingroup members to each other and to the outgroup members, we can determine which characteristics are evolutionary modifications determining the branch points of the ingroup’s phylogeny.

If a characteristic is found in all of the members of a group, it is a shared ancestral characterbecause there has been no change in the trait during the descent of each of the members of the clade. Although these traits appear interesting because they unify the clade, in cladistics they are considered not helpful when we are trying to determine the relationships of the members of the clade because every member is the same. In contrast, consider the amniotic egg characteristic of Figure **23.2.4**. Only some of the organisms have this trait, and to those that do, it is called a shared derived character because this trait changed at some point during descent. This character does tell us about the relationships among the members of the clade; it tells us that lizards, rabbits, and humans group more closely together than any of these organisms do with fish, lampreys, and lancelets.

A sometimes confusing aspect of “ancestral” and “derived” characters is that these terms are relative. The same trait could be either ancestral or derived depending on the diagram being used and the organisms being compared. Scientists find these terms useful when distinguishing between clades during the building of phylogenetic trees, but it is important to remember that their meaning depends on context.

Choosing the Right Relationships

Constructing a phylogenetic tree, or cladogram, from the character data is a monumental task that is usually left up to a computer. The computer draws a tree such that all of the clades share the same list of derived characters. But there are other decisions to be made, for example, what if a species presence in a clade is supported by all of the shared derived characters for that clade except one? One conclusion is that the trait evolved in the ancestor, but then changed back in that one species. Also a character state that appears in two clades must be assumed to have evolved independently in those clades. These inconsistencies are common in trees drawn from character data and complicate the decision-making process about which tree most closely represents the real relationships among the taxa.

To aid in the tremendous task of choosing the best tree, scientists often use a concept called maximum parsimony, which means that events occurred in the simplest, most obvious way. This means that the “best” tree is the one with the fewest number of character reversals, the fewest number of independent character changes, and the fewest number of character changes throughout the tree. Computer programs search through all of the possible trees to find the small number of trees with the simplest evolutionary pathways. Starting with all of the homologous traits in a group of organisms, scientists can determine the order of evolutionary events of which those traits occurred that is the most obvious and simple.

CONCEPT IN ACTION



Practice Parsimony: Go to this website to learn how maximum parsimony is used to create phylogenetic trees (be sure to continue to the second page).

These tools and concepts are only a few of the strategies scientists use to tackle the task of revealing the evolutionary history of life on Earth. Recently, newer technologies have uncovered surprising discoveries with unexpected relationships, such as the fact that people seem to be more closely related to fungi than fungi are to plants. Sound unbelievable? As the information about DNA sequences grows, scientists will become closer to mapping the evolutionary history of all life on Earth.

Section Summary

To build phylogenetic trees, scientists must collect character information that allows them to make evolutionary connections between organisms. Using morphologic and molecular data, scientists work to identify homologous characteristics and genes. Similarities between organisms can stem either from shared evolutionary history (homologies) or from separate evolutionary paths (analogies). After homologous information is identified, scientists use cladistics to organize these events as a means to determine an evolutionary timeline. Scientists apply the concept of maximum parsimony, which states that the likeliest order of events is probably the simplest shortest path. For evolutionary events, this would be the path with the least number of major divergences that correlate with the evidence.

Art Connections

Figure **23.2.3**: Which animals in this figure belong to a clade that includes animals with hair? Which evolved first: hair or the amniotic egg?

Answer

Rabbits and humans belong in the clade that includes animals with hair. The amniotic egg evolved before hair, because the Amniota clade branches off earlier than the clade that encompasses animals with hair.

Footnotes

1. 1 Gibbons, A. (2012, June 13). *Science Now*. Retrieved from news.sciencemag.org/scienceno...sequenced.html
2. 2 *Background on comparative genomic analysis*. (2002, December). Retrieved from http://www.genome.gov/10005835
3. 3 Harris, S.R. et al. 2010. Evolution of MRSA during hospital transmission and intercontinental spread. *Science* 327:469–474.
4. 4 Isaac NJ, Turvey ST, Collen B, Waterman C, Baillie JE (2007) Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny. PLoS ONE 2(3): e296. doi:10.1371/journal.pone.0000296

Glossary

analogous structure
a character found in two taxa that looks similar because of convergent evolution, not because of descent from a common ancestor

clade
a group of taxa with the same set of shared derived characters, including an ancestral species and all its descendants

cladistics
a method used to organize homologous traits to describe phylogenies using common descendent as the primary criterion used to classify organisms

maximum parsimony
applying the simplest, most obvious way with the least number of steps

molecular systematics
the methods of using molecular evidence to identify phylogenetic relationships

monophyletic group

(also, clade) organisms that share a single ancestor

shared ancestral character

a character on a phylogenetic branch that is shared by a particular clade

shared derived character

a character on a phylogenetic tree that is shared only by a certain clade of organisms

Contributors and Attributions

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23.3: Systematics and Classification

All life on Earth evolved from a common ancestor. Biologists map how organisms are related by constructing phylogenetic trees. In other words, a “tree of life” can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms, as shown in Figure **23.3.1**. Notice that from a single point, the three domains of Archaea, Bacteria, and Eukarya diverge and then branch repeatedly. The small branch that plants and animals (including humans) occupy in this diagram shows how recently these groups had their origin compared with other groups.

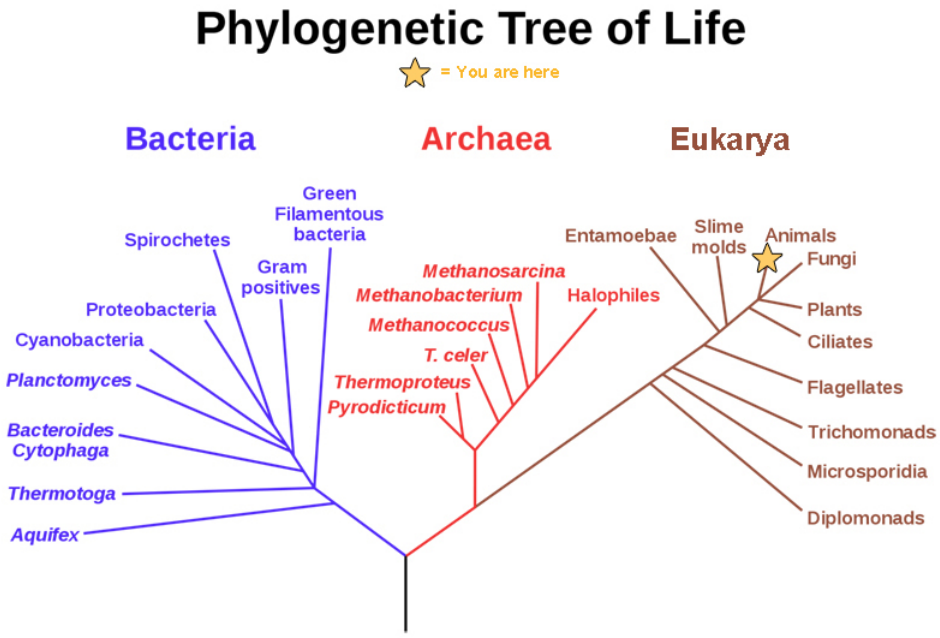


Figure 23.3.1: In the evolution of life on Earth, the three domains of life—Archaea, Bacteria, and Eukarya—branch from a single point. (credit: modification of work by Eric Gaba)

The phylogenetic tree in Figure **23.3.1** illustrates the pathway of evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing backward to any branch point, the organisms related to it by various degrees of closeness can be identified.

A phylogeny is the evolutionary history and the relationships among a species or group of species. The study of organisms with the purpose of deriving their relationships is called systematics.

Many disciplines within the study of biology contribute to understanding how past and present life evolved over time, and together they contribute to building, updating, and maintaining the “tree of life.” Information gathered may include data collected from fossils, from studying morphology, from the structure of body parts, or from molecular structure, such as the sequence of amino acids in proteins or DNA nucleotides. By considering the trees generated by different sets of data scientists can put together the phylogeny of a species.

Scientists continue to discover new species of life on Earth as well as new character information, thus trees change as new data arrive.

The Levels of Classification

Taxonomy (which literally means “arrangement law”) is the science of naming and grouping species to construct an internationally shared classification system. The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish naturalist) uses a hierarchical model. A hierarchical system has levels and each group at one of the levels includes groups at the next lowest level, so that at the lowest level each member belongs to a series of nested groups. An analogy is the nested series of directories on the main disk drive of a computer. For example, in the most inclusive grouping, scientists divide organisms into three domains: Bacteria, Archaea, and Eukarya. Within each domain is a second level called a kingdom. Each domain contains

several kingdoms. Within kingdoms, the subsequent categories of increasing specificity are: phylum, class, order, family, genus, and species.

As an example, the classification levels for the domestic dog are shown in Figure **23.3.2**. The group at each level is called a taxon (plural: taxa). In other words, for the dog, Carnivora is the taxon at the order level, Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, such as domestic dog, or wolf. Each taxon name is capitalized except for species, and the genus and species names are italicized. Scientists refer to an organism by its genus and species names together, commonly called a scientific name, or Latin name. This two-name system is called binomial nomenclature. The scientific name of the wolf is therefore *Canis lupus*. Recent study of the DNA of domestic dogs and wolves suggest that the domestic dog is a subspecies of the wolf, not its own species, thus it is given an extra name to indicate its subspecies status, *Canis lupus familiaris*.

Figure **23.3.2** also shows how taxonomic levels move toward specificity. Notice how within the domain we find the dog grouped with the widest diversity of organisms. These include plants and other organisms not pictured, such as fungi and protists. At each sublevel, the organisms become more similar because they are more closely related. Before Darwin's theory of evolution was developed, naturalists sometimes classified organisms using arbitrary similarities, but since the theory of evolution was proposed in the 19th century, biologists work to make the classification system reflect evolutionary relationships. This means that all of the members of a taxon should have a common ancestor and be more closely related to each other than to members of other taxa.

Recent genetic analysis and other advancements have found that some earlier taxonomic classifications do not reflect actual evolutionary relationships, and therefore, changes and updates must be made as new discoveries take place. One dramatic and recent example was the breaking apart of prokaryotic species, which until the 1970s were all classified as bacteria. Their division into Archaea and Bacteria came about after the recognition that their large genetic differences warranted their separation into two of three fundamental branches of life.

ART CONNECTION

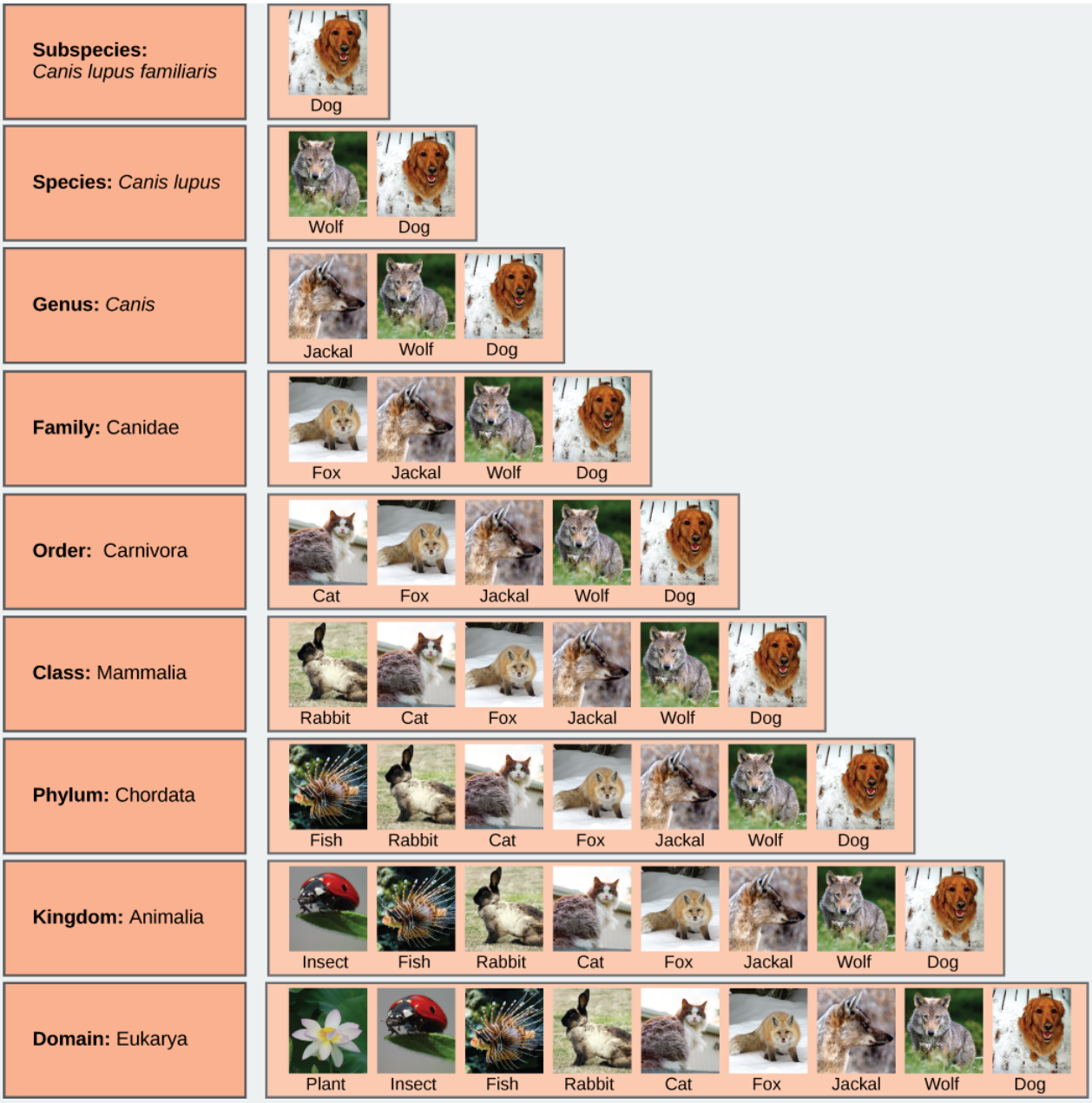


Figure 23.3.2: At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of work by "berduchwal"/Flickr; credit “insect”: modification of work by Jon Sullivan; credit “fish”: modification of work by Christian Mehlführer; credit “rabbit”: modification of work by Aidan Wojtas; credit “cat”: modification of work by Jonathan Lidbeck; credit “fox”: modification of work by Kevin Bacher, NPS; credit “jackal”: modification of work by Thomas A. Hermann, NBII, USGS; credit “wolf” modification of work by Robert Dewar; credit “dog”: modification of work by "digital_image_fan"/Flickr)

In what levels are cats and dogs considered to be part of the same group?

CONCEPT IN ACTION

Visit this site to learn more about taxonomy.

Classification and Phylogeny

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and relationships between organisms. A phylogenetic tree is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. The hierarchical classification of groups nested within more inclusive groups is reflected in diagrams. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past because one cannot go back through time to confirm the proposed relationships.

Unlike with a taxonomic classification, a phylogenetic tree can be read like a map of evolutionary history, as shown in Figure **23.3.3**. Shared characteristics are used to construct phylogenetic trees. The point where a split occurs in a tree, called a branch point, represents where a single lineage evolved into distinct new ones. Many phylogenetic trees have a single branch point at the base representing a common ancestor of all the branches in the tree. Scientists call such trees rooted, which means there is a single ancestral taxon at the base of a phylogenetic tree to which all organisms represented in the diagram descend from. When two lineages stem from the same branch point, they are called sister taxa, for example the two species of orangutans. A branch point with more than two groups illustrates a situation for which scientists have not definitively determined relationships. An example is illustrated by the three branches leading to the gorilla subspecies; their exact relationships are not yet understood. It is important to note that sister taxa share an ancestor, which does not mean that one taxon evolved from the other. The branch point, or split, represents a common ancestor that existed in the past, but that no longer exists. Humans did not evolve from chimpanzees (nor did chimpanzees evolve from humans) although they are our closest living relatives. Both humans and chimpanzees evolved from a common ancestor that lived, scientists believe, six million years ago and looked different from both modern chimpanzees and modern humans.

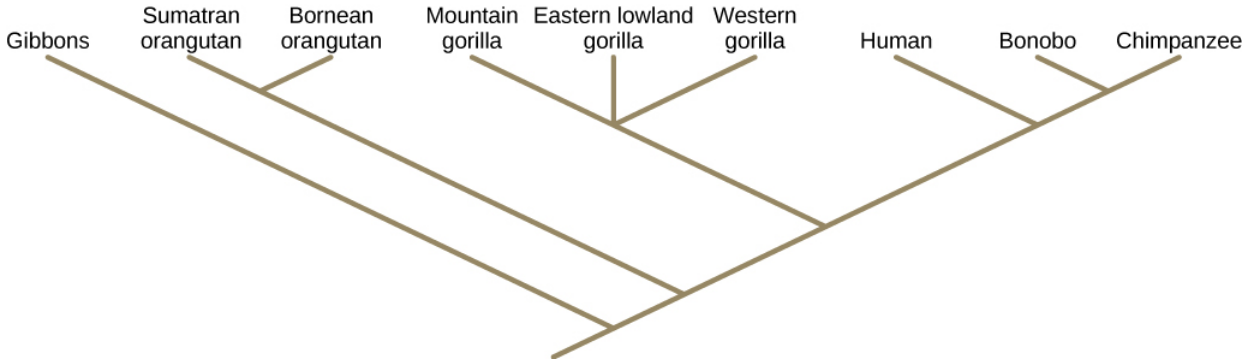


Figure 23.3.3: A phylogenetic tree is rooted and shows how different organisms, in this case the species and subspecies of living apes, evolved from a common ancestor.

The branch points and the branches in phylogenetic tree structure also imply evolutionary change. Sometimes the significant character changes are identified on a branch or branch point. For example, in Figure **23.3.4**, the branch point that gives rise to the mammal and reptile lineage from the frog lineage shows the origin of the amniotic egg character. Also the branch point that gives rise to organisms with legs is indicated at the common ancestor of mammals, reptiles, amphibians, and jawed fishes.

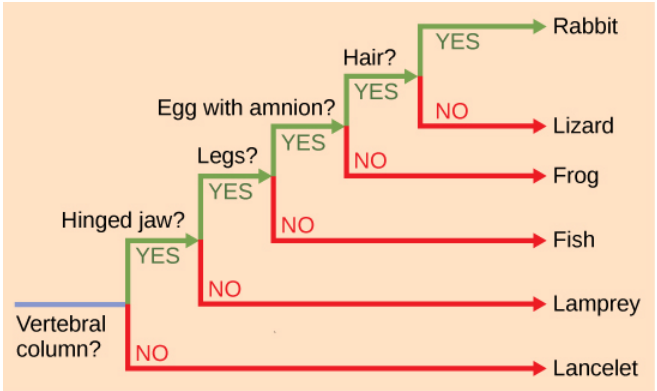


Figure 23.3.4: This phylogenetic tree is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups.

Limitations of Phylogenetic Trees

It is easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly different surroundings or after the evolution of a major new adaptation, they may look quite different from each other, even more so than other groups that are not as closely related. For example, the phylogenetic tree in Figure **23.3.4** shows that lizards and rabbits both have amniotic eggs, whereas salamanders (within the frog lineage) do not; yet on the surface, lizards and salamanders appear more similar than the lizards and rabbits.

Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not show length of time, they show only the order in time of evolutionary events. In other words, a long branch does not necessarily mean more time passed, nor does a short branch mean less time passed— unless specified on the diagram. For example, in Figure **23.3.4**, the tree does not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the order in which things took place. Again using Figure **23.3.4**, the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and similar to a real tree, it does not grow in only one direction after a new branch develops. So, for the organisms in Figure **23.3.4**, just because a vertebral column evolved does not mean that invertebrate evolution ceased, it only means that a new branch formed. Also, groups that are not closely related, but evolve under similar conditions, may appear more similar to each other than to a close relative.

Section Summary

Scientists continually obtain new information that helps to understand the evolutionary history of life on Earth. Each group of organisms went through its own evolutionary journey, called its phylogeny. Each organism shares relatedness with others, and based on morphologic and genetic evidence scientists attempt to map the evolutionary pathways of all life on Earth. Historically, organisms were organized into a taxonomic classification system. However, today many scientists build phylogenetic trees to illustrate evolutionary relationships and the taxonomic classification system is expected to reflect evolutionary relationships.

Art Connections

Figure **23.3.2**: In what levels are cats and dogs considered to be part of the same group?

Answer

Cats and dogs are part of the same group at five levels: both are in the domain Eukarya, the kingdom Animalia, the phylum Chordata, the class Mammalia, and the order Carnivora.

Glossary

binomial nomenclature
a system of two-part scientific names for an organism, which includes genus and species names

branch point
a point on a phylogenetic tree where a single lineage splits to distinct new ones

class
the category in the taxonomic classification system that falls within phylum and includes orders

domain
the highest level category in the classification system and that includes all taxonomic classifications below it; it is the most inclusive taxon

family
the category in the taxonomic classification system that falls within order and includes genera

genus
the category in the taxonomic classification system that falls within family and includes species; the first part of the scientific name

kingdom
the category in the taxonomic classification system that falls within domain and includes phyla

order
the category in the taxonomic classification system that falls within class and includes families

phylogenetic tree
diagram used to reflect the evolutionary relationships between organisms or groups of organisms

phylogeny
evolutionary history and relationship of an organism or group of organisms

phylum
the category in the taxonomic classification system that falls within kingdom and includes classes

rooted
describing a phylogenetic tree with a single ancestral lineage to which all organisms represented in the diagram relate

sister taxa
two lineages that diverged from the same branch point

species
the most specific category of classification

systematics
the science of determining the evolutionary relationships of organisms

taxon
a single level in the taxonomic classification system

taxonomy
the science of classifying organisms

Contributors

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23.4: Phylogenetics and Comparative Biology

Learning Objectives

- Explain the difference between homologous and analogous structures

Two Options for Similarities

In general, organisms that share similar physical features and genomes tend to be more closely related than those that do not. Such features that overlap both morphologically (in form) and genetically are referred to as homologous structures; they stem from developmental similarities that are based on evolution. For example, the bones in the wings of bats and birds have homologous structures.

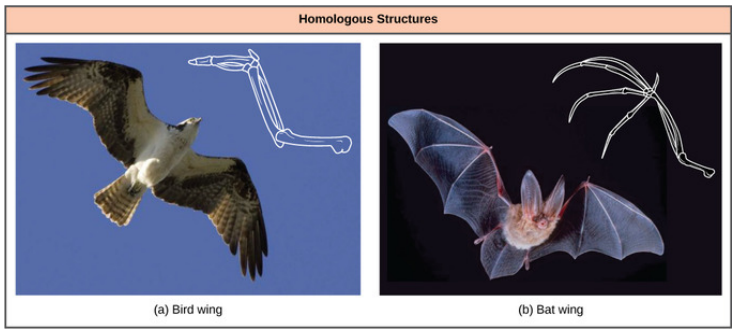


Figure **23.4.1**: Homologous structures: Bat and bird wings are homologous structures, indicating that bats and birds share a common evolutionary past.

Notice it is not simply a single bone, but rather a grouping of several bones arranged in a similar way. The more complex the feature, the more probable that any overlap is due to a common evolutionary past. Imagine two people from different countries both inventing a car with all the same parts and in exactly the same arrangement without any previous or shared knowledge. That outcome would be highly improbable. However, if two people both invented a hammer, it would be reasonable to conclude that both could have the original idea without the help of the other. The same relationship between complexity and shared evolutionary history is true for homologous structures in organisms.

Misleading Appearances

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. Similarly, unrelated organisms may be distantly related, but appear very similar. This usually happens because both organisms developed common adaptations that evolved within similar environmental conditions. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is called an analogy or homoplasy. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different. These are called analogous structures.

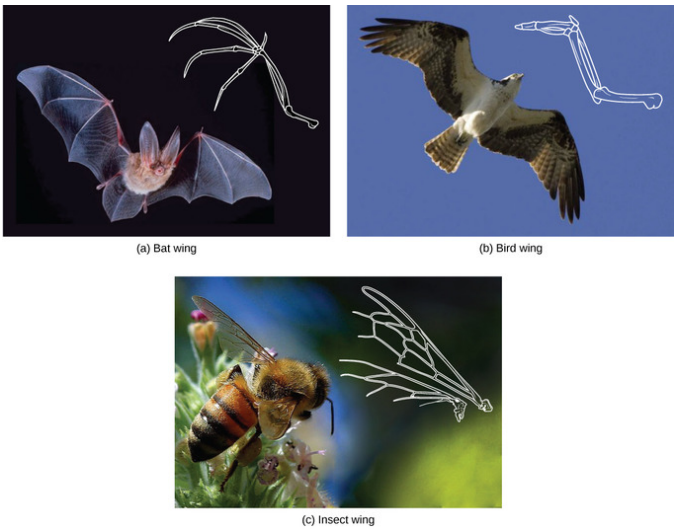


Figure **23.4.1**: Analogous structures: The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, the honeybee wing is not composed of bones and has a distinctly-different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate an analogy: similar structures that do not share an evolutionary history.

Similar traits can be either homologous or analogous. Homologous structures share a similar embryonic origin; analogous organs have a similar function. For example, the bones in the front flipper of a whale are homologous to the bones in the human arm. These structures are not analogous. The wings of a butterfly and the wings of a bird are analogous, but not homologous. Some structures are both analogous and homologous: the wings of a bird and the wings of a bat are both homologous and analogous. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.

Molecular Comparisons

With the advancement of DNA technology, the area of molecular systematics, which describes the use of information on the molecular level including DNA analysis, has blossomed. New computer programs not only confirm many earlier classified organisms, but also uncover previously-made errors. As with physical characteristics, even the DNA sequence can be tricky to read in some cases. For some situations, two very closely-related organisms can appear unrelated if a mutation occurred that caused a shift in the genetic code. An insertion or deletion mutation would move each nucleotide base over one place, causing two similar codes to appear unrelated.

Sometimes two segments of DNA code in distantly-related organisms randomly share a high percentage of bases in the same locations, causing these organisms to appear closely related when they are not. For both of these situations, computer technologies have been developed to help identify the actual relationships. Ultimately, the coupled use of both morphologic and molecular information is more effective in determining phylogeny.

Key Points

- Organisms may be very closely related, even though they look quite different, due to a minor genetic change that caused a major morphological difference.
- Unrelated organisms may appear very similar because both organisms developed common adaptations that evolved within similar environmental conditions.
- To determine the phylogeny of an organism, scientists must determine whether a similarity is homologous or analogous.
- The advancement of DNA technology, the area of molecular systematics, describes the use of information on the molecular level, including DNA analysis.

Key Terms

- **analogous**: when similar similar physical features occur in organisms because of environmental constraints and not due to a close evolutionary relationship
- **homologous**: when similar physical features and genomes stem from developmental similarities that are based on evolution

- **phylogeny**: the evolutionary history of an organism
- **molecular systematics**: molecular phylogenetics is the analysis of hereditary molecular differences, mainly in DNA sequences, to gain information on an organism's evolutionary relationships

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23.5: Phylogenetics and Disease Evolution

What is an evolutionary tree?

On a grand scale, the process of speciation leads to an evolutionary pattern that is something like a forking road. A lineage may persist for many generations and then split, with each resulting lineage taking its own path. Some paths end up leading to dead-ends (i.e., extinction); others diverge many more times, leading to new lineages. The result of this process is a tree-like structure that links together all species that have ever lived on planet Earth.

Imagine if we humans could turn around and walk backwards on the branch of our own evolutionary history. We'd soon meet up with routes leading to our now-extinct hominin relatives, and then greet the ancient ancestors of chimpanzees and bonobos as our routes converged. Eventually, we'd be crossing paths with ancient ancestors of birds and dinosaurs, then the ancestors of sharks, starfish, insects, and plants, ultimately, reaching the point where all evolutionary paths converge — the single-celled organisms that are the great-great-great-great-great … great-grandparents of all species that have ever lived on Earth.

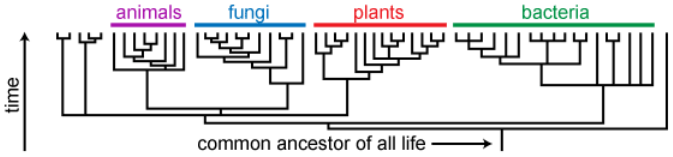


Figure **23.5.1**: Tree adapted from Gómez, J. M.; Verdú, M. & Perfectti, F. 2010. Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature* 465: 918-

Evolutionary trees, also known as phylogenetic trees, are visual representations of this branching pattern of evolution. A phylogenetic tree may represent the full diversity of life springing from our universal common ancestor (as does the tree above) or a single branch of the full tree of life, such as the vertebrate, fungus, or beetle lineages. Trees may include both extant and extinct organisms. As shown here, there are many ways to depict an evolutionary tree.



Figure **23.5.2**: Evolutionary trees may be visually depicted in many different ways.

The pattern of evolutionary history is mainly branching. However, biologists are discovering more and more cases in which lineages have merged with one another over the course of evolution (e.g., in bacteria, this is common). Such events can still be represented on tree-like structures with cross branches between lineages; however, we will not address this situation here since by far the most common evolutionary trees focus on lineages with a strictly branching pattern of evolution.

How to read trees

To understand how trees represent evolution, imagine the tree shown here beginning as a single lineage and growing outwards in a branching pattern over time (click the button to view the animation). That first lineage represents the oldest lineage on the tree — the lineage that is ancestral to all the other organisms on the tree. The tips of the branches (called taxa) represent the youngest lineages on the tree. These taxa are often species — but not always. Some trees represent the relationships among major groups of organisms, species, populations, individuals, or even genes.

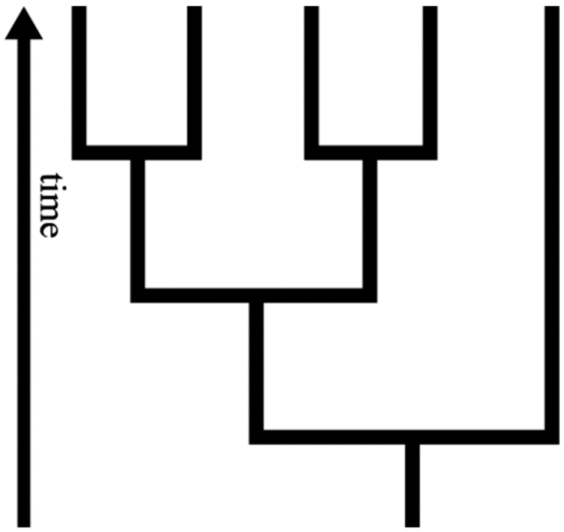


Figure **23.5.31**:

The branches of the tree correspond to ancestor/descendent relationships within a lineage: the part of the branch nearer the base of the tree represents the lineage that is ancestral to the part of the branch nearer the tips. The branching points, or nodes, of the tree represent the splitting of an ancestral lineage into multiple descendent lineages through the process of speciation. If you take any two taxa and trace their branches backwards, the node at which the two paths meet represents the point in evolutionary time when their common ancestor split into two lineages.

Understanding evolutionary relationships

So how do you tell which organisms on a tree are most closely related to one another? It's tempting to focus on the *order* of the branch tips on a tree (i.e., which lineage goes to the right and which goes to the left), but in fact, this ordering is not meaningful at all. Instead, the key to understanding evolutionary relationships is common ancestry. Common ancestry refers to the fact that distinct descendent lineages have the same ancestral lineage in common with one another, as shown in the diagram below.

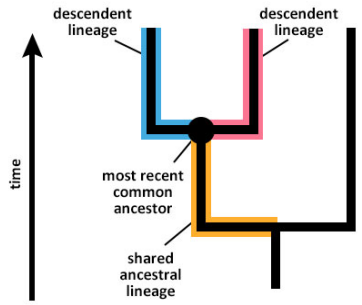


Figure **23.5.4**: Common ancestry refers to the fact that distinct descendent lineages have the same ancestral lineage in common with one another

So how do you tell which organisms on a tree are most closely related to one another? It's tempting to focus on the *order* of the branch tips on a tree (i.e., which lineage goes to the right and which goes to the left), but in fact, this ordering is not meaningful at all. Instead, the key to understanding evolutionary relationships is common ancestry. Common ancestry refers to the fact that distinct descendent lineages have the same ancestral lineage in common with one another, as shown in the diagram below.

Any set of taxa has a most recent common ancestor — that is, the youngest common ancestor that they all have in common. To find the most recent common ancestor of a set of taxa on a phylogenetic tree, follow each taxon's lineage back in time (towards the base of the tree) until all the lineages meet up. That node represents their most recent common ancestor. Test your understanding of most

recent common ancestors with the tree shown here. Which node represents the most recent common ancestor of the square taxon and the star taxon? Click the button to see the answer.

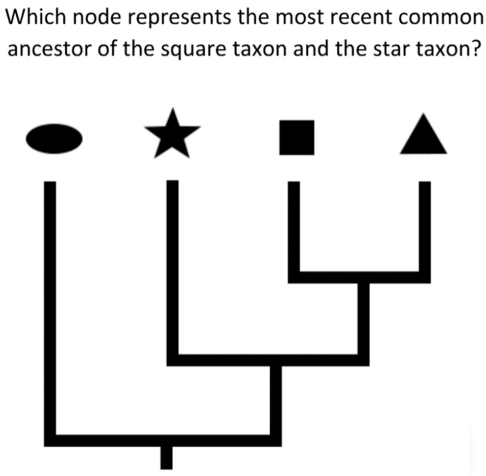


Figure **23.5.5**: the triangle and square taxa are more closely related to one another than either is to the star taxon

Taxa that share a *more* recent common ancestor with one another are more closely related than are taxa whose most recent common ancestor is older. As shown in the diagram above, because the triangle taxon shares a more recent common ancestor with the square taxon than either does with the star taxon, we can say that the triangle and square taxa are more closely related to one another than either is to the star taxon.

Disease detectives

At the most basic level, evolutionary trees tell us which groups of organisms (i.e., clades) are closely related and which are more distant cousins. This can be useful in a couple of ways. First, if a particular organism is unfamiliar, placing it on an evolutionary tree can reveal its origins. This might seem like a no brainer (after all, if the organism is a dog, it must be closely related to other dogs); however, in practice it is often not so simple. Viruses and bacteria often can't be identified based on their appearances, but can be placed on a phylogenetic tree based on their genetic sequences. For example, the origins of HIV were a mystery to medical researchers until samples of the HIV virus and many others were sequenced and used to construct a phylogenetic tree. The tree made it obvious that HIV evolved from the Simian Immunodeficiency Virus (SIV) and that, on a few different occasions, SIV had jumped from another primate to a human host and, over many generations, was selected for the traits that we now associate with HIV. HIV evolved not just once, but several different times![1] Clearly, when humans come into close contact with our nearest relatives, the risk of passing infectious diseases to one another is relatively high.

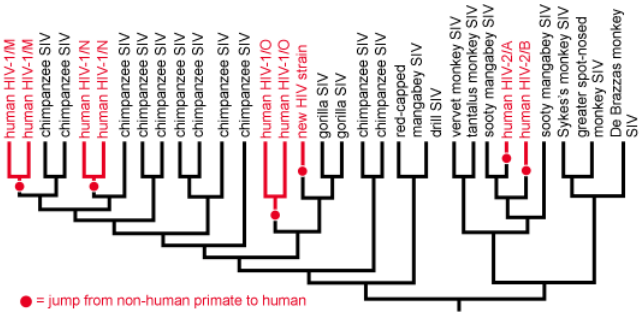


Figure **23.5.6**: Phylogenetics reveals that HIV has evolved from SIV several times. Tree based on Frontline and Plantier, J., M. Leoz, J.E. Dickerson, F. De Oliveira, F. Cordonnier, V. Lemée, … and F. Simon. 2009. A new human immunodeficiency virus derived from gorillas. *Nature Medicine* 15:871-872.

Understanding the relationships among groups of organisms has been useful for much more than just identifying the origins of HIV. The same basic approach has helped uncover the roots of SARS (from bats), malaria (from primates), and other diseases.

Understanding how infectious diseases got their starts in humans may help us prevent other animal-borne diseases from starting to infect humans. It also allows researchers to study the disease in other contexts — potentially resulting in new treatments. The same approach has been useful in non-medical contexts as well. For example, whale species being illegally sold in Japanese meat markets and alligator being sold as turtle meat in the southern U.S. have all been identified on the basis of phylogenetic trees linking suspect meat samples to known species.[2]

1. Keele, B.F., F. Van Heuverswyn, Y. Li, E. Bailes, J. Takehisa, M.L. Santiago, … and B.H. Hahn. 2006. Chimpanzee reservoirs of pandemic and nonpandemic HIV-*Nature* 313:523-526.

2. C.S. Baker, G.M. Lento, F. Cipriano, M.L. Dalebout, and S.R. Palumbi. (2000). Scientific whaling: Source of illegal products for market? *Science* 290:1695. Baker, C.S., and S.R. Palumbi. 1996. Population structure, molecular

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CHAPTER OVERVIEW

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24.3: Evolution within Genomes

24.3.1: Eukaryotic Transcription

24.3.2: Perspectives on the Phylogenetic Tree

24.4: Gene Function and Expression Patterns

24.5: Applying Comparative Genomics

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24.1: Comparative Genomics

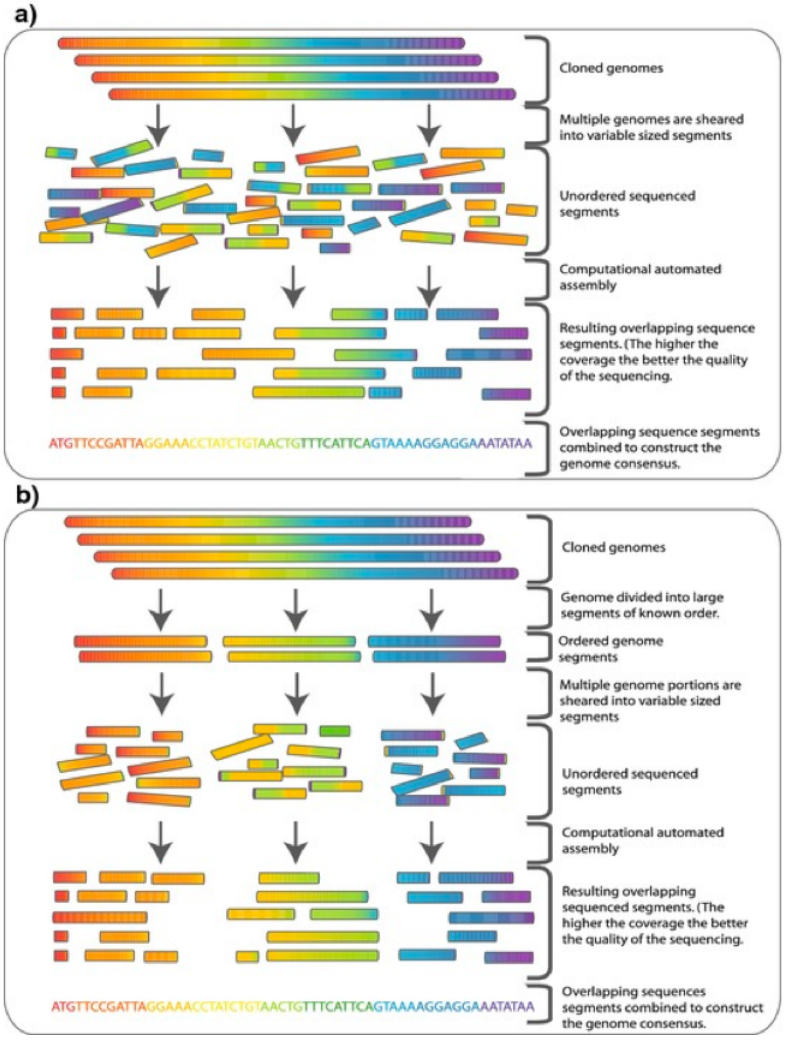
Genomics is a field that studies the entire collection of an organism's DNA or genome. It involves sequencing, analyzing, and comparing the information contained within genomes. Since sequencing has become much less expensive and more efficient, vast amounts of genomic information is now available about a wide variety of organisms, but particularly microbes, with their smaller genome size. In fact, the biggest bottleneck currently is not the lack of information but the lack of computing power to process the information!

Sequencing

Sequencing, or determining the base order of an organism's DNA or RNA, is often one of the first steps to finding out detailed information about an organism. A bacterial genome can range from 130 kilobase pairs (kbp) to over 14 Megabase pairs (Mbp), while a viral genome ranges from 0.859 to 2473 kbp. For comparison, the human genome contains about 3 billion base pairs.

Shotgun sequencing

Shotgun sequencing initially involves construction of a **genomic library**, where the genome is broken into randomly sized fragments that are inserted into vectors to produce a library of clones. The fragments are sequenced and then analyzed by a computer, which searches for overlapping regions to form a longer stretch of sequence. Eventually all the sequences are aligned to give the complete genome sequence. Errors are reduced because many of the clones contain identical or near identical sequences, resulting in good "coverage" of the genome.



Shotgun Sequencing. By Commins, J., Toft, C., Fares, M. A. [CC BY-SA 2.5], via Wikimedia Commons

Second generation DNA sequencing

Second-generation DNA sequencing uses **massively parallel methods**, where multiple samples are sequenced side-by-side. DNA fragments of a few hundred bases each are amplified by PCR and then attached to small bead, so that each bead carries several copies of the same section of DNA. The beads are put into a plate containing more than a million wells, each with one bead, and the DNA fragments are sequenced.

Third- and fourth-generation DNA sequencing

Third-generation DNA sequencing involves the sequencing of single molecules of DNA. Fourth-generation DNA sequencing, also known as “post light sequencing,” utilizes methods other than optical detection for sequencing.

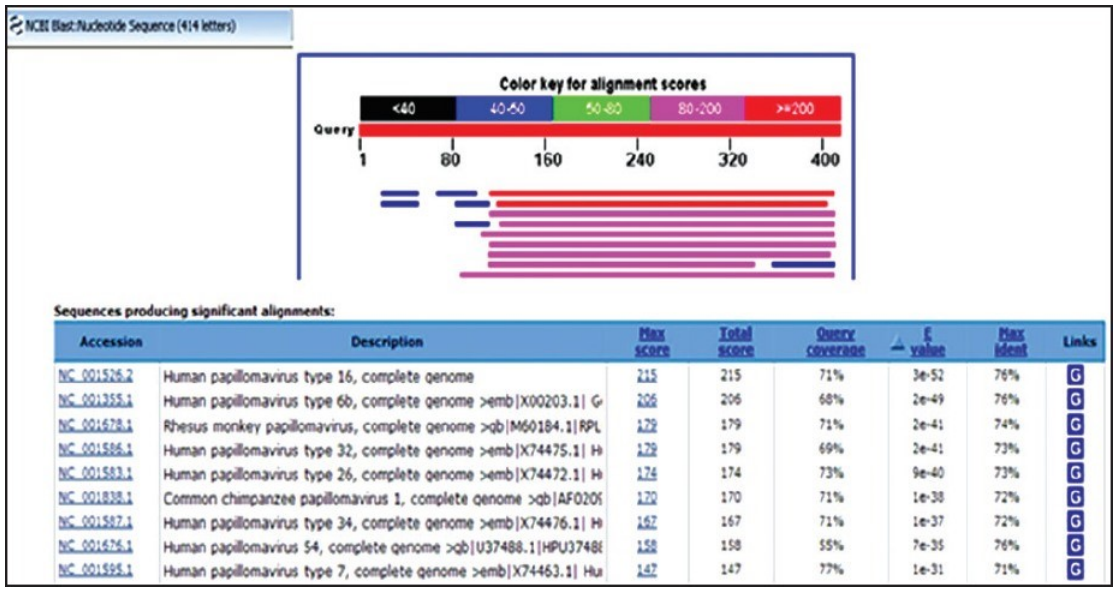
Bioinformatics

After sequencing, it is time to make sense of the information. The field of **bioinformatics** combines many fields together (i.e. biology, computer science, statistics) to use the power of computers to analyze information contained in the genomic sequence. Locating specific genes within a genome is referred to as **genome annotation**.

Open Reading Frames (ORFS)

An **open reading frame** or **ORF** denotes a possible protein-coding gene. For double-stranded DNA, there are six reading frames to be analyzed, since the DNA is read in sets of three bases at a time and there are two strands of DNA. An ORF typically has at least 100 codons before a stop codon, with 3’ terminator sequences. A **functional ORF** is one that is actually used by the organism to encode a protein. Computers are used to search the DNA sequence looking for ORFs, with those presumed to encode protein further analyzed by a bioinformaticist.

It is often helpful for the sequence to be compared against a database of sequences coding for known proteins. GenBank is a database of over 200 billion base pairs of sequences that scientists can access, to try and find matches to the sequence of interest. The database search tool **BLAST** (**basic local alignment search tool**) has programs for comparing both nucleotide sequences and amino acid sequences, providing a ranking of results in order of decreasing similarity.



BLAST Results.

Comparative Genomics

Once the sequences of organisms have been obtained, meaningful information can be gathered using **comparative genomics**. For this genomes are assessed for information regarding size, organization, and gene content.

Comparison of the genome of microbial strains has given scientists a better picture regarding the genes that organisms pick up. A group of multiple strains share a **core genome**, genes coding for essential cellular functions that they all have in common. The **pan genome** represents all the genes found in all the members of species, so provides a good idea of the diversity of a group. Most of these "extra" genes are probably picked up by horizontal gene transfer.

Comparative genomics also shows that many genes are derived as a result of gene duplication. Genes within a single organism that likely came about because of gene duplication are referred to as **paralogs**. In many cases one of the genes might be altered to take on a new function. It is also possible for gene duplication to be found in different organisms, as a result of acquiring the original gene from a common ancestor. These genes are called **orthologs**.

Functional Genomics

The sequence of a genome and the location of genes provide part of the picture, but in order to fully understand an organism we need an idea of what the cell is doing with its genes. In other words, what happens when the genes are expressed? This is where **functional genomics** comes in – placing the genomic information in context.

The first step in gene expression is transcription or the manufacture of RNA. **Transcriptome** refers to the entire complement of RNA that a cell can make from its genome, while **proteome** refers to all the proteins encoded by an organisms' genome, in the final step of gene expression.

Microarrays

Microarrays or **gene chips** are solid supports upon which multiple spots of DNA are placed, in a grid-like fashion. Each spot of DNA represents a single gene or ORF. Known fragments of nucleic acid are labeled and used as **probes**, with a signal produced if binding occurs. Microarrays can be used to determine what genes might be turned on or off under particular conditions, such as comparing the growth of a bacterial pathogen inside the host versus outside of the host.

Proteomics

The study of the proteins of an organism (or the proteome) is referred to as **proteomics**. Much of the interest focuses on **functional proteomics**, which examines the functions of the cellular proteins and the ways in which they interact with one another.

One common technique used in the study of proteins is **two-dimensional gel electrophoresis**, which first separates proteins based on their isoelectric points. This is accomplished by using a pH gradient, which separates the proteins based on their amino acid content. The separated proteins are then run through a polyacrylamide gel, providing the second dimension as proteins are separated by size.

Structural proteomics focuses on the three-dimensional structure of proteins, which is often determined by protein modeling, using computer algorithms to predict the most likely folding of the protein based on amino acid information and known protein patterns.

Metabolomics

Metabolomics strives to identify the complete set of metabolic intermediates produced by an organism. This can be extremely complicated, since many metabolites are used by cells in multiple pathways.

Metagenomics

Metagenomics or **environmental genomics** refers to the extraction of pooled DNA directly from a specific environment, without the initial isolation and identification of organisms within that environment. Since many microbial species are difficult to culture in the laboratory, studying the **metagenome** of an environment allows scientists to consider all organisms that might be present. Taxa can even be identified in the absence of organism isolation using nucleic acid sequences alone, where the taxon is known as **phylotype**.

Key Words

genomics, sequencing, shotgun sequencing, genomic library, second generation DNA sequencing, massively parallel methods, third- and fourth-generation DNA sequencing, bioinformatics, genome annotation, open reading frame/ORF, functional ORF, GenBank, BLAST/basic local alignment search tool, comparative genomics, core genome, pan genome, paralog, ortholog,

functional genomics, transcriptome, proteome, microarray/gene chips, probe, proteomics, functional proteomics, two-dimensional gel electrophoresis, structural proteomics, metabolomics, metagenomics/environmental genomics, metagenome, phylotype.

Study Questions

1. What does the field of genomics encompass?
2. What is shotgun sequencing and how does this allow for the complete sequencing of an organism's genome?
3. What are the basic differences among 2nd, 3rd, and 4th generation sequencing?
4. What is an open reading frame and how can scientists use it to determine information about a genome and its products?
5. How does functional genomics differ from comparative genomics? What are the tools used in functional genomics and what information can be obtained from each?

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24.2: Genome Size

The genome of an organism is the complete set of genes specifying how its phenotype will develop (under a certain set of environmental conditions). In this sense, then, **diploid** organisms (like ourselves) contain two genomes, one inherited from our mother, the other from our father. The table below presents a selection of representative genome sizes from the rapidly-growing list of organisms whose genomes have been sequenced.

Table of Genome Sizes (haploid)

https://bio.libretexts.org/@go/page/74237

	Base pairs	Genes	Notes
φX174	5,386	11	virus of E. coli
Human mitochondrion	16,569	37	
Nasuia deltocephalinicola	112,091	137	smallest genome yet found in a bacterium. This β-proteobacterium lives in a mutualistic relationship within a special organ of an insect (a leaf hopper) which it supplies with essential amino acids.
Epstein-Barr virus (EBV)	172,282	80	causes mononucleosis
nucleomorph of *Guillardia theta*	551,264	511	all that remains of the nuclear genome of a red alga (a eukaryote) engulfed long ago by another eukaryote
Mycoplasma genitalium	580,073	525	two of the smallest true organisms
Mycoplasma pneumoniae	816,394	679	
Rickettsia prowazekii	1,111,523	834	bacterium that causes epidemic typhus
Treponema pallidum	1,138,011	1,039	bacterium that causes syphilis
Pelagibacter ubique	1,308,759	1,354	smallest genome yet found in a **free-living** organism (marine α-proteobacterium)
Helicobacter pylori	1,667,867	1,589	chief cause of stomach ulcers (not stress and diet)
Methanocaldococcus jannaschii	1,664,970	1,783	These unicellular microbes look like typical bacteria but their genes are so different from those of either bacteria or eukaryotes that they are classified in a third kingdom: **Archaea**.
Aeropyrum pernix	1,669,695	1,885	
Methanothermobacter thermoautotrophicus	1,751,377	2,008	
Streptococcus pneumoniae	2,160,837	2,236	the pneumococcus
Pandoravirus	2,473,870	2556	A **virus** (of an amoeba) with a genome larger than that of the bacteria and archaea above and about the same as that of some parasitic **eukaryotes.**
Listeria monocytogenes	2,944,528	2,926	2,853 of these encode proteins; the rest RNAs
Synechocystis	3,573,470	4,003	a marine cyanobacterium ("blue-green alga")
E. coli K-12	4,639,221	4,377	4,290 of these genes encode proteins; the rest RNAs

	Base pairs	Genes	Notes
E. coli O157:H7	5.44×10^6	5,416	strain that is pathogenic for humans; has 1,346 genes not found in E. coli K-12
Schizosaccharomyces pombe	12,462,637	4,929	Fission yeast. A **eukaryote** with fewer genes than the three bacteria below.
Agrobacterium tumefaciens	4,674,062	5,419	Useful vector for making transgenic plants; shares many genes with *Sinorhizobium meliloti*
Pseudomonas aeruginosa	6.3×10^6	5,570	Increasingly common cause of opportunistic infections in humans.
Sinorhizobium meliloti	6,691,694	6,204	The rhizobial symbiont of alfalfa. Genome consists of one chromosome and 2 large plasmids.
Saccharomyces cerevisiae	12,495,682	5,770	Budding yeast. A eukaryote.
Neurospora crassa	38,639,769	10,082	Plus 498 RNA genes.
Thalassiosira pseudonana	34.5×10^6	11,242	A diatom. Plus 144 chloroplast and 40 mitochondrial genes encoding proteins
Naegleria gruberi	41×10^6	15,727	This free-living unicellular organism lives as both an amoeboid and a flagellated form. 4,133 of its genes are also found in other eukaryotes suggesting that they were present in the common ancestor of all eukaryotes. The great variety of functions encoded by these genes also suggests that the common ancestor of all eukaryotes was itself as complex as many of the present-day unicellular members.
Drosophila melanogaster	122,653,977	~17,000	the "fruit fly"
Caenorhabditis elegans	100,258,171	21,733	
Humans	3.3×10^9	~21,000	
Tetraodon nigroviridis (a pufferfish)	3.42×10^8	27,918	Although Tetraodon seems to have more protein-encoding genes than we do, it has much less non-coding DNA so its total genome is about a tenth the size of ours.

	Base pairs	Genes	Notes
Mouse	2.8×10^9	~23,000	
Amphibians	10^9–10^{11}	?	
Arabidopsis thaliana	0.135×10^9	27,407	a flowering plant (angiosperm) with one of the smallest genomes known in the plant kingdom.
Picea abies	19.6×10^9	28,354	the Norway spruce, a conifer (gymnosperm). Even though it has only ~900 more genes than Arabidopsis, it has 145 times as much DNA. Most of this appears to be derived from transposons.
Psilotum nudum	2.5×10^{11}	?	

Even though *Psilotum nudum* (sometimes called the "whisk fern") is a far simpler plant than Arabidopsis (it has no true leaves, flowers, or fruit), it has 3000 times as much DNA. No one knows why, but 80% or more of it is repetitive DNA containing no genetic information. This is also the case for some amphibians, which contain 30 times as much DNA as we do, but certainly are not 30 times as complex. The total amount of DNA in the haploid genome is called its C value. The lack of a consistent relationship between the C value and the complexity of an organism (e.g., amphibians vs. mammals) is called the C value paradox.

Not all genes are Indispensable

The scientists at The Institute for Genomic Research (now known as the J. Craig Venter Institute) who determined the ***Mycoplasma genitalium*** sequence have followed this work by systematically destroying its genes (by mutating them with insertions) to see which ones are essential to life and which are dispensable. Of the 485 protein-encoding genes, they have concluded that only 381 of them are essential to life. In other words, the loss of any one of the 381 is lethal; the loss of any one of the others is not. (This is not to say that all the organism needs are those 381 — see "A Minimal Genome?" below.)

Using similar techniques, three groups have recently found that only about 10% of the genes in the human genome (~2000 of them) must be present for human cells to grow successfully in culture. These genes encode proteins for such essential functions as controlling the cell cycle, DNA replication, DNA transcription and RNA translation. The cells can tolerate the loss of any one of the other ~18,000 genes. Thus the human genome appears to have redundant pathways that can often compensate for the loss of a single gene at least for cells growing in culture. Probably others will turn out to be essential for the development and functioning of the various types of differentiated cells in the intact body.

A Minimal Genome?

In March of 2016, workers at the J. Craig Venter Institute reported that they had created a strain of *mycoplasma* containing only 473 genes. This synthetic organism, which grows vigorously in culture, now holds the record for the smallest genome of a free-living organism.

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SECTION OVERVIEW

24.3: Evolution within Genomes

Skills to Develop

- Describe how a karyogram is created
- Explain how nondisjunction leads to disorders in chromosome number
- Compare disorders caused by aneuploidy
- Describe how errors in chromosome structure occur through inversions and translocations

Inherited disorders can arise when chromosomes behave abnormally during meiosis. Chromosome disorders can be divided into two categories: abnormalities in chromosome number and chromosomal structural rearrangements. Because even small segments of chromosomes can span many genes, chromosomal disorders are characteristically dramatic and often fatal.

Identification of Chromosomes

The isolation and microscopic observation of chromosomes forms the basis of cytogenetics and is the primary method by which clinicians detect chromosomal abnormalities in humans. A karyotype is the number and appearance of chromosomes, and includes their length, banding pattern, and centromere position. To obtain a view of an individual's karyotype, cytologists photograph the chromosomes and then cut and paste each chromosome into a chart, or karyogram, also known as an ideogram (Figure **24.3.1**).

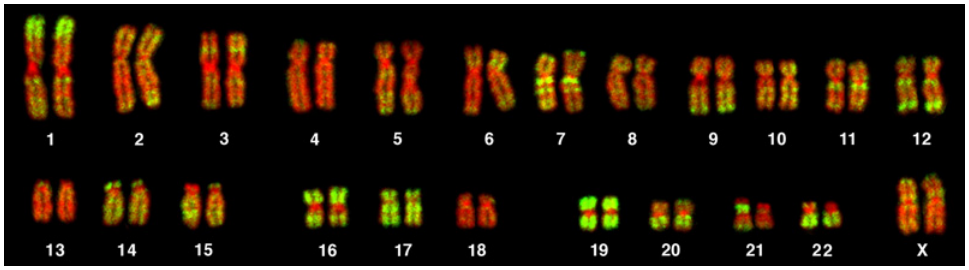


Figure **24.3.1**: This karyotype is of a female human. Notice that homologous chromosomes are the same size, and have the same centromere positions and banding patterns. A human male would have an XY chromosome pair instead of the XX pair shown. (credit: Andreas Blozer et al)

In a given species, chromosomes can be identified by their number, size, centromere position, and banding pattern. In a human karyotype, autosomes or "body chromosomes" (all of the non–sex chromosomes) are generally organized in approximate order of size from largest (chromosome 1) to smallest (chromosome 22). The X and Y chromosomes are not autosomes. However, chromosome 21 is actually shorter than chromosome 22. This was discovered after the naming of Down syndrome as trisomy 21, reflecting how this disease results from possessing one extra chromosome 21 (three total). Not wanting to change the name of this important disease, chromosome 21 retained its numbering, despite describing the shortest set of chromosomes. The chromosome "arms" projecting from either end of the centromere may be designated as short or long, depending on their relative lengths. The short arm is abbreviated *p* (for "petite"), whereas the long arm is abbreviated *q* (because it follows "p" alphabetically). Each arm is further subdivided and denoted by a number. Using this naming system, locations on chromosomes can be described consistently in the scientific literature.

Career Connection: Geneticists Use Karyograms to Identify Chromosomal Aberrations

Although Mendel is referred to as the "father of modern genetics," he performed his experiments with none of the tools that the geneticists of today routinely employ. One such powerful cytological technique is karyotyping, a method in which traits characterized by chromosomal abnormalities can be identified from a single cell. To observe an individual's karyotype, a person's cells (like white blood cells) are first collected from a blood sample or other tissue. In the laboratory, the isolated cells are stimulated to begin actively dividing. A chemical called colchicine is then applied to cells to arrest condensed chromosomes in metaphase. Cells are then made to swell using a hypotonic solution so the chromosomes spread apart. Finally, the sample is preserved in a fixative and applied to a slide.

The geneticist then stains chromosomes with one of several dyes to better visualize the distinct and reproducible banding patterns of each chromosome pair. Following staining, the chromosomes are viewed using bright-field microscopy. A common stain choice is the Giemsa stain. Giemsa staining results in approximately 400–800 bands (of tightly coiled DNA and condensed proteins) arranged along all of the 23 chromosome pairs; an experienced geneticist can identify each band. In addition to the banding patterns, chromosomes are further identified on the basis of size and centromere location. To obtain the classic depiction of the karyotype in which homologous pairs of chromosomes are aligned in numerical order from longest to shortest, the geneticist obtains a digital image, identifies each chromosome, and manually arranges the chromosomes into this pattern (Figure **24.3.1**).

At its most basic, the karyogram may reveal genetic abnormalities in which an individual has too many or too few chromosomes per cell. Examples of this are Down Syndrome, which is identified by a third copy of chromosome 21, and Turner Syndrome, which is characterized by the presence of only one X chromosome in women instead of the normal two. Geneticists can also identify large deletions or insertions of DNA. For instance, Jacobsen Syndrome—which involves distinctive facial features as well as heart and bleeding defects—is identified by a deletion on chromosome 11. Finally, the karyotype can pinpoint translocations, which occur when a segment of genetic material breaks from one chromosome and reattaches to another chromosome or to a different part of the same chromosome. Translocations are implicated in certain cancers, including chronic myelogenous leukemia.

During Mendel's lifetime, inheritance was an abstract concept that could only be inferred by performing crosses and observing the traits expressed by offspring. By observing a karyogram, today's geneticists can actually visualize the chromosomal composition of an individual to confirm or predict genetic abnormalities in offspring, even before birth.

Disorders in Chromosome Number

Of all of the chromosomal disorders, abnormalities in chromosome number are the most obviously identifiable from a karyogram. Disorders of chromosome number include the duplication or loss of entire chromosomes, as well as changes in the number of complete sets of chromosomes. They are caused by nondisjunction, which occurs when pairs of homologous chromosomes or sister chromatids fail to separate during meiosis. Misaligned or incomplete synapsis, or a dysfunction of the spindle apparatus that facilitates chromosome migration, can cause nondisjunction. The risk of nondisjunction occurring increases with the age of the parents.

Nondisjunction can occur during either meiosis I or II, with differing results (Figure **24.3.2**). If homologous chromosomes fail to separate during meiosis I, the result is two gametes that lack that particular chromosome and two gametes with two copies of the chromosome. If sister chromatids fail to separate during meiosis II, the result is one gamete that lacks that chromosome, two normal gametes with one copy of the chromosome, and one gamete with two copies of the chromosome.

Art Connection

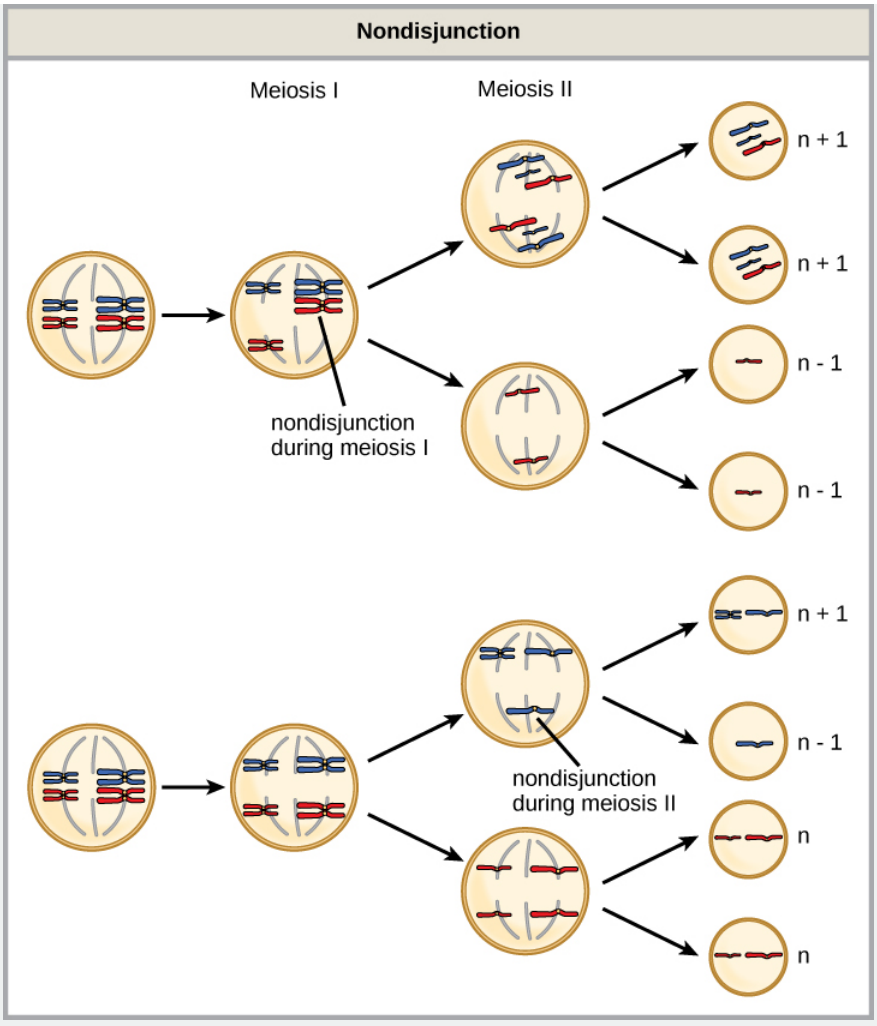


Figure **24.3.2**: Nondisjunction occurs when homologous chromosomes or sister chromatids fail to separate during meiosis, resulting in an abnormal chromosome number. Nondisjunction may occur during meiosis I or meiosis II.

Which of the following statements about nondisjunction is true?

A. Nondisjunction only results in gametes with n+1 or n–1 chromosomes.
B. Nondisjunction occurring during meiosis II results in 50 percent normal gametes.
C. Nondisjunction during meiosis I results in 50 percent normal gametes.
D. Nondisjunction always results in four different kinds of gametes.

Aneuploidy

An individual with the appropriate number of chromosomes for their species is called euploid; in humans, euploidy corresponds to 22 pairs of autosomes and one pair of sex chromosomes. An individual with an error in chromosome number is described as aneuploid, a term that includes monosomy (loss of one chromosome) or trisomy (gain of an extraneous chromosome). Monosomic human zygotes missing any one copy of an autosome invariably fail to develop to birth because they lack essential genes. This underscores the importance of “gene dosage” in humans. Most autosomal trisomies also fail to develop to birth; however, duplications of some of the smaller chromosomes (13, 15, 18, 21, or 22) can result in offspring that survive for several weeks to many years. Trisomic individuals suffer from a different type of genetic imbalance: an excess in gene dose. Individuals with an extra chromosome may synthesize an abundance of the gene products encoded by that chromosome. This extra dose (150 percent) of specific genes can lead to a number of functional challenges and often precludes development. The most common trisomy among viable births is that of chromosome 21, which corresponds to Down Syndrome. Individuals with this inherited disorder are characterized by short stature and stunted digits, facial distinctions that include a broad skull and large tongue, and significant

developmental delays. The incidence of Down syndrome is correlated with maternal age; older women are more likely to become pregnant with fetuses carrying the trisomy 21 genotype (Figure **24.3.3**).

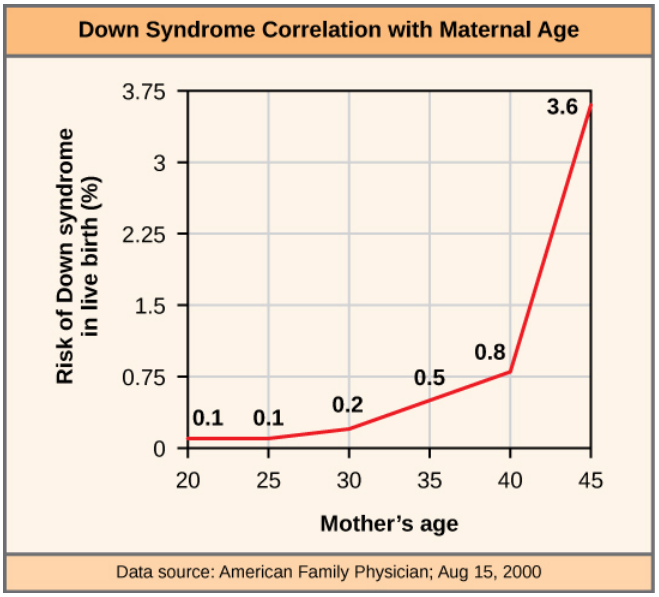


Figure **24.3.3**: The incidence of having a fetus with trisomy 21 increases dramatically with maternal age.

Link to Learning



Visualize the addition of a chromosome that leads to Down syndrome in this video simulation.

Polyploidy

An individual with more than the correct number of chromosome sets (two for diploid species) is called polyploid. For instance, fertilization of an abnormal diploid egg with a normal haploid sperm would yield a triploid zygote. Polyploid animals are extremely rare, with only a few examples among the flatworms, crustaceans, amphibians, fish, and lizards. Polyploid animals are sterile because meiosis cannot proceed normally and instead produces mostly aneuploid daughter cells that cannot yield viable zygotes. Rarely, polyploid animals can reproduce asexually by haplodiploidy, in which an unfertilized egg divides mitotically to produce offspring. In contrast, polyploidy is very common in the plant kingdom, and polyploid plants tend to be larger and more robust than euploids of their species (Figure **24.3.4**).



Figure **24.3.4**: As with many polyploid plants, this triploid orange daylily (*Hemerocallis fulva*) is particularly large and robust, and grows flowers with triple the number of petals of its diploid counterparts. (credit: Steve Karg)

Sex Chromosome Nondisjunction in Humans

Humans display dramatic deleterious effects with autosomal trisomies and monosomies. Therefore, it may seem counterintuitive that human females and males can function normally, despite carrying different numbers of the X chromosome. Rather than a gain or loss of autosomes, variations in the number of sex chromosomes are associated with relatively mild effects. In part, this occurs because of a molecular process called X inactivation. Early in development, when female mammalian embryos consist of just a few thousand cells (relative to trillions in the newborn), one X chromosome in each cell inactivates by tightly condensing into a quiescent (dormant) structure called a Barr body. The chance that an X chromosome (maternally or paternally derived) is inactivated in each cell is random, but once the inactivation occurs, all cells derived from that one will have the same inactive X chromosome or Barr body. By this process, females compensate for their double genetic dose of X chromosome. In so-called "tortoiseshell" cats, embryonic X inactivation is observed as color variegation (Figure **24.3.5**). Females that are heterozygous for an X-linked coat color gene will express one of two different coat colors over different regions of their body, corresponding to whichever X chromosome is inactivated in the embryonic cell progenitor of that region.



Figure 24.3.5: In cats, the gene for coat color is located on the X chromosome. In the embryonic development of female cats, one of the two X chromosomes is randomly inactivated in each cell, resulting in a tortoiseshell pattern if the cat has two different alleles for coat color. Male cats, having only one X chromosome, never exhibit a tortoiseshell coat color. (credit: Michael Bodega)

An individual carrying an abnormal number of X chromosomes will inactivate all but one X chromosome in each of her cells. However, even inactivated X chromosomes continue to express a few genes, and X chromosomes must reactivate for the proper maturation of female ovaries. As a result, X-chromosomal abnormalities are typically associated with mild mental and physical defects, as well as sterility. If the X chromosome is absent altogether, the individual will not develop in utero.

Several errors in sex chromosome number have been characterized. Individuals with three X chromosomes, called triplo-X, are phenotypically female but express developmental delays and reduced fertility. The XXY genotype, corresponding to one type of Klinefelter syndrome, corresponds to phenotypically male individuals with small testes, enlarged breasts, and reduced body hair. More complex types of Klinefelter syndrome exist in which the individual has as many as five X chromosomes. In all types, every X chromosome except one undergoes inactivation to compensate for the excess genetic dosage. This can be seen as several Barr bodies in each cell nucleus. Turner syndrome, characterized as an X0 genotype (i.e., only a single sex chromosome), corresponds to a phenotypically female individual with short stature, webbed skin in the neck region, hearing and cardiac impairments, and sterility.

Duplications and Deletions

In addition to the loss or gain of an entire chromosome, a chromosomal segment may be duplicated or lost. Duplications and deletions often produce offspring that survive but exhibit physical and mental abnormalities. Duplicated chromosomal segments may fuse to existing chromosomes or may be free in the nucleus. Cri-du-chat (from the French for “cry of the cat”) is a syndrome associated with nervous system abnormalities and identifiable physical features that result from a deletion of most of 5p (the small arm of chromosome 5) (Figure 24.3.6). Infants with this genotype emit a characteristic high-pitched cry on which the disorder’s name is based.

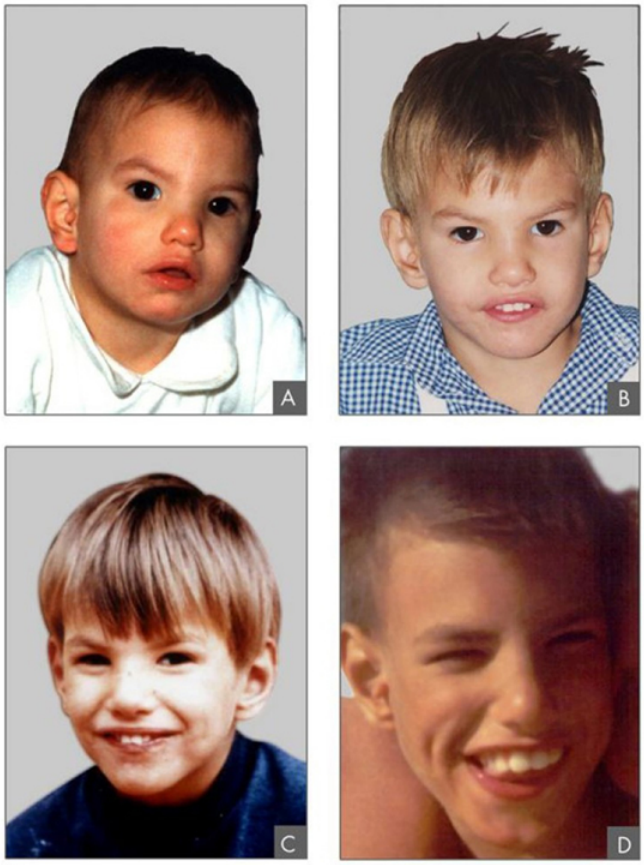


Figure **24.3.6**: This individual with cri-du-chat syndrome is shown at two, four, nine, and 12 years of age. (credit: Paola Cerruti Mainardi)

Chromosomal Structural Rearrangements

Cytologists have characterized numerous structural rearrangements in chromosomes, but chromosome inversions and translocations are the most common. Both are identified during meiosis by the adaptive pairing of rearranged chromosomes with their former homologs to maintain appropriate gene alignment. If the genes carried on two homologs are not oriented correctly, a recombination event could result in the loss of genes from one chromosome and the gain of genes on the other. This would produce aneuploid gametes.

Chromosome Inversions

A chromosome inversion is the detachment, 180° rotation, and reinsertion of part of a chromosome. Inversions may occur in nature as a result of mechanical shear, or from the action of transposable elements (special DNA sequences capable of facilitating the rearrangement of chromosome segments with the help of enzymes that cut and paste DNA sequences). Unless they disrupt a gene sequence, inversions only change the orientation of genes and are likely to have more mild effects than aneuploid errors. However, altered gene orientation can result in functional changes because regulators of gene expression could be moved out of position with respect to their targets, causing aberrant levels of gene products.

An inversion can be pericentric and include the centromere, or paracentric and occur outside of the centromere (). A pericentric inversion that is asymmetric about the centromere can change the relative lengths of the chromosome arms, making these inversions easily identifiable.

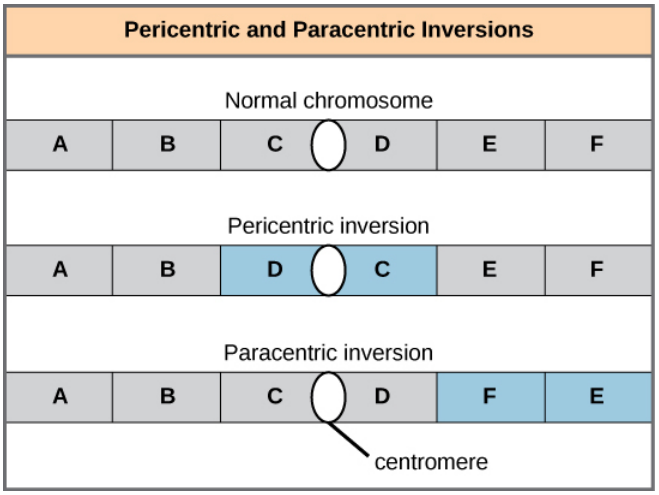


Figure **24.3.7**: Pericentric inversions include the centromere, and paracentric inversions do not. A pericentric inversion can change the relative lengths of the chromosome arms; a paracentric inversion cannot.

When one homologous chromosome undergoes an inversion but the other does not, the individual is described as an inversion heterozygote. To maintain point-for-point synapsis during meiosis, one homolog must form a loop, and the other homolog must mold around it. Although this topology can ensure that the genes are correctly aligned, it also forces the homologs to stretch and can be associated with regions of imprecise synapsis (Figure **24.3.8**).

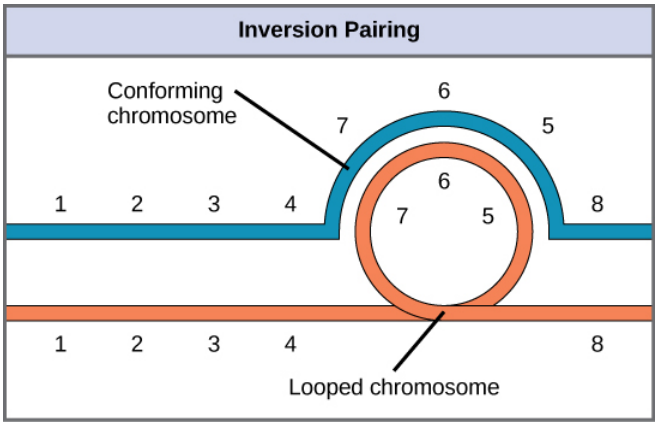


Figure **24.3.8**: When one chromosome undergoes an inversion but the other does not, one chromosome must form an inverted loop to retain point-for-point interaction during synapsis. This inversion pairing is essential to maintaining gene alignment during meiosis and to allow for recombination.

Evolution Connection: The Chromosome 18 Inversion

Not all structural rearrangements of chromosomes produce nonviable, impaired, or infertile individuals. In rare instances, such a change can result in the evolution of a new species. In fact, a pericentric inversion in chromosome 18 appears to have contributed to the evolution of humans. This inversion is not present in our closest genetic relatives, the chimpanzees. Humans and chimpanzees differ cytogenetically by pericentric inversions on several chromosomes and by the fusion of two separate chromosomes in chimpanzees that correspond to chromosome two in humans.

The pericentric chromosome 18 inversion is believed to have occurred in early humans following their divergence from a common ancestor with chimpanzees approximately five million years ago. Researchers characterizing this inversion have suggested that approximately 19,000 nucleotide bases were duplicated on 18p, and the duplicated region inverted and reinserted on chromosome 18 of an ancestral human.

A comparison of human and chimpanzee genes in the region of this inversion indicates that two genes—*ROCK1* and *USP14*—that are adjacent on chimpanzee chromosome 17 (which corresponds to human chromosome 18) are more distantly positioned on human chromosome 18. This suggests that one of the inversion breakpoints occurred between these two genes. Interestingly, humans and chimpanzees express *USP14* at distinct levels in specific cell types, including cortical cells and

fibroblasts. Perhaps the chromosome 18 inversion in an ancestral human repositioned specific genes and reset their expression levels in a useful way. Because both *ROCK1* and *USP14* encode cellular enzymes, a change in their expression could alter cellular function. It is not known how this inversion contributed to hominid evolution, but it appears to be a significant factor in the divergence of humans from other primates.[1]

Translocations

A translocation occurs when a segment of a chromosome dissociates and reattaches to a different, nonhomologous chromosome. Translocations can be benign or have devastating effects depending on how the positions of genes are altered with respect to regulatory sequences. Notably, specific translocations have been associated with several cancers and with schizophrenia. Reciprocal translocations result from the exchange of chromosome segments between two nonhomologous chromosomes such that there is no gain or loss of genetic information (Figure **24.3.9**).

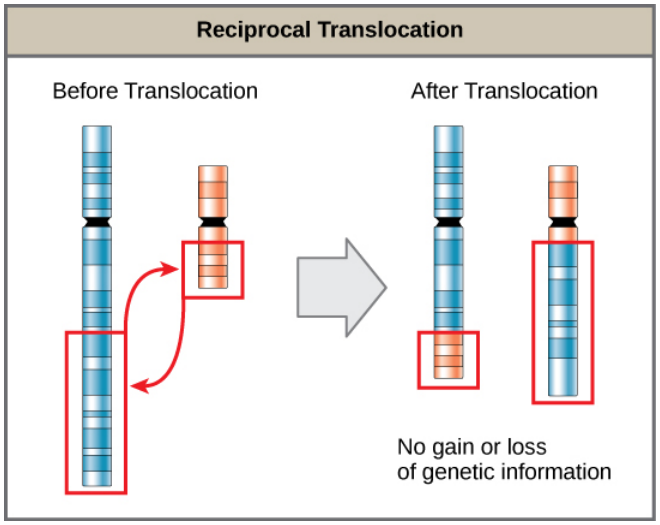


Figure **24.3.9**: A reciprocal translocation occurs when a segment of DNA is transferred from one chromosome to another, nonhomologous chromosome. (credit: modification of work by National Human Genome Research/USA)

Summary

The number, size, shape, and banding pattern of chromosomes make them easily identifiable in a karyogram and allows for the assessment of many chromosomal abnormalities. Disorders in chromosome number, or aneuploidies, are typically lethal to the embryo, although a few trisomic genotypes are viable. Because of X inactivation, aberrations in sex chromosomes typically have milder phenotypic effects. Aneuploidies also include instances in which segments of a chromosome are duplicated or deleted. Chromosome structures may also be rearranged, for example by inversion or translocation. Both of these aberrations can result in problematic phenotypic effects. Because they force chromosomes to assume unnatural topologies during meiosis, inversions and translocations are often associated with reduced fertility because of the likelihood of nondisjunction.

Art Connections

Figure **24.3.2**: Which of the following statements about nondisjunction is true?

A. Nondisjunction only results in gametes with n+1 or n–1 chromosomes.
B. Nondisjunction occurring during meiosis II results in 50 percent normal gametes.
C. Nondisjunction during meiosis I results in 50 percent normal gametes.
D. Nondisjunction always results in four different kinds of gametes.

Answer

B.

Footnotes

1. 1 Violaine Goidts et al., “Segmental duplication associated with the human-specific inversion of chromosome 18: a further example of the impact of segmental duplications on karyotype and genome evolution in primates,” *Human Genetics*. 115 (2004):116-122

Glossary

aneuploid
individual with an error in chromosome number; includes deletions and duplications of chromosome segments

autosome
any of the non-sex chromosomes

chromosome inversion
detachment, 180° rotation, and reinsertion of a chromosome arm

euploid
individual with the appropriate number of chromosomes for their species

karyogram
photographic image of a karyotype

karyotype
number and appearance of an individuals chromosomes; includes the size, banding patterns, and centromere position

monosomy
otherwise diploid genotype in which one chromosome is missing

nondisjunction
failure of synapsed homologs to completely separate and migrate to separate poles during the first cell division of meiosis

paracentric
inversion that occurs outside of the centromere

pericentric
inversion that involves the centromere

polyploid
individual with an incorrect number of chromosome sets

translocation
process by which one segment of a chromosome dissociates and reattaches to a different, nonhomologous chromosome

trisomy
otherwise diploid genotype in which one entire chromosome is duplicated

X inactivation
condensation of X chromosomes into Barr bodies during embryonic development in females to compensate for the double genetic dose

24.3.1: Eukaryotic Transcription

24.3.2: Perspectives on the Phylogenetic Tree

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24.3.1: Eukaryotic Transcription

Skills to Develop

- List the steps in eukaryotic transcription
- Discuss the role of RNA polymerases in transcription
- Compare and contrast the three RNA polymerases
- Explain the significance of transcription factors

Prokaryotes and eukaryotes perform fundamentally the same process of transcription, with a few key differences. The most important difference between prokaryotes and eukaryotes is the latter's membrane-bound nucleus and organelles. With the genes bound in a nucleus, the eukaryotic cell must be able to transport its mRNA to the cytoplasm and must protect its mRNA from degrading before it is translated. Eukaryotes also employ three different polymerases that each transcribe a different subset of genes. Eukaryotic mRNAs are usually monogenic, meaning that they specify a single protein.

Initiation of Transcription in Eukaryotes

Unlike the prokaryotic polymerase that can bind to a DNA template on its own, eukaryotes require several other proteins, called transcription factors, to first bind to the promoter region and then help recruit the appropriate polymerase.

The Three Eukaryotic RNA Polymerases

The features of eukaryotic mRNA synthesis are markedly more complex those of prokaryotes. Instead of a single polymerase comprising five subunits, the eukaryotes have three polymerases that are each made up of 10 subunits or more. Each eukaryotic polymerase also requires a distinct set of transcription factors to bring it to the DNA template.

RNA polymerase I is located in the nucleolus, a specialized nuclear substructure in which ribosomal RNA (rRNA) is transcribed, processed, and assembled into ribosomes (Table **24.3.1.1**). The rRNA molecules are considered structural RNAs because they have a cellular role but are not translated into protein. The rRNAs are components of the ribosome and are essential to the process of translation. RNA polymerase I synthesizes all of the rRNAs except for the 5S rRNA molecule. The "S" designation applies to "Svedberg" units, a nonadditive value that characterizes the speed at which a particle sediments during centrifugation.

Table **24.3.1.1**: Locations, Products, and Sensitivities of the Three Eukaryotic RNA Polymerases

RNA Polymerase	Cellular Compartment	Product of Transcription	α-Amanitin Sensitivity
I	Nucleolus	All rRNAs except 5S rRNA	Insensitive
II	Nucleus	All protein-coding nuclear pre-mRNAs	Extremely sensitive
III	Nucleus	5S rRNA, tRNAs, and small nuclear RNAs	Moderately sensitive

RNA polymerase II is located in the nucleus and synthesizes all protein-coding nuclear pre-mRNAs. Eukaryotic pre-mRNAs undergo extensive processing after transcription but before translation. For clarity, this module's discussion of transcription and translation in eukaryotes will use the term "mRNAs" to describe only the mature, processed molecules that are ready to be translated. RNA polymerase II is responsible for transcribing the overwhelming majority of eukaryotic genes.

RNA polymerase III is also located in the nucleus. This polymerase transcribes a variety of structural RNAs that includes the 5S pre-rRNA, transfer pre-RNAs (pre-tRNAs), and small nuclear pre-RNAs. The tRNAs have a critical role in translation; they serve as the adaptor molecules between the mRNA template and the growing polypeptide chain. Small nuclear RNAs have a variety of functions, including "splicing" pre-mRNAs and regulating transcription factors.

A scientist characterizing a new gene can determine which polymerase transcribes it by testing whether the gene is expressed in the presence of a particular mushroom poison, α-amanitin (table above). Interestingly, α-amanitin produced by *Amanita phalloides*, the

Death Cap mushroom, affects the three polymerases very differently. RNA polymerase I is completely insensitive to α-amanitin, meaning that the polymerase can transcribe DNA in vitro in the presence of this poison. In contrast, RNA polymerase II is extremely sensitive to α-amanitin, and RNA polymerase III is moderately sensitive. Knowing the transcribing polymerase can clue a researcher into the general function of the gene being studied. Because RNA polymerase II transcribes the vast majority of genes, we will focus on this polymerase in our subsequent discussions about eukaryotic transcription factors and promoters.

Structure of an RNA Polymerase II Promoter

Eukaryotic promoters are much larger and more complex than prokaryotic promoters, but both have a TATA box. For example, in the mouse thymidine kinase gene, the TATA box is located at approximately -30 relative to the initiation (+1) site (Figure **24.3.1.1**). For this gene, the exact TATA box sequence is TATAAAA, as read in the 5' to 3' direction on the nontemplate strand. This sequence is not identical to the *E. coli* TATA box, but it conserves the A–T rich element. The thermostability of A–T bonds is low and this helps the DNA template to locally unwind in preparation for transcription.

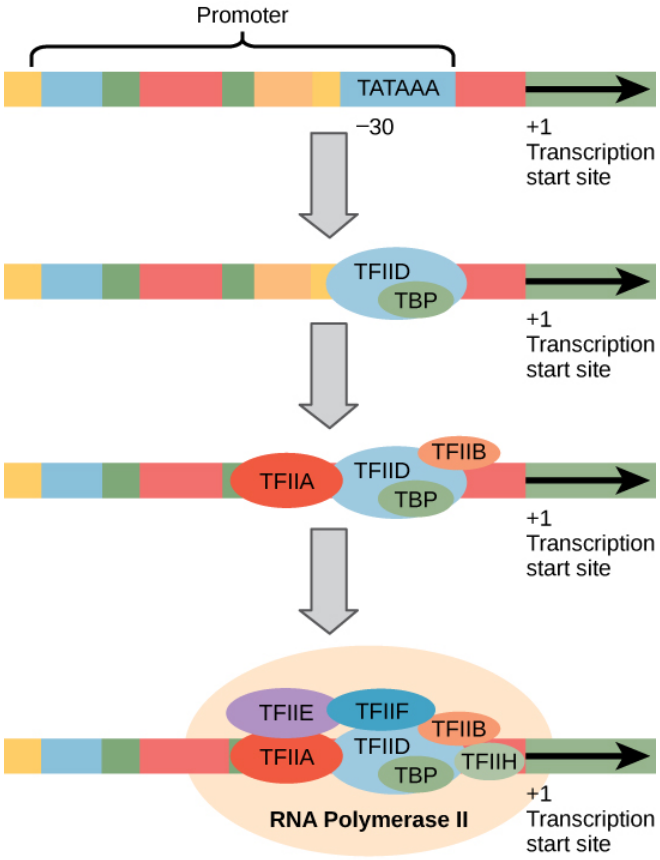


Figure **24.3.1.1**: A generalized promoter of a gene transcribed by RNA polymerase II is shown. Transcription factors recognize the promoter. RNA polymerase II then binds and forms the transcription initiation complex.

Art Connection

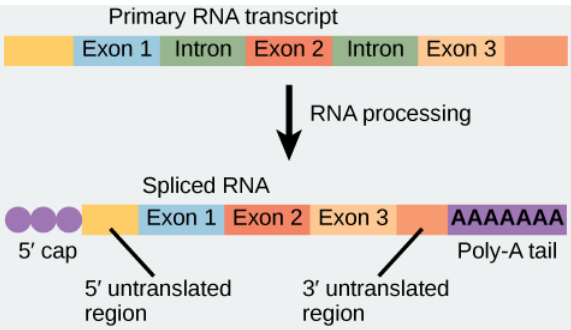


Figure **24.3.1.2**: Eukaryotic mRNA contains introns that must be spliced out. A 5' cap and 3' poly-A tail are also added.

A scientist splices a eukaryotic promoter in front of a bacterial gene and inserts the gene in a bacterial chromosome. Would you expect the bacteria to transcribe the gene?

The mouse genome includes one gene and two pseudogenes for cytoplasmic thymidine kinase. Pseudogenes are genes that have lost their protein-coding ability or are no longer expressed by the cell. These pseudogenes are copied from mRNA and incorporated into the chromosome. For example, the mouse thymidine kinase promoter also has a conserved CAAT box (GGCCAATCT) at approximately -80. This sequence is essential and is involved in binding transcription factors. Further upstream of the TATA box, eukaryotic promoters may also contain one or more GC-rich boxes (GGCG) or octamer boxes (ATTTGCAT). These elements bind cellular factors that increase the efficiency of transcription initiation and are often identified in more “active” genes that are constantly being expressed by the cell.

Transcription Factors for RNA Polymerase II

The complexity of eukaryotic transcription does not end with the polymerases and promoters. An army of basal transcription factors, enhancers, and silencers also help to regulate the frequency with which pre-mRNA is synthesized from a gene. Enhancers and silencers affect the efficiency of transcription but are not necessary for transcription to proceed. Basal transcription factors are crucial in the formation of a preinitiation complex on the DNA template that subsequently recruits RNA polymerase II for transcription initiation.

The names of the basal transcription factors begin with “TFII” (this is the transcription factor for RNA polymerase II) and are specified with the letters A–J. The transcription factors systematically fall into place on the DNA template, with each one further stabilizing the preinitiation complex and contributing to the recruitment of RNA polymerase II.

The processes of bringing RNA polymerases I and III to the DNA template involve slightly less complex collections of transcription factors, but the general theme is the same. Eukaryotic transcription is a tightly regulated process that requires a variety of proteins to interact with each other and with the DNA strand. Although the process of transcription in eukaryotes involves a greater metabolic investment than in prokaryotes, it ensures that the cell transcribes precisely the pre-mRNAs that it needs for protein synthesis.

Evolution Connection: The Evolution of Promoters

The evolution of genes may be a familiar concept. Mutations can occur in genes during DNA replication, and the result may or may not be beneficial to the cell. By altering an enzyme, structural protein, or some other factor, the process of mutation can transform functions or physical features. However, eukaryotic promoters and other gene regulatory sequences may evolve as well. For instance, consider a gene that, over many generations, becomes more valuable to the cell. Maybe the gene encodes a structural protein that the cell needs to synthesize in abundance for a certain function. If this is the case, it would be beneficial to the cell for that gene’s promoter to recruit transcription factors more efficiently and increase gene expression.

Scientists examining the evolution of promoter sequences have reported varying results. In part, this is because it is difficult to infer exactly where a eukaryotic promoter begins and ends. Some promoters occur within genes; others are located very far upstream, or even downstream, of the genes they are regulating. However, when researchers limited their examination to human core promoter sequences that were defined experimentally as sequences that bind the preinitiation complex, they found that promoters evolve even faster than protein-coding genes.

> It is still unclear how promoter evolution might correspond to the evolution of humans or other higher organisms. However, the evolution of a promoter to effectively make more or less of a given gene product is an intriguing alternative to the evolution of the genes themselves.[1]

Promoter Structures for RNA Polymerases I and III

In eukaryotes, the conserved promoter elements differ for genes transcribed by RNA polymerases I, II, and III. RNA polymerase I transcribes genes that have two GC-rich promoter sequences in the -45 to +20 region. These sequences alone are sufficient for transcription initiation to occur, but promoters with additional sequences in the region from -180 to -105 upstream of the initiation site will further enhance initiation. Genes that are transcribed by RNA polymerase III have upstream promoters or promoters that occur within the genes themselves.

Eukaryotic Elongation and Termination

Following the formation of the preinitiation complex, the polymerase is released from the other transcription factors, and elongation is allowed to proceed as it does in prokaryotes with the polymerase synthesizing pre-mRNA in the 5' to 3' direction. As discussed previously, RNA polymerase II transcribes the major share of eukaryotic genes, so this section will focus on how this polymerase accomplishes elongation and termination.

Although the enzymatic process of elongation is essentially the same in eukaryotes and prokaryotes, the DNA template is more complex. When eukaryotic cells are not dividing, their genes exist as a diffuse mass of DNA and proteins called chromatin. The DNA is tightly packaged around charged histone proteins at repeated intervals. These DNA–histone complexes, collectively called nucleosomes, are regularly spaced and include 146 nucleotides of DNA wound around eight histones like thread around a spool.

For polynucleotide synthesis to occur, the transcription machinery needs to move histones out of the way every time it encounters a nucleosome. This is accomplished by a special protein complex called FACT, which stands for “facilitates chromatin transcription.” This complex pulls histones away from the DNA template as the polymerase moves along it. Once the pre-mRNA is synthesized, the FACT complex replaces the histones to recreate the nucleosomes.

The termination of transcription is different for the different polymerases. Unlike in prokaryotes, elongation by RNA polymerase II in eukaryotes takes place 1,000–2,000 nucleotides beyond the end of the gene being transcribed. This pre-mRNA tail is subsequently removed by cleavage during mRNA processing. On the other hand, RNA polymerases I and III require termination signals. Genes transcribed by RNA polymerase I contain a specific 18-nucleotide sequence that is recognized by a termination protein. The process of termination in RNA polymerase III involves an mRNA hairpin similar to rho-independent termination of transcription in prokaryotes.

Summary

Transcription in eukaryotes involves one of three types of polymerases, depending on the gene being transcribed. RNA polymerase II transcribes all of the protein-coding genes, whereas RNA polymerase I transcribes rRNA genes, and RNA polymerase III transcribes rRNA, tRNA, and small nuclear RNA genes. The initiation of transcription in eukaryotes involves the binding of several transcription factors to complex promoter sequences that are usually located upstream of the gene being copied. The mRNA is synthesized in the 5' to 3' direction, and the FACT complex moves and reassembles nucleosomes as the polymerase passes by. Whereas RNA polymerases I and III terminate transcription by protein- or RNA hairpin-dependent methods, RNA polymerase II transcribes for 1,000 or more nucleotides beyond the gene template and cleaves the excess during pre-mRNA processing.

Art Connections

Figure **24.3.1.2**: A scientist splices a eukaryotic promoter in front of a bacterial gene and inserts the gene in a bacterial chromosome. Would you expect the bacteria to transcribe the gene?

Answer

No. Prokaryotes use different promoters than eukaryotes.

Footnotes

1. 1 H Liang et al., “Fast evolution of core promoters in primate genomes,” *Molecular Biology and Evolution* 25 (2008): 1239–44.

Glossary

CAAT box
(GGCCAATCT) essential eukaryotic promoter sequence involved in binding transcription factors

FACT
complex that “facilitates chromatin transcription” by disassembling nucleosomes ahead of a transcribing RNA polymerase II and reassembling them after the polymerase passes by

GC-rich box
(GGCG) nonessential eukaryotic promoter sequence that binds cellular factors to increase the efficiency of transcription; may be present several times in a promoter

Octamer box
(ATTTGCAT) nonessential eukaryotic promoter sequence that binds cellular factors to increase the efficiency of transcription; may be present several times in a promoter

preinitiation complex
cluster of transcription factors and other proteins that recruit RNA polymerase II for transcription of a DNA template

small nuclear RNA
molecules synthesized by RNA polymerase III that have a variety of functions, including splicing pre-mRNAs and regulating transcription factors

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24.3.2: Perspectives on the Phylogenetic Tree

Skills to Develop

- Describe horizontal gene transfer
- Illustrate how prokaryotes and eukaryotes transfer genes horizontally
- Identify the web and ring models of phylogenetic relationships and describe how they differ from the original phylogenetic tree concept

The concepts of phylogenetic modeling are constantly changing. It is one of the most dynamic fields of study in all of biology. Over the last several decades, new research has challenged scientists' ideas about how organisms are related. New models of these relationships have been proposed for consideration by the scientific community.

Many phylogenetic trees have been shown as models of the evolutionary relationship among species. Phylogenetic trees originated with Charles Darwin, who sketched the first phylogenetic tree in 1837 (Figure **24.3.2.1**a), which served as a pattern for subsequent studies for more than a century. The concept of a phylogenetic tree with a single trunk representing a common ancestor, with the branches representing the divergence of species from this ancestor, fits well with the structure of many common trees, such as the oak (Figure **24.3.2.1**b). However, evidence from modern DNA sequence analysis and newly developed computer algorithms has caused skepticism about the validity of the standard tree model in the scientific community.



(a) (b)

Figure **24.3.2.1**: The (a) concept of the "tree of life" goes back to an 1837 sketch by Charles Darwin. Like an (b) oak tree, the "tree of life" has a single trunk and many branches. (credit b: modification of work by "Amada44"/Wikimedia Commons)

Limitations to the Classic Model

Classical thinking about prokaryotic evolution, included in the classic tree model, is that species evolve clonally. That is, they produce offspring themselves with only random mutations causing the descent into the variety of modern-day and extinct species known to science. This view is somewhat complicated in eukaryotes that reproduce sexually, but the laws of Mendelian genetics explain the variation in offspring, again, to be a result of a mutation within the species. The concept of genes being transferred between unrelated species was not considered as a possibility until relatively recently. Horizontal gene transfer (HGT), also known as lateral gene transfer, is the transfer of genes between unrelated species. HGT has been shown to be an ever-present phenomenon, with many evolutionists postulating a major role for this process in evolution, thus complicating the simple tree model. Genes have been shown to be passed between species which are only distantly related using standard phylogeny, thus adding a layer of complexity to the understanding of phylogenetic relationships.

The various ways that HGT occurs in prokaryotes is important to understanding phylogenies. Although at present HGT is not viewed as important to eukaryotic evolution, HGT does occur in this domain as well. Finally, as an example of the ultimate gene transfer, theories of genome fusion between symbiotic or endosymbiotic organisms have been proposed to explain an event of great importance—the evolution of the first eukaryotic cell, without which humans could not have come into existence.

Horizontal Gene Transfer

Horizontal gene transfer (HGT) is the introduction of genetic material from one species to another species by mechanisms other than the vertical transmission from parent(s) to offspring. These transfers allow even distantly related species to share genes, influencing their phenotypes. It is thought that HGT is more prevalent in prokaryotes, but that only about 2% of the prokaryotic genome may be transferred by this process. Some researchers believe such estimates are premature: the actual importance of HGT to evolutionary processes must be viewed as a work in progress. As the phenomenon is investigated more thoroughly, it may be revealed to be more common. Many scientists believe that HGT and mutation appear to be (especially in prokaryotes) a significant source of genetic variation, which is the raw material for the process of natural selection. These transfers may occur between any two species that share an intimate relationship (Table **24.3.2.1**).

Table **24.3.2.1**: Summary of Mechanisms of Prokaryotic and Eukaryotic HGT

	Mechanism	Mode of Transmission	Example
Prokaryotes	transformation	DNA uptake	many prokaryotes
	transduction	bacteriophage (virus)	bacteria
	conjugation	pilus	many prokaryotes
	gene transfer agents	phage-like particles	purple non-sulfur bacteria
Eukaryotes	from food organisms	unknown	aphid
	jumping genes	transposons	rice and millet plants
	epiphytes/parasites	unknown	yew tree fungi
	from viral infections		

HGT in Prokaryotes

The mechanism of HGT has been shown to be quite common in the prokaryotic domains of Bacteria and Archaea, significantly changing the way their evolution is viewed. The majority of evolutionary models, such as in the Endosymbiont Theory, propose that eukaryotes descended from multiple prokaryotes, which makes HGT all the more important to understanding the phylogenetic relationships of all extant and extinct species.

The fact that genes are transferred among common bacteria is well known to microbiology students. These gene transfers between species are the major mechanism whereby bacteria acquire resistance to antibiotics. Classically, this type of transfer has been thought to occur by three different mechanisms:

1. Transformation: naked DNA is taken up by a bacteria
2. Transduction: genes are transferred using a virus
3. Conjugation: the use of a hollow tube called a pilus to transfer genes between organisms

More recently, a fourth mechanism of gene transfer between prokaryotes has been discovered. Small, virus-like particles called gene transfer agents (GTAs) transfer random genomic segments from one species of prokaryote to another. GTAs have been shown to be responsible for genetic changes, sometimes at a very high frequency compared to other evolutionary processes. The first GTA was characterized in 1974 using purple, non-sulfur bacteria. These GTAs, which are thought to be bacteriophages that lost the ability to reproduce on their own, carry random pieces of DNA from one organism to another. The ability of GTAs to act with high frequency has been demonstrated in controlled studies using marine bacteria. Gene transfer events in marine prokaryotes, either by

GTAs or by viruses, have been estimated to be as high as 10^{13} per year in the Mediterranean Sea alone. GTAs and viruses are thought to be efficient HGT vehicles with a major impact on prokaryotic evolution.

As a consequence of this modern DNA analysis, the idea that eukaryotes evolved directly from Archaea has fallen out of favor. While eukaryotes share many features that are absent in bacteria, such as the TATA box (found in the promoter region of many genes), the discovery that some eukaryotic genes were more homologous with bacterial DNA than Archaea DNA made this idea less tenable. Furthermore, the fusion of genomes from Archaea and Bacteria by endosymbiosis has been proposed as the ultimate event in eukaryotic evolution.

HGT in Eukaryotes

Although it is easy to see how prokaryotes exchange genetic material by HGT, it was initially thought that this process was absent in eukaryotes. After all, prokaryotes are but single cells exposed directly to their environment, whereas the sex cells of multicellular organisms are usually sequestered in protected parts of the body. It follows from this idea that the gene transfers between multicellular eukaryotes should be more difficult. Indeed, it is thought that this process is rarer in eukaryotes and has a much smaller evolutionary impact than in prokaryotes. In spite of this fact, HGT between distantly related organisms has been demonstrated in several eukaryotic species, and it is possible that more examples will be discovered in the future.

In plants, gene transfer has been observed in species that cannot cross-pollinate by normal means. Transposons or “jumping genes” have been shown to transfer between rice and millet plant species. Furthermore, fungal species feeding on yew trees, from which the anti-cancer drug TAXOL® is derived from the bark, have acquired the ability to make taxol themselves, a clear example of gene transfer.

In animals, a particularly interesting example of HGT occurs within the aphid species (Figure **24.3.2.2**). Aphids are insects that vary in color based on carotenoid content. Carotenoids are pigments made by a variety of plants, fungi, and microbes, and they serve a variety of functions in animals, who obtain these chemicals from their food. Humans require carotenoids to synthesize vitamin A, and we obtain them by eating orange fruits and vegetables: carrots, apricots, mangoes, and sweet potatoes. On the other hand, aphids have acquired the ability to make the carotenoids on their own. According to DNA analysis, this ability is due to the transfer of fungal genes into the insect by HGT, presumably as the insect consumed fungi for food. A carotenoid enzyme called a desaturase is responsible for the red coloration seen in certain aphids, and it has been further shown that when this gene is inactivated by mutation, the aphids revert back to their more common green color (Figure **24.3.2.2**).



(a) (b)

Figure **24.3.2.2**: (a) Red aphids get their color from red carotenoid pigment. Genes necessary to make this pigment are present in certain fungi, and scientists speculate that aphids acquired these genes through HGT after consuming fungi for food. If genes for making carotenoids are inactivated by mutation, the aphids revert back to (b) their green color. Red coloration makes the aphids a lot more conspicuous to predators, but evidence suggests that red aphids are more resistant to insecticides than green ones. Thus, red aphids may be more fit to survive in some environments than green ones. (credit a: modification of work by Benny Mazur; credit b: modification of work by Mick Talbot)

Genome Fusion and the Evolution of Eukaryotes

Scientists believe the ultimate in HGT occurs through genome fusion between different species of prokaryotes when two symbiotic organisms become endosymbiotic. This occurs when one species is taken inside the cytoplasm of another species, which ultimately results in a genome consisting of genes from both the endosymbiont and the host. This mechanism is an aspect of the Endosymbiont Theory, which is accepted by a majority of biologists as the mechanism whereby eukaryotic cells obtained their mitochondria and chloroplasts. However, the role of endosymbiosis in the development of the nucleus is more controversial. Nuclear and mitochondrial DNA are thought to be of different (separate) evolutionary origin, with the mitochondrial DNA being derived from the circular genomes of bacteria that were engulfed by ancient prokaryotic cells. Mitochondrial DNA can be regarded as the smallest chromosome. Interestingly enough, mitochondrial DNA is inherited only from the mother. The mitochondrial DNA degrades in sperm when the sperm degrades in the fertilized egg or in other instances when the mitochondria located in the flagellum of the sperm fails to enter the egg.

Within the past decade, the process of genome fusion by endosymbiosis has been proposed by James Lake of the UCLA/NASA Astrobiology Institute to be responsible for the evolution of the first eukaryotic cells (Figure **24.3.2.3**a). Using DNA analysis and a new mathematical algorithm called conditioned reconstruction (CR), his laboratory proposed that eukaryotic cells developed from an endosymbiotic gene fusion between two species, one an Archaea and the other a Bacteria. As mentioned, some eukaryotic genes resemble those of Archaea, whereas others resemble those from Bacteria. An endosymbiotic fusion event, such as Lake has proposed, would clearly explain this observation. On the other hand, this work is new and the CR algorithm is relatively unsubstantiated, which causes many scientists to resist this hypothesis.

More recent work by Lake (Figure **24.3.2.3**b) proposes that gram-negative bacteria, which are unique within their domain in that they contain two lipid bilayer membranes, indeed resulted from an endosymbiotic fusion of archaeal and bacterial species. The double membrane would be a direct result of the endosymbiosis, with the endosymbiont picking up the second membrane from the host as it was internalized. This mechanism has also been used to explain the double membranes found in mitochondria and chloroplasts. Lake's work is not without skepticism, and the ideas are still debated within the biological science community. In addition to Lake's hypothesis, there are several other competing theories as to the origin of eukaryotes. How did the eukaryotic nucleus evolve? One theory is that the prokaryotic cells produced an additional membrane that surrounded the bacterial chromosome. Some bacteria have the DNA enclosed by two membranes; however, there is no evidence of a nucleolus or nuclear pores. Other proteobacteria also have membrane-bound chromosomes. If the eukaryotic nucleus evolved this way, we would expect one of the two types of prokaryotes to be more closely related to eukaryotes.

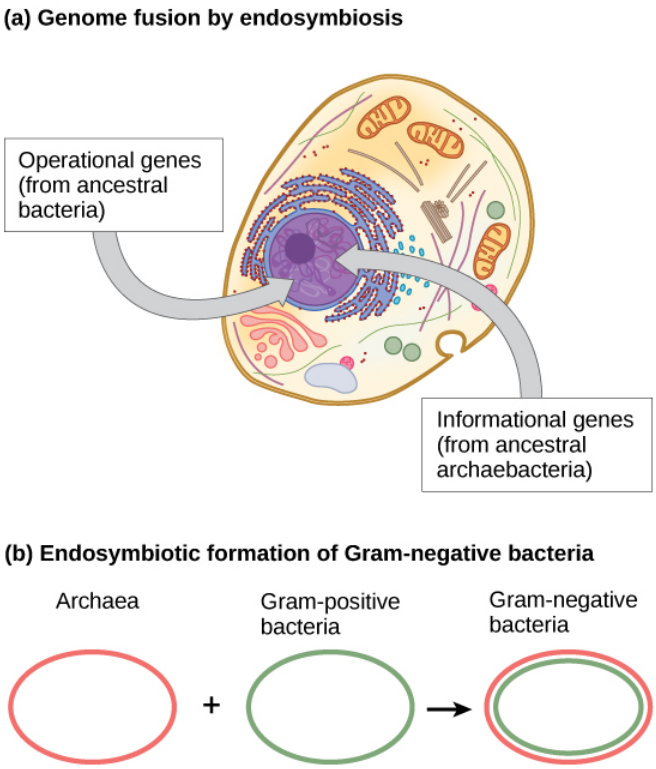


Figure **24.3.2.3**: The theory that mitochondria and chloroplasts are endosymbiotic in origin is now widely accepted. More controversial is the proposal that (a) the eukaryotic nucleus resulted from the fusion of archaeal and bacterial genomes, and that (b) Gram-negative bacteria, which have two membranes, resulted from the fusion of Archaea and Gram-positive bacteria, each of which has a single membrane.

The nucleus-first hypothesis proposes that the nucleus evolved in prokaryotes first (Figure **24.3.2.4**a), followed by a later fusion of the new eukaryote with bacteria that became mitochondria. The mitochondria-first hypothesis proposes that mitochondria were first established in a prokaryotic host (Figure **24.3.2.4**b), which subsequently acquired a nucleus, by fusion or other mechanisms, to become the first eukaryotic cell. Most interestingly, the eukaryote-first hypothesis proposes that prokaryotes actually evolved from eukaryotes by losing genes and complexity (Figure **24.3.2.4**c). All of these hypotheses are testable. Only time and more experimentation will determine which hypothesis is best supported by data.

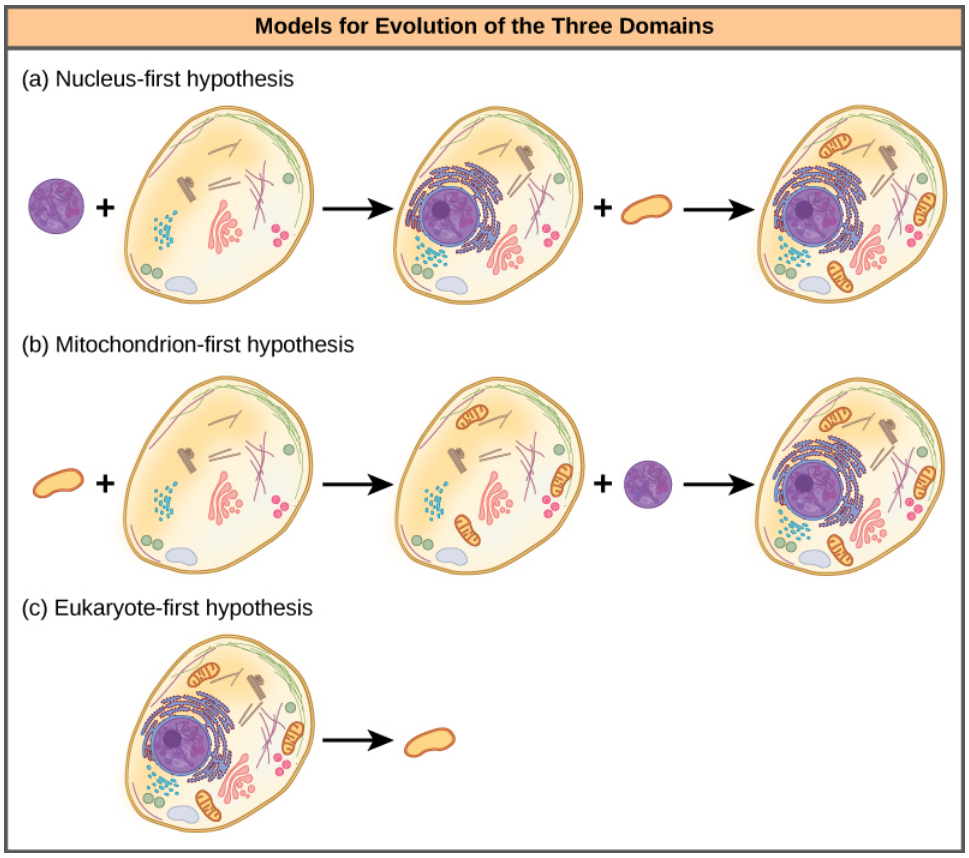
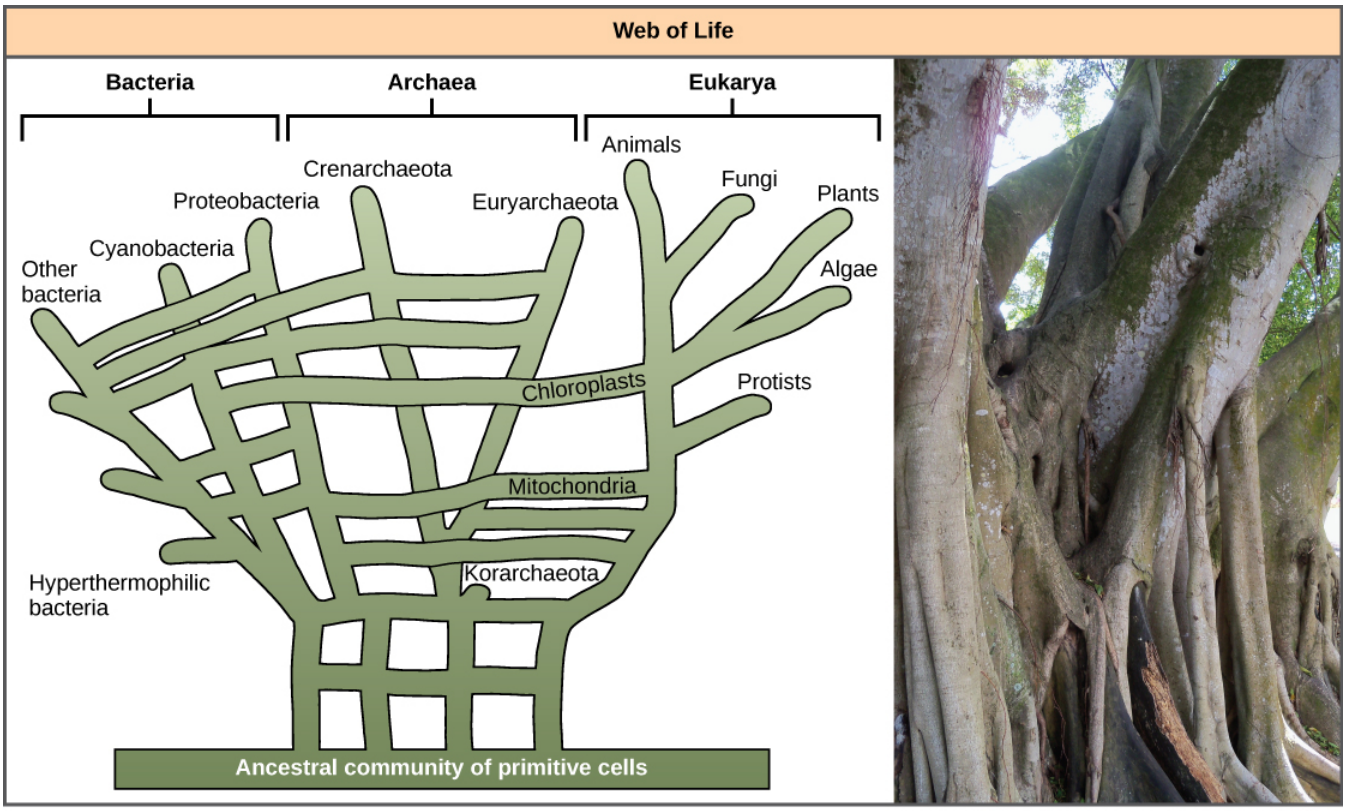


Figure **24.3.2.4**: Three alternate hypotheses of eukaryotic and prokaryotic evolution are (a) the nucleus-first hypothesis, (b) the mitochondrion-first hypothesis, and (c) the eukaryote-first hypothesis.

Web and Network Models

The recognition of the importance of HGT, especially in the evolution of prokaryotes, has caused some to propose abandoning the classic "tree of life" model. In 1999, W. Ford Doolittle proposed a phylogenetic model that resembles a web or a network more than a tree. The hypothesis is that eukaryotes evolved not from a single prokaryotic ancestor, but from a pool of many species that were sharing genes by HGT mechanisms. As shown in Figure **24.3.2.5**a, some individual prokaryotes were responsible for transferring the bacteria that caused mitochondrial development to the new eukaryotes, whereas other species transferred the bacteria that gave rise to chloroplasts. This model is often called the "web of life." In an effort to save the tree analogy, some have proposed using the *Ficus* tree (Figure **24.3.2.5**b) with its multiple trunks as a phylogenetic to represent a diminished evolutionary role for HGT.



(a) (b)

Figure **24.3.2.5**: In the (a) phylogenetic model proposed by W. Ford Doolittle, the “tree of life” arose from a community of ancestral cells, has multiple trunks, and has connections between branches where horizontal gene transfer has occurred. Visually, this concept is better represented by (b) the multi-trunked **Ficus** than by the single trunk of the oak similar to the tree drawn by Darwin (Figure **24.3.2.1**). (credit b: modification of work by "psyberartist"/Flickr)

Ring of Life Models

Others have proposed abandoning any tree-like model of phylogeny in favor of a ring structure, the so-called “ring of life” (Figure **24.3.2.6**); a phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes. Lake, again using the conditioned reconstruction algorithm, proposes a ring-like model in which species of all three domains—Archaea, Bacteria, and Eukarya—evolved from a single pool of gene-swapping prokaryotes. His laboratory proposes that this structure is the best fit for data from extensive DNA analyses performed in his laboratory, and that the ring model is the only one that adequately takes HGT and genomic fusion into account. However, other phylogeneticists remain highly skeptical of this model.

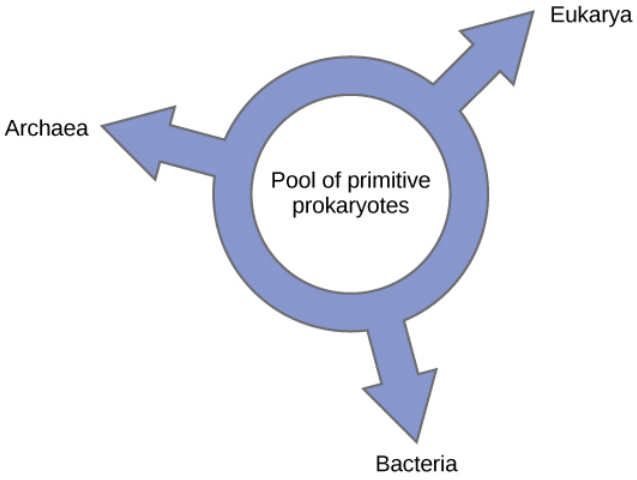


Figure **24.3.2.6**: According to the "ring of life" phylogenetic model, the three domains of life evolved from a pool of primitive prokaryotes.

In summary, the "tree of life" model proposed by Darwin must be modified to include HGT. Does this mean abandoning the tree model completely? Even Lake argues that all attempts should be made to discover some modification of the tree model to allow it to accurately fit his data, and only the inability to do so will sway people toward his ring proposal.

This doesn't mean a tree, web, or a ring will correlate completely to an accurate description of phylogenetic relationships of life. A consequence of the new thinking about phylogenetic models is the idea that Darwin's original conception of the phylogenetic tree is too simple, but made sense based on what was known at the time. However, the search for a more useful model moves on: each model serving as hypotheses to be tested with the possibility of developing new models. This is how science advances. These models are used as visualizations to help construct hypothetical evolutionary relationships and understand the massive amount of data being analyzed.

Summary

The phylogenetic tree, first used by Darwin, is the classic "tree of life" model describing phylogenetic relationships among species, and the most common model used today. New ideas about HGT and genome fusion have caused some to suggest revising the model to resemble webs or rings.

Glossary

eukaryote-first hypothesis
proposal that prokaryotes evolved from eukaryotes

gene transfer agent (GTA)
bacteriophage-like particle that transfers random genomic segments from one species of prokaryote to another

genome fusion
fusion of two prokaryotic genomes, presumably by endosymbiosis

horizontal gene transfer (HGT)
(also, lateral gene transfer) transfer of genes between unrelated species

mitochondria-first hypothesis
proposal that prokaryotes acquired a mitochondrion first, followed by nuclear development

nucleus-first hypothesis
proposal that prokaryotes acquired a nucleus first, and then the mitochondrion

ring of life

phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes

web of life

phylogenetic model that attempts to incorporate the effects of horizontal gene transfer on evolution

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24.4: Gene Function and Expression Patterns

Learning Objectives

- Understand the concept of gene expression.
- Understand transcriptional regulation of gene expression.
- Understand epigenetic gene regulation.4
- Understand post-transcriptional regulation of gene expression (RNA level).
- Understand post-translational protein modification and regulation.

Introduction

Every cell in a plant contains the same genetic information, the same set of genes. Yet Therefore different sets of genes are required for the various functions of different cells or tissues, as well as for plant responses to environmental stimuli or stresses. This is achieved by regulating the activity of genes according to the physiological demands of a particular cell type, developmental stage, or environmental condition. This regulation of activity is known as **gene expression**.

The term **expression** can be used in different ways that are sometimes confusing. Typically, if a gene product is produced, the gene is considered “expressed”. However, it sometimes occurs that a transcript might be produced but not a protein, or that a protein is produced but it is in an inactive state. In such cases, although a gene product is produced, the biological activity encoded by that gene is not present. For the purposes of this section, the key point is how the biological activity encoded by a gene is regulated.

The expression of genes in specific plant cells, tissues, and organs and the timing of this expression require a precise level of regulation. Expression, or genetic function, can potentially be regulated at any of the steps from transcription, RNA processing, translation, through post-translational protein modification, as discussed in lesson 1. Regulation can be qualitative (i.e. gene expression is either “on” or “off”) or quantitative (i.e. expression levels can be modulated “up” or “down”). Fluctuations in the intensities of external stimuli coupled to changes that occur at the genomic level result in different developmental outcomes or physiological states. Regulation of gene expression at the level of transcription can be brought about through chromatin and histone modifications. Also, a gene sequence can be differentially spliced to produce mRNA products of variable lengths leading to new protein products with novel functions. Some genes do not encode proteins but short forms of RNAs with regulatory functions such as induction of flowering. Finally, proteins products can be subjected to modifications such as phosphorylation or dephosphorylation to alter their functions, or can be completely degraded to turn off a gene.

Transcriptional gene regulation

Since transcription is the first step in gene expression, it makes sense in terms of cellular economy, to regulate expression at this point, and in fact this is one of the most important regulatory points. We already described the involvement of RNA polymerase in the transcription process, but in fact there are other protein factors that are required. Proteins involved in transcriptional regulation are known as transcription factors. It is the interaction of these transcription factors with specific DNA sequences that regulate the process of gene transcription.

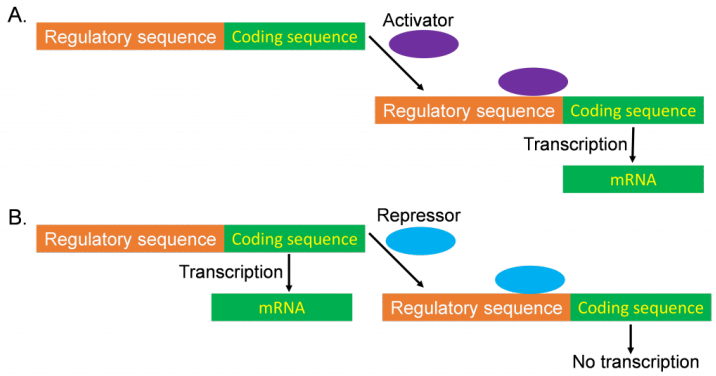


Figure 1. Positive regulation of gene transcription (A) occurs when a transcriptional factor (activator) turns on gene transcription. Negative regulation of gene transcription (B) occurs when a transcription factor (repressor) turns off gene transcription. Image by Walter Suza.

A. The concept of differential (regulated) gene expression

As just described, not every gene is expressed all the time. When a gene displays different levels of expression in different circumstances, this is known as **differential expression**. Circumstances that might apply include, but are not limited to, different plant tissues (root vs. leaf), different developmental stages (germination vs. reproductive development), or in response to different environmental stimuli (cold stress or pathogen attack).

The term differential expression can also be used to compare the expression of different genes. If two genes show different expression patterns (among plant tissues or in response to environmental stimuli), they are considered differentially expressed, whereas genes that showed very similar patterns of expression would be considered **co-expressed**.

B. Promoters

As mentioned, transcription is regulated through the interactions of proteins, transcription factors, with specific DNA sequences. Most regulatory DNA sequences governing gene transcription are located on the 5′ border of the transcribed region. This region is called the gene **promoter**.

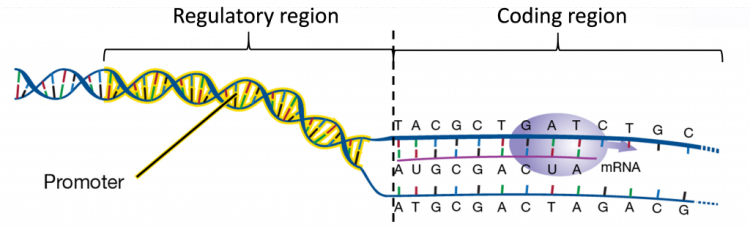


Figure 2. Promoters are part of gene regulatory sequence. Adapted from Illustration by NIH-NHGRI.

Promoters contain a core, which is required for the binding of the “basal transcriptional machinery”, including RNA polymerase. The “TATA” box, with a consensus sequence TATAA, is located within the core promoter, usually 25-30 nucleotides upstream of the transcription initiation site. Promoters also contain regulatory sequences that determine when, where, and to what level genes are transcribed. Promoters can vary in length from a hundred to a few thousand nucleotides.

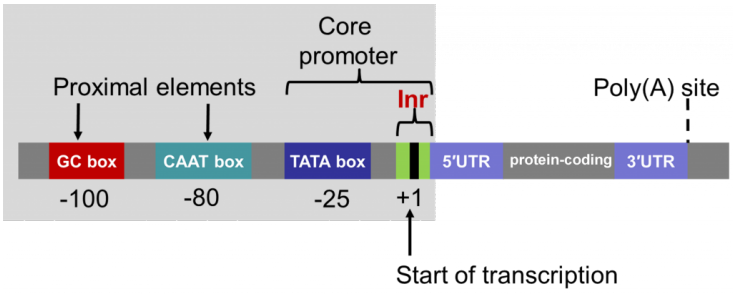


Figure 3. The promoter contains core and proximal elements. Image by Walter Suza.

The full promoter sequences of different genes that are expressed in a similar manner may be different. However, such promoters often contain short sequence “motifs” that are similar, referred to as cis elements. Early work (Benfy and Chua, 1990) to understand the function of different promoter elements in regulating gene expression in plant cells and tissues revealed that various combinations of cis elements are able to be interpreted by the cell and control gene expression. Sometimes cis elements promote gene transcription and sometimes they function to restrict transcription of genes in particular cells and tissues.

Promoter analysis is facilitated through the use of **reporter genes**. The reporter gene produces effects that are easily identifiable and quantifiable, which can be used to determine the function of a regulatory region of another gene (promoter, promoter elements, or enhancers) in cells, tissues, or organs. Such analyses are critical to crop biotechnology where targeted expression of genes in particular tissues is often desirable. To test whether a promoter is effective in conferring the expression of a gene to a particular tissue, scientists fuse the putative promoter to a reporter gene and introduce the promoter-gene fusion into plants. An example of a reporter is the GUS gene, which encodes a GUS enzyme (beta-Glucuronidase) that, when expressed, produces a blue color upon addition of a substrate. Figure 1 shows an example of GUS expression in maize seed using two promoters that act either in the endosperm or the embryo.

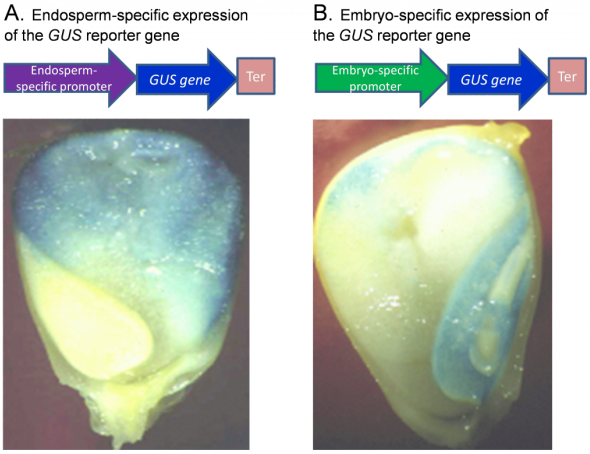


Figure 4. Promoters direct the expression of genes in plant tissues. (A) The expression of the GUS transgene is restricted to the endosperm of maize seed by an endosperm-specific promoter. (B) When the GUS transgene is fused to an embyo-specific promoter the activity of the GUS enzyme (production of the blue coloration after addition of a GUS substrate) is restricted to the embryonic tissue. Image by Shui-zhang Fei.

C. Enhancers

Enhancers are DNA sequences that increase the rate of transcription of a gene when they are present, although alone they cannot cause transcription to occur. Enhancers are usually position and orientation independent. Although they are normally located upstream of the promoter, they can also be located on the 3’ region of the gene or even with the coding region. Enhancers can increase the transcription when added to genes that they are not normally associated with. This is a useful property for biotechnology, allowing promoters to be manipulated for increased levels of transcriptional regulation. Some enhancers function at all times in all cells and tissues and they are referred to as constitutive. Other enhancers function in specific tissues at specific developmental stages. Some are active only in response to environmental signals. The AACCA enhancer on the promoter of soybean β-conglycinin gene encoding a seed storage protein functions specifically in seeds. Enhancers are thought to interact with specific nuclear proteins involved in transcription. For example, enhancers might facilitate the binding of transcription factors and direct these factors along the DNA strand to the direction of the promoter. Alternatively, enhancers may facilitate changes in DNA structure such as modification of the chromatin structure.

The counterpart of an enhancer is a **silencer**. Silencers have all the properties just described for enhancers, except they function to dampen, or decrease, the levels of transcription controlled by a promoter.

D. Transcription factors

RNA polymerase binds the promoter at the TATA box and in cooperation with other proteins drives gene transcription. The proteins that interact with RNA polymerase to facilitate its binding to the promoter and to regulate its activity are known as **transcription**

factors. Some transcription factors, known as “basal transcription factors” are fundamental to RNA polymerase binding and function, and are expressed in all living cells.

Other transcription factors bind to cis regulatory DNA sequences of promoters, enhancers or silencers. These proteins interact in complex ways with the basal transcription machinery, to regulate the activity of RNA polymerase, and therefore gene transcription. Thus, transcription factors regulate when or where individual genes are expressed, and to what level.

Transcription factors can function as either positive or negative regulators. That is, they can either function to induce (increase) gene transcription or to repress it. The consequence of many transcription factors depends on their interactions with other proteins. Two factors together may be required for gene activity, and exclusion of one of the factors in space and time offers a mechanism for differential gene expression. Some transcription factors might function as a positive regulator in one context but as a negative regulator in another context, depending on what other cis elements and/or transcription factors might be present.

Epigenetic regulation

A. Chromatin structure and histone modification

At the molecular level chromatin is a product of an ordered and tight packaging of the double stranded DNA around nucleosomes (a core of proteins named histones), and an association with additional proteins.

Transcriptional regulation often involves modification of chromatin structure mediated by post-translational regulation (changes in acetylation and methylation) of histones. Histone acetylation involves the addition of acetyl groups and when histones are heavily acetylated the DNA is less tightly associated with them. This often correlates with increased transcriptional activity of specific genes. The idea is that when DNA is loosely associated with histones, it is more accessible to transcription factors that require interaction with the DNA to initiate transcription. Consequently, histone deacetylation (removal of acetyl groups) by histone deacetylase enzymes (for example, FLD, p462) stabilizes nucleosomes and represses transcription. On the other hand, histone acetylation by histone ecetyltransferase destabilizes nucleosomes and promotes transcription.

As described in the text, another form of histone modification is the addition of methyl groups to histone proteins, which similarly regulates chromatin condensation or decondensation.

B. DNA methylation

The nucleotide bases of DNA can be modified by the attachment of methyl groups at various locations. The addition of these methyl groups happens after the DNA has been synthesized and is controlled by enzymes that add methyl moieties to specific regions of DNA. The most common modified nucleotide base is C5 methylcytosine (m5C) due the activity of the enzyme DNA (cytosine-5) methyltransferase (MET). MET recognizes the unmethylated newly-replicated DNA strand and incorporates a methyl group if the template strand was methylated (hemimethylated).

Methylation status is correlated with gene expression (Figure 5) as demonstrated by the low level of methylation in regions of the genome undergoing active transcription.

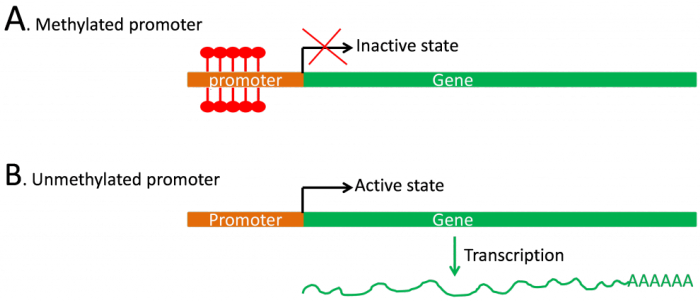


Figure 5. Absence of methylation correlates with gene expression. (A) The promoter region may be methylated during development or environmental conditions such that a gene is inactivated. (B) The same gene is activated upon the removal of the methyl groups.

Studies have shown that altering a plant’s overall DNA methylation status can affect growth and development. For example, cold treatment (vernalization) induces flowering in biannuals such as Arabidopsis and winter wheat, and lowers the level of methylation of particular genes. Also, treating plants with the drug 5 azacytidine prevents methylation at the 5 position of cytosine and

stimulates flowering. Recent studies also suggest a relationship between epigenetic gene regulation and heterosis, with hybrids showing higher global levels of transcription, higher histone acetylation levels and lower DNA methylation levels (reviewed in He et al., 2011).

RNA-level regulation

Regulation of gene expression occurs at many levels, including post-transcriptionally. From the standpoint of the expression level for a given gene, a critical factor is the level of fully processed, mature mRNA. When we consider the level of the mature form a particular transcript at any given time reflects the steady state balance between synthesis, processing and degradation. The Post-transcriptional regulation of RNA occurs through several mechanisms.

RNA stability and degradation

The control of mRNA degradation rate, or turnover, is an important regulatory mechanism in gene expression. As mentioned, the level of a particular transcript at any given time reflects the steady state balance between synthesis and degradation. Thus, even though a gene may be transcribed at a high rate, a high rate of RNA turnover could effectively shut off the gene. The stability of mRNA can be regulated globally, to affect all or most transcripts, or it can be very specific to a particular mRNA. Regulated mRNA turnover may be particularly important in plants, since plants cannot move to avoid harsh environmental conditions and stresses are known to induce specific changes in RNA stability. Other factors such as light and plant hormones are also known to regulate mRNA stability.

The degradation of mRNA is catalyzed by enzymes called ribonucleases. Ribonucleases include exonucleases, which degrade only from one end of the transcript, and endonucleases, which can attack the mRNA molecule internally.

Therefore, controlling ribonuclease access to the mRNA substrate is an important regulatory mechanism in gene expression. This control is achieved through various mechanisms including, controlling the amount of nucleases present, regulating the activity of the nuclease, sequestering the nuclease to particular cellular locations to restrict its access to RNA, and to control the stability of the mRNA by decreasing accessibility to nuclease.

Four regions of an mRNA are important for its overall stability. These include, the 5′ untranslated region and the cap, coding region, 3’ untranslated region, and the poly(A) tail.

The cap at the 5′ end protects the mRNA from exonucleases that degrade RNA from the 5′ to the 3′ direction.

The 3′ untranslated region may contain short sequences that influence mRNA stability. For example, the repetition of the sequence AUUUA in the 3′ untranslated region of many animal and plant genes is associated with mRNAs with short half-lives (the time it takes for half the RNA to be degraded, after transcription is stopped).

The poly(A) tail increases mRNA stability but is not sufficient alone. It only provides stability when bound by proteins such as poly(A) binding protein (PABP). Test-tube experiments have shown that, removing PABP from a stable mRNA destabilizes it, while adding back purified PABP restores stability.

Translational regulation

As described, for most genes it is the protein product that performs the biological function. As such, regulating the amount of protein production effectively regulates gene expression. There are several known mechanisms by which the process of translation is known to be regulated. A detailed consideration of these mechanisms is beyond the scope of this course, but in general it is important to bear in mind their importance. For example, under certain stress conditions, “normal” translation is halted and only mRNAs related to stress tolerance are selectively permitted to be translated into proteins. This selective translation is important to allow plants to quickly respond to stress and to conserve energy under stress conditions.

Translation of mRNAs can play an important role in determining their overall stability. Mutations that add premature stop codons often lead to rapid degradation of the mRNA. Ribonucleases (figure 9) or other factors involved in degradation may recognize the number or spacing of ribosomes on an mRNA, and degrade those that are not produced properly. This may help prevent synthesis of proteins with incorrect functions which will negatively impact cellular processes. Errors during transcription could add or omit nucleotides which would alter the proper codon sequence creating mutant proteins.

Protein-level regulation

After translation, proteins are subject to a variety of modifications that can regulate their activity. There are many different ways by which proteins can potentially be modified and thereby regulated, and only a few of the basic mechanisms will be considered here.

Common types of post-translational modifications

The first mechanism is covalent modification by the addition of various chemical groups. A wide variety of groups can be involved, including small organic groups (methylation, acetylation) lipids (myristoylation, farnesylation, palmitylation), carbohydrates (glycosylation, glucosylation), small proteins (ubiquitination, sumoylation) and inorganic molecules (phosphorylation, sulfation). Such covalent modifications are generally accomplished by the activity of enzymes specialized to perform these modifications. Many of these modifications are also reversible; that is these groups can be added to a protein and subsequently removed. Phosphorylation is a particularly noteworthy reversible modification that is common in the regulation of many proteins. Enzymes that add phosphate groups to other proteins are called protein kinases, and those that remove phosphates are called phosphatases. As such, protein kinases and phosphatases are central to many cellular regulatory systems.

A second common mechanism of protein modification is through proteolytic cleavage. Proteolysis occurs as part of the general turnover of cellular proteins, which is required to eliminate damaged proteins and recycle amino acids. Proteolysis is important for the processing of certain proteins, for example in the removal of the signal peptide of proteins targeted to specific cellular compartments. It can also occur in a highly specific manner whereby particular proteins are targeted for degradation or for cleavage at a specific site within the protein. Proteolytic modifications are non-reversible.

Proteins can undergo modification through complex formation. Such complexes can occur among proteins or between a protein and a cofactor.

Proteins can also be modified according to conditions of the cellular environment. The redox state can result in oxidation or reduction of proteins, particularly of sulfhydryl side groups. Cellular pH can affect the charge of ionizable side groups.

Common types of protein regulation

All of the above mentioned types of protein modification can alter protein conformations and thus have regulatory consequences on protein function or activity. Protein regulation is highly complex and there are a myriad of different ways by which this occurs. Again we will just briefly consider a few of the more common mechanisms.

One major way protein modification can regulate protein function is by **altering their activity**. This can be true for many types of proteins including, but not limited to, enzymes, transcription factors, signaling proteins, and structural proteins.

Cells are **compartmentalized** into several membrane bound organelles, including the nucleus, chloroplasts, mitochondria, peroxisomes, endoplasmic reticulum (ER), golgi, and vacuoles. Each of these compartments performs unique metabolic functions that require a set of proteins. Compartmentation is regulated for some proteins. For example, upon exposure to light the phytochrome protein moves into the nucleus where it affects the expression of light-regulated genes.

Proteolytic processing is involved in several important regulatory processes. Many proteins are synthesized in an inactive form that requires proteolytic cleavage for activation. The full-length translation product before processing is often called the precursor, or a preprotein. As mentioned, cells contain membrane-bound compartments. Since membranes are impermeable to most proteins, an active mechanism is necessary to move a protein across a membrane. For proper delivery to their organellar destinations, specific amino acid sequences, called target signals must be present in a protein (to serve as an “address”). For example, entry into the chloroplast is achieved by the presence of a target signal called the transit peptide. This is at the amino terminal end of the protein and is proteolytically cleaved during import.

Another example of proteolytic processing is seen in a plant defense response in members of the solanaceae (for example, tomato and potato). An 18-amino acid peptide hormone called systemin is secreted by plant cells that are damaged by insects or mechanical wounding. Systemin production by wounded cells is required to induce the synthesis of proteins involved in defense. Systemin induces defense responses in wounded cells, and throughout the plant. Analogous to animal peptide hormones (e.g., insulin), systemin is initially synthesized as a much larger (200 amino acids) precursor called pro-systemin. Pro-system is inactive; however, upon wounding it undergoes proteolytic cleavage to produce activated systemin.

Targeted protein degradation

The amount of protein present in a cell or tissue is determined by both its rate of synthesis and its rate of degradation. Therefore, protein degradation is an important mechanism by which the plant can regulate biological activity (i.e., a genetic function). For example, one way to shut down a metabolic pathway is by degrading one of the key enzymes controlling the rate of the entire pathway. Therefore, protein degradation is an essential component of gene regulation to meet cellular demands for growth, development, and defense.

Protein degradation must be carefully controlled to fine tune gene expression to allow plants to adapt to new environmental conditions. Often, cells will adopt several complex mechanisms for proteolytic degradation of proteins. Enzymes that cleave or degrade proteins are referred to as proteases. For example, plant vacuoles are rich in proteases that play a similar function in protein degradation as that of lysosomes in animal cells. Protease activity must be tightly regulated to prevent accidental degradation of essential proteins. Sequestering proteases in particular organelles like the vacuole separates them from other organelles and is one of to control their activity.

An important mechanism by which specific proteins are targeted for degradation is through ubiquitin-mediated proteasomal degradation. The proteasome is a large complex of multiple protein subunits that have a protease activity to degrade proteins. Proteins get marked for proteasomal degradation with a small protein called ubiquitin. Ubiquitin is covalently attached to specific proteins in response to environmental or developmental signals. This allows plants to quickly adapt to changing conditions by eliminating proteins whose functions are not advantageous under the new conditions. For example, the photoreceptor phytochrome mentioned above becomes targeted for degradation when light is no longer available. This allows plants to change their physiological functions going from daylight to night conditions. Protein degradation by the proteasome system is also an important regulatory mechanism for plant hormone signaling, for example the signaling of the defense hormone jasmonic acid, and growth hormone gibberellic acid.

Proteins have lifetimes that range from a few minutes to weeks or more. Cells continuously make proteins from and break them down to amino acids. One of the functions of protein degradation is to eliminate aberrant or damaged proteins which could harm the cell. The second function is to facilitate the recycling of amino acids. For example, most of the amino acids required for growth of the seedling are derived from the degradation of seed storage proteins. Conversely, in annual crop plants, many of the amino acids in seed storage proteins are derived from proteins degraded in leaves and other plant parts during senescence.

Lesson Summary

The expression of genes in specific plant cells, tissues, and organs and the timing of this expression require a precise level of regulation. A single promoter may not be sufficient to regulate the expression of such gene(s) in space and time. Therefore, coding regions with the same function may have different promoters, and such genes are referred to as differentially regulated. Most regulatory sequences governing gene expression are located on the 5’ border of the coding region. Transcription is often initiated between 20 and 60 nucleotides upstream of the ATG start site. Enhancers are usually position and orientation independent. Although they are normally located upstream of the promoter, they can also be located on the 3’ region of the gene or even with the coding region. Enhancers can increase the transcription when added to genes that they are not associated with. RNA polymerase binds the promoter at the TATA box and in cooperation with other proteins drives gene transcription. The proteins that interact with RNA polymerase bind to regulatory sequences upstream and downstream of the transcription site.

Transcription factors can play a regulatory role by determining where individual genes are expressed. Transcriptional regulation often involves modification of chromatin by changes in acetylation and methylation of histone. The nucleotide bases of DNA can be modified by the attachment of methyl groups at various locations. Methylation status is correlated with gene expression. Alternative splicing describes an alternative mechanism of pre-mRNA processing to generate mRNAs that have different combinations of exons. The control of mRNA degradation rate, or turnover, is an important regulatory mechanism in gene expression. RNA interference (RNAi) is a post-transcriptional process involving the degradation of mRNA initiated by the formation of double-stranded RNA (dsRNA) of the target mRNA. Translation of mRNAs can play an important role in determining their overall stability. Mutations that add premature stop codons often lead to rapid degradation of the mRNA. Protein degradation is an essential component of gene regulation to meet cellular demands for growth, development, and defense. The plant can alter the activity of a metabolic pathway, by degrading one of the key enzymes controlling the rate of the entire pathway.

Exercises

1a. Which of the following could alter gene regulation

i. Deleting a promoter
ii. Altering fertilizer application rate
iii. Raising the temperature of the greenhouse
iv. Herbicide application
v. Reduce irrigation frequency

1b. The detection of a gene product, for example, RNA or protein at any one moment is a reflection of the “steady state” of the product. Describe the term “steady state” in this context.

2. You are studying expression of a gene responsible for resistance to a pathogen. You cloned the gene and made antibody to detect the protein it encodes by a procedure called Western blot analysis, and the mRNA by a procedure called reverse transcription PCR. Explain the type of regulation from the scenarios in the table.

Scenarios			
	Not treated with pathogen		**Treated with pathogen**
	mRNA	**Protein**	**mRNA**	**Protein**
1	Absent	Absent	Present	Present
2	Present	Absent	Present	Present
3	Present	Present	Absent	Absent
4	Present	Present	Present	Present

Absent

5

Present

Present

Present

Present

3. You are studying the expression of a gene controlling height in your crop species. You have cloned the gene and are interested in determining its expression in different parts of the plant. You use the RT-PCR procedure as in the previous problem. After the PCR part, you load products on a gel and observe the following pattern. Explain your results in the context of gene regulation.

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- **1.9: Regulation of Gene Expression** by Donald Lee, Marjorie Hanneman, Philip Becraft, Walter Suza is licensed CC BY-NC-SA 4.0. Original source: https://iastate.pressbooks.pub/genagbiotech.

24.5: Applying Comparative Genomics

Recall that every cell in a plant contains the same genetic information. The genetic information of a cell constitutes its genome. Therefore, a genome is made up of genes and their regulatory elements. The genome size varies in different species of animals and plants. For example, the human genome is 3.2 Gb while that of hexaploid wheat is 16 Gb. Certainly, a human is very different from a wheat plant. Despite having a smaller genome, a human can think and move but a wheat plant cannot. What then brings about such stark differences? To answer this question we need to compare the genomes of these two organisms for features such as gene content, organization, and function. This type of research is referred to as comparative genomics. Using bioinformatics programs, genome sequences are aligned and the alignments are examined for their evolutionary relationship. Are they homologous, or do they share a common ancestor? Comparative analysis can also be done for genomes of different strains of a species or species that are distantly related. Differences of genomes can therefore be linked to functional consequences, or phenotypes.

Learning Objectives

- Understand the difference between genetic and physical maps
- Familiarize with comparative genomics tools
- Understand the challenges in comparative genomics
- Familiarize with the application of comparative mapping

Introduction to Structural Genomics

Overview

To conduct comparative genomics we need to know the structure of the genomes we wish to compare. We also need tools/approaches to perform such an analysis. The following sections describe mapping concepts and the fundamentals of comparative genomics.

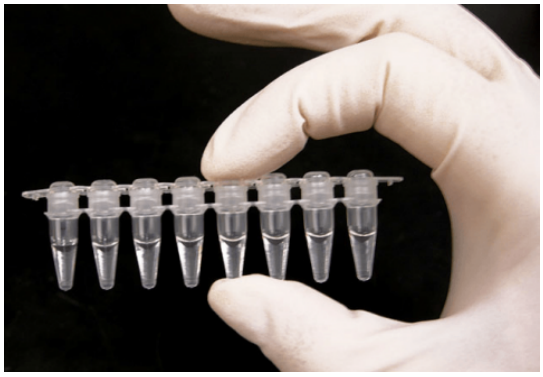


Fig. 1 Sample tubes used in PCR analysis. Photo by Madprime. Liscensed under CC BY-SA 3.0 via Wikimedia Commons.

Genetic Maps

The purpose of genetic maps (also called linkage maps) is to report the length of chromosome intervals, chromosomes, and whole genomes. Genetic maps are based on the rate of recombination. Thus, genetic distances reflect the number of crossover events “observed” for the region, chromosome, or genome of interest. Figure 2 is an example of a genetic map in tomato. Compare the linkage map of molecular markers with the classical genetic map. Molecular markers are super abundance and a single cross allows mapping thousands of markers. Classical maps based on morphological markers are less dense and require integration of maps developed from many crosses. Compare the molecular map with the cytological map on the right. The markers are highly dense in the heterochromatic regions containing the centromeres. This is because of the reduced or suppressed recombination rates in the heterochromatic regions.

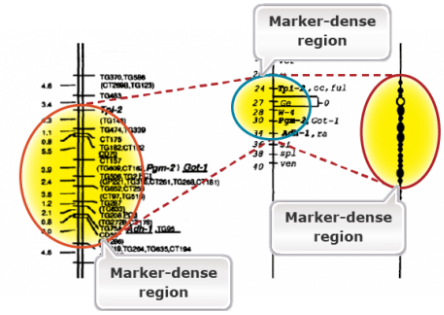


Fig. 2 Molecular linkage map of the tomato genome (left) and comparison with classical map (center) and cytological (pachytene) map (right). Adapted from Tanksley et al. (1992).

Physical Maps

While a genetic map is based on the rates of crossing over and is arbitrary, physical maps provide physical locations of markers. Fluorescence in situ hybridization (FISH) mapping of genetic markers on the pachytene chromosomes can allow us to develop a physical map that corresponds to a genetic map (Fig. 2). Note that in Fig. 2, certain regions are expanded in the genetic map due to higher rates of recombination. The reverse is true for the heterochromatic regions including the centromeres due to reduced recombination rates. Thus, crossover events are not evenly distributed across the chromosomes. Crossover events tend to be suppressed in centromeres and repetitive DNA-rich heterochromatic regions, whereas they are enhanced generally in gene-rich, euchromatic regions. With the sequencing of the entire genomes of crop species, one can now have physical maps of individual chromosomes based on nucleotide sequence. Genome browsers (e.g., Phytozome for soybean) can allow us to navigate the physical maps for gene sequences or molecular markers to the nucleotide level.

Restriction Mapping

Restriction mapping can also allow us to generate a physical map of small DNA fragments cloned in a plasmid vector or larger fragments cloned in BAC (bacterial artificial chromosome) or YAC (yeast artificial chromosome) vectors. This requires determination of the positions of restriction sites on DNA. Consider a piece of linear DNA of 28 kb. The DNA was cut first by *Hind*III alone, then by *Pst*I alone, and, finally, by both *Hind*III and *Pst*I together. The following results were obtained:

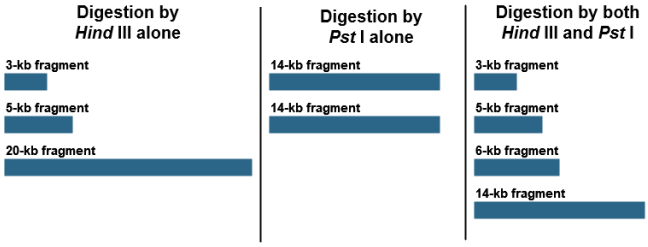


Fig. 3 Results of DNA digestion by different enzymes.

Using these results, draw a map of the *Hind*III and *Pst*I restriction site on this 28-kb piece of DNA, indicating the relative positions of the restriction sites and the distances between them.

Physical Maps and Genome Sequencing

With progress in sequencing technology, an increased number of plant genomes have been sequenced. As a result, physical maps have gained importance. The assembly of the whole-genome sequence relies on both genetic and physical maps for aligning sequenced fragments. Recall in Lesson 5 that BAC and YAC clones are used to prepare genomic libraries for sequencing. The cloned DNA fragments in a YAC or BAC are aligned to form continuous stretches of DNA for subsequent sequencing processes (Fig. 4).

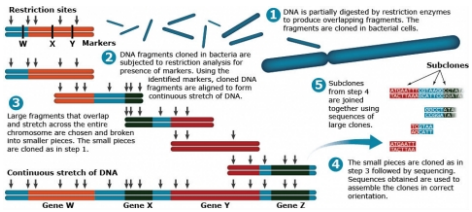


Fig. 4 Physical maps are used to order cloned DNA fragments facilitating genome sequencing. Adapted from Pierce (2010).

Comparative Mapping

Description

Comparative mapping is a study how the genomes relate across species and genera and even families. The concept started with comparative mapping experiments using RFLP markers between two species that led to the discovery of conserved linear orders of marker loci across related species.

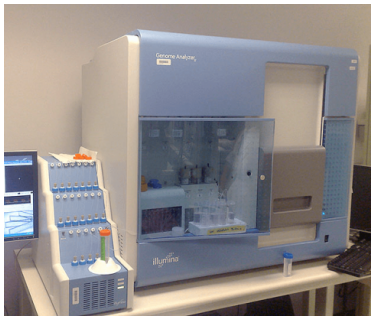


Fig. 5 The Illumina Genome Analyzer II System. Photo by Jon Callas. Licensed under CC BY 2.0 via Wikimedia Commons.

Colinearity and Synteny

The terms synteny and colinearity have been broadly used to describe the presence of conserved gene orders on chromosomes across species, genera or families. Colinearity describes the conservation of the gene order within a chromosomal segment between different species (Fig. 7). The term colinearity is used to explain conservation of loci at the chromosome level, and micro-colinearity at the locus level (Fig. 8). Synteny was originally used to describe the physical mapping without the linkage assumption. Now the term is used to define chromosomal segments or to gene loci in different organisms located on a chromosomal region originating from a common ancestor (Keller and Feuillet 2000). Genetic loci that arose from a common ancestor are defined as orthologous loci; whereas, paralogous loci are evolved through tandem duplication within a species and located side by side in a chromosomal segment. The examples of colinearity and micro-colinearity are shown in Figures 7 and 8, respectively.

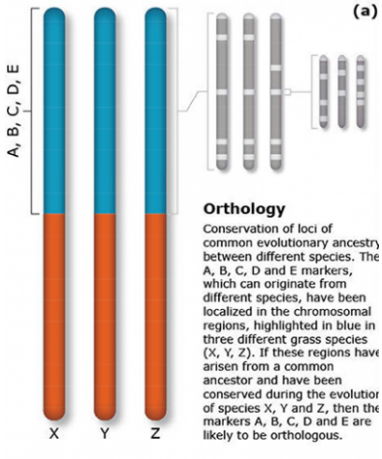


Fig. 6 Different levels of conservation between the grass genomes. Orthology. Adapted from Trends in Plant Science.

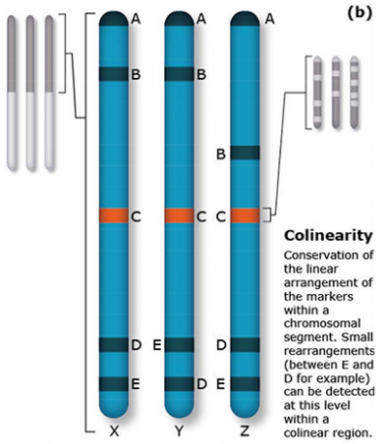


Fig. 7 Different levels of conservation between the grass genomes. Colinearity. Adapted from Trends in Plant Science.

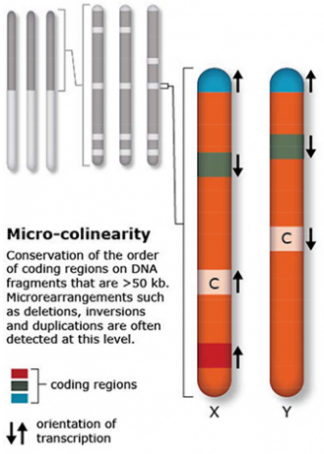


Fig. 8 Different levels of conservation between the grass genomes. colinearity. Adapted from Trends in Plant Science.

Orthology Example

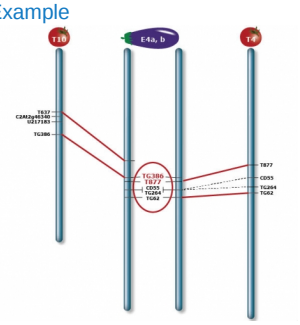


Fig. 9 Chromosomal rearrangement between genomes of eggplant and tomato. Adapted from Wu and Tanksley (2010).

The eggplant chromosome E4 combines two segments (E4a and E4b) orthologous to tomato T4 and T10 respectively, indicating a translocation between the two genomes. The breakpoint is located between markers TG386 and T677 (highlighted in red), and the region is indicated by a black bar beside E4. Orthologous marker pairs are connected by lines. A dash line indicates a marker of low mapping confidence on either or both maps that is not used for deduction of inversions. Vertical arrows beside E4 depict inversions in E4 with respect to T10.

Micro-Colinearity Example

The genetic map of bread wheat (*Triticum aestivum*) is used to analyze micro-colinearity of the Q locus of *T. monococcum*, *Brachypodium sylvaticum*, and rice (*Oryza sativa*). Genes are shown as colored boxes along the physical maps of each species.

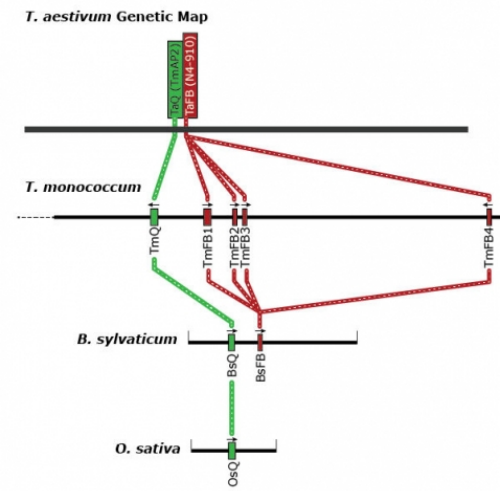


Fig. 10 The genetic map of bread wheat (Triticum aestivum) is used to analyze micro-colinearity of the Q locus of T. monococcum, Brachypodium sylvaticum, and rice (Oryza sativa). Selected genes are shown as colored boxes along the physical maps of each species, and transcriptional orientations are indicated by arrows above the boxes.

Orthology and Mapping

Comparative mapping is the alignment of chromosomes of related species based on genetic mapping of common DNA markers. Thus, comparative mapping involves the development of linkage maps (Fig. 1). The construction of comparative maps depends on orthology predictions to identify gene pairs of two species. Orthologous loci are loci in different species originating from the same ancestral locus. In contrast, paralagous loci are loci in different (or the same) species that arose due to a duplication of an ancestral locus.

Once the gene pairs have been established, blocks of conserved syteny are established using the positions of each gene in their respective map. The comparative studies in Solanaceae species revealed a modest and consistent rate of chromosomal changes across the family (0.03 ~ 0.12 rearrangements per chromosome per million years). Closely related species showed more conservation of gene orders than the distantly related species. For example, a high conservation of marker orders was observed between tomato and eggplant or tomato and potato than between tomato and pepper. Also, hot spots of chromosomal breakages were identified to suggest that breakpoints are not randomly distributed across the genome. In general, a higher frequency of inversions than translocations was observed among the Solaneaceous species.

Grass Genome Map

Early research to evaluate synteny in grass species suggested the grouping of grasses of the Poaceae families as a single genetic system (Bennetzen and Freeling, 1993). This early synteny work revealed that a large degree of colinearity exists among diverse grasses. For instance, a high conservation across grass species was observed in regions ranging from 5-10 cM. Also, most genes are homologous across species, i.e. all species have essentially the same genes. Additional fine structure mapping revealed insertions of repeated sequences among grass genomes. Overall, these efforts led to the development of the circular grass genome map.

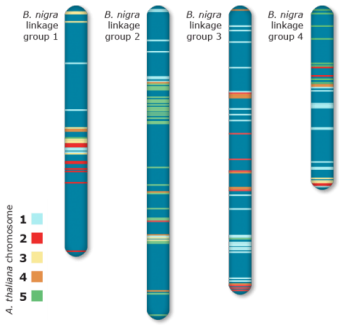


Fig. 11 A linear comparative map of Arabidopsis thaliana and Brassica nigra. Four out of eight linkage groups (G1-G4) of B. nigra are represented by vertical lines. The chromosomal location of A. thaliana loci detected by the A. thaliana markers are shown with different colors. Adapted from Lagercrantz (1998).

Linear Comparative Map

The average conserved segments between Arabidopsis and B. nigra was estimated to be ~8 cMs (Fig. 11). This estimate correspondsto ~90 rearrangements since divergence of the two species; much higher than other species.

Soybean and Arabidopsis Linkage

The majority of the comparative mapping studies were based on conservation of nucleotide sequences among closely related species. In 2000, synteny between soybean and *Arabidopsis* chromosomes was observed when linear orders of predicted protein sequences of genes were compared between the two species (Figure

12). This study also showed that *Arabidopsis* contains large scale duplicated genomic regions (Grant et al. 2000).

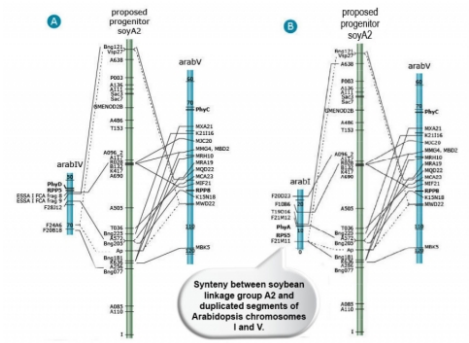


Fig. 12 Only those loci that had significant homology to Arabidopsis sequences on arabIV or arabV are connected by lines, although tic marks for every soybean sequence analyzed are shown on the proposed progenitor soyA2 map. Thin lines indicate soybean sequences that had homologs on only one Arabidopsis chromosome. Broken lines are used to indicate uncertainty in syntenic relationships because of duplicated loci in soybean. Known genes in Arabidopsis are shown in bold type. Tic marks and numbers indicate 10-cM intervals on the Arabidopsis chromosomes. Adapted from Grant et at. (2000).

Web-Based Mapping Tools

Web-based applications are available for mapping purposes. For example, the Comparative Map Viewer (CMap) available from GRAMENE (Fig. 13) allows comparisons of different maps.

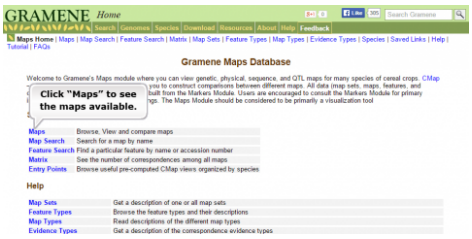


Fig. 13 Gramene's Maps module allows viewing of genetic, physical, and comparative maps for cereal crops.

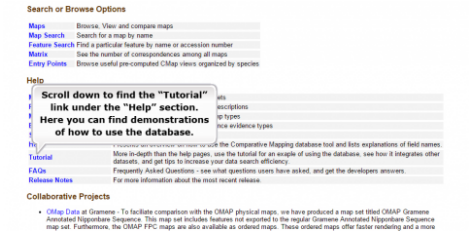
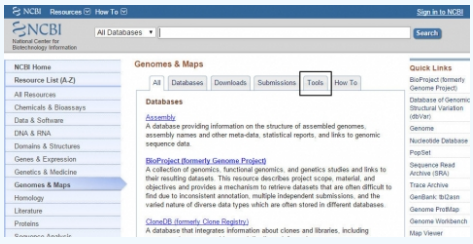


Fig. 14 Gramene's Maps module allows viewing of genetic, physical, and comparative maps for cereal crops.

Try This: NCBI MapViewer

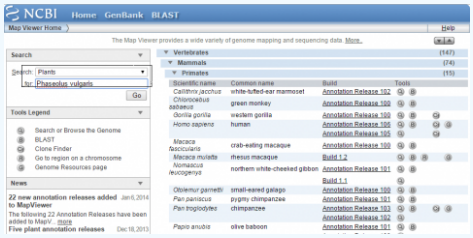
1. In the "Introduction to Bioinformatics" module, you learned about bioinformatics web tools. Go to NCBI and access MapViewer within Genomes & Maps.

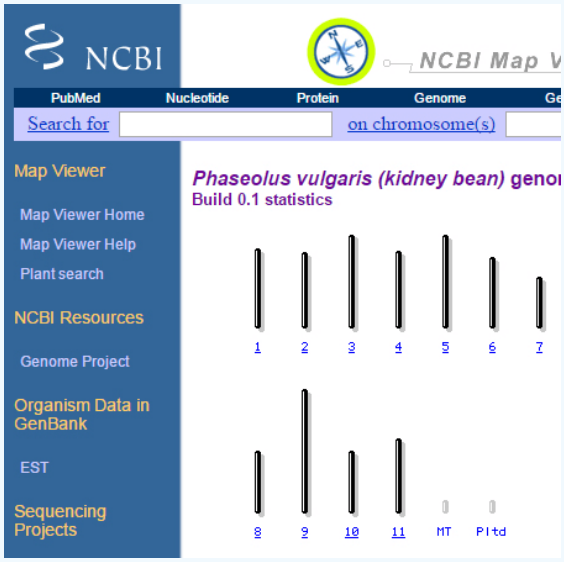


2. In "Introduction to Bioinformatics" module, you learned about bioinformatic webtools. Go to NCBI and access MapViewer within Genomes & Maps.



3. Search for plants, and select Phaseolus vulgaris (kidney bean).





How many chromosomes does kidney bean have?

4. Select chromosome 1, and answer the following:

- How many maps are available for chromosome 1?
- Are the maps physical or genetic? What is the estimated length for each map?
- List the types of markers used to develop each map?
- Try the zoom-in function in the left corner – what do you see?

Comparative Genomics

With the advent of nextgen sequencing, there has been a continuous supply of genome sequence data in the literature. Now the concept of comparing genome maps looking for linear order of genes or synteny has been changed to comparative genomics. It is now feasible to compare related or distant species or genera at the genome level with the aid of available genome sequences. Comparative genomics will have an impact on advancing our knowledge not only in the evolution of crop species, but also in answering biological questions. For example, traditional studies on domestication traits were focused on dozens of loci involved in a variety of functions. Many of the traits were not amenable to study using conventional mapping approaches. Through comparative genomics, it is now known that about 24% of loci in the maize genome were involved in either domestication or subsequent improvement. Through comparative genomics studies, it is now known

that in both maize and sunflowers there some loci related to amino acid biosynthesis are enriched. Selection of genes for amino acid biosynthesis during domestication may suggest that protein metabolism has an important role in heterosis. In barley, allelic variation at a flowering time locus in European cultivars appears to have arisen by introgression from barley that was independently domesticated in Central Asia.

Gene Prediction

The availability of genome sequence information makes it possible to apply comparative genomics for identification of genes. Gene prediction by comparative analysis involves identification of local similarities by sequence alignment programs in pairs of closely or distantly related genomes. For example, the mouse genome helped increase the accuracy of predicting human genes (Parra et al. 2003).

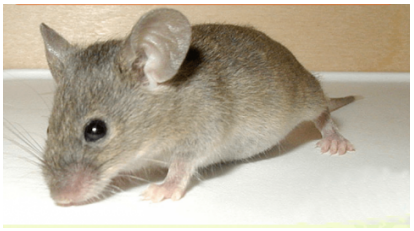
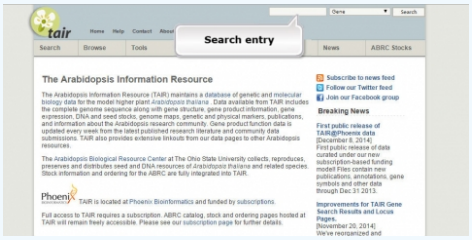


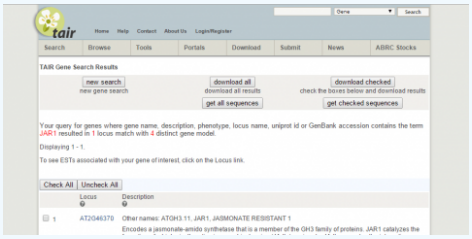
Fig. 16 Analysis of the mouse genome helped increase the accuracy of predicting human genes. Photo licensed under CC BY-SA 3.0 via Wikimedia Commons.

Try This: Arabidopsis Analysis

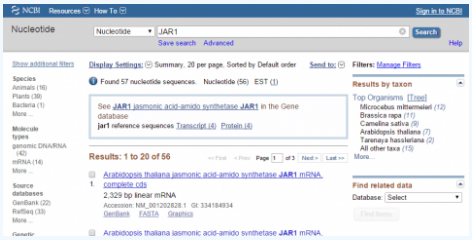
1. Go to the Arabidopsis Information Resource and search for a gene called JAR1.



2. What is the function of JAR1 (AT2G46370)?



3. Go to NCBI and search for nucleotide sequence for JAR1 (NM_001202828.1).



4. Within NCBI, perform a BLAST search for sequences similar to JAR1 (remember to exclude Arabidopsis thaliana in your query). After obtaining sequences producing significant alignments evaluate the four top sequences (maximum identity of 85-99 %). Use your results to answer the following:

- Give the name of the organism from which the sequence was obtained
- Provide the title of the research and the name of the Journal that published the research
- List GenBank id or NCBI reference sequence number of each hit

Detecting Copy Number Variations

The traditional view of comparative genomics was the analysis of synteny (gene order) and sequence comparisons among related species. With the emergence of powerful computational approaches, the examination of the genomic distribution of large insertions and deletions (indels) and copy number variants (CNVs) are becoming the norm.

Copy number variations may result from deletions, causing some individuals to contain only a single copy of a DNA sequence, or may be due to duplications, having certain individuals with more than two copies.



Fig. 17 A technician places a strip of eight PCR tubes into a thermal cycler at the University of Tartu in Estonia. Photo by Karl Mumm. Licensed under CC BY-SA 3.0 via Wikimedia Commons.

Comparative Genomic Hybridization

Detecting DNA Copy Number Variations

Comparative genomic hybridization (CGH) is a method for genome-wide screening for DNA copy number variations. CGH uses two genomes, a test and a control, which are labeled differentially with fluorescence probes and allowed to competitively hybridize to metaphase chromosomes. The fluorescence signal intensity from test samples compared to controls is plotted across each chromosome, allowing detection of copy number variation. Array-based CGH does not use metaphase chromosomes. Instead, synthetic oligonucleotide probes, or fragments from genomic clones such as BAC or YAC clones are arrayed onto glass slides. The basic method for aCGH is shown in Fig. 18.

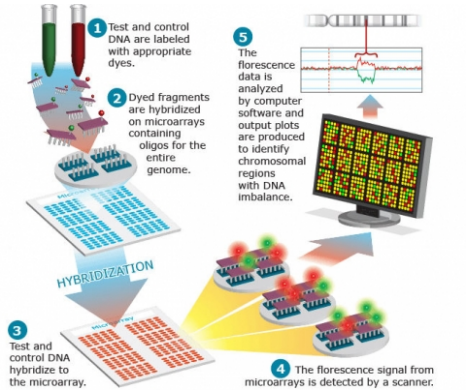


Fig. 18 The array-based (aCGH) process.

Gene Cloning



Fig. 19 Blight resistance in the potato plant was aided by genomic information from tomato. Photo by U.S. Department of Agriculture.

After predicting gene location, the next step is to predict the function of the gene. One of the approaches is to clone the gene using recombinant DNA approaches. Tests for gene function may involve in vitro biochemical analyses for the activity of an enzyme, or complementation of a mutant phenotype by the wild type allele. One can use information from comparative analysis of a species with a simple genome to clone genes from a species with a complex genome. For example, the isolation of the R3a blight resistance gene in potato utilized genomic information from tomato (Huang et al., 2005).

Analysis of Genome Evolution

Evolution of a species is a result of numerous processes including gene duplication and loss, whole genome duplication, variation in ploidy level, retrotransposon activity, and genome rearrangements. Genome evolution describes how the genome has been rearranged through time. Thus, to understand the evolution of a species we need to analyze genome evolution. Genome analysis involves construction of a map in one species and comparison of the map with maps from closely related species by the means of common markers (or common single gene traits).

An understanding of crop origins has long been held as central to the identification of useful genetic resources for crop improvement. The number of times that a species has been domesticated influences the genetic architecture of agronomic traits and the levels of genetic diversity in crop genomes. Domestication shapes the genetic variation that is available to modern breeders as it influences levels of nucleotide diversity and patterns of LD (linkage disequilibrium) genome-wide. The demographic history of domestication also informs our expectations of the genetic architecture of traits and thus our ability to identify causal genetic variants for crop improvement.

Genome Evolution: Details

There is evidence for both single domestications (such as maize and soybeans) and multiple domestications (such as avocados, common beans and barley); but for most crops it is not known whether single or multiple domestication events were involved. Following domestication, extensive admixture with wild relatives may occur; and this may be one explanation for the continued controversy regarding the origins of the domesticated indica and japonica rice.

Isolation of genes encoding domestication traits bears evolutionary importance. Until recently, traits that facilitated domestication, i.e. 'domestication syndrome' including decreased dispersal, reduced branching, loss of seed dormancy, reduced natural defenses and increased size of certain morphological features were investigated using mapping strategies. Thus, the study was limited to only a handful traits or loci. Whole-genome data of crops and their wild relatives will facilitate identification of complex demographic histories of many crops. Population genetic approaches, e.g. genome wide association studies (GWAS) will help identify loci that have no known phenotypes; e.g., 2-4% of loci in the maize were affected by artificial selection during domestication. Also, Nextgen sequencing will reveal genome-wide polymorphisms among the accessions leading to discovering demographic history and geographic origins of crop plants.



Fig. 20 Sunflowers in Fargo, ND. Studies suggest that the domestication of sunflowers may contribute to heterosis. Photo by the U.S. Department of Agriculture.

Domestication and Heterosis

Analysis of Genome Evolution

Comparative genetic mapping studies between species suggested some similarity in the genetic basis of domestication syndrome traits (orthology). Comparative genomics studies in both maize and sunflowers suggest selection on genes for amino acid biosynthesis (unknowingly) during domestication contributes to heterosis.

Challenges: Large Genomes

Most genome tools were not developed for plant genomics studies. First generation molecular markers were isozyme markers that were available in the late 1960s for mapping plant genomes. But such markers are limited in number, and DNA markers paved the way towards construction of high-density molecular maps in 1990s.

Despite the availability of DNA markers, large size of plant genomes remains the greatest challenge in plant comparative genomics.

Challenges: Transposable Content

Large genome sizes for plant species are a result of amplification of retrotransposable elements (Fig. 21). In addition, plants genomes contain multi-gene families and paralogous genes that are tandem-duplicated; for example, plant disease resistance genes.

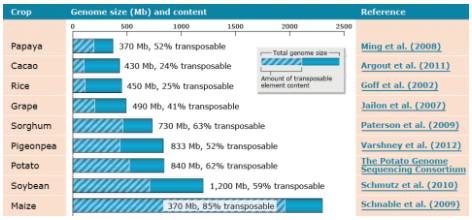


Fig. 21 Genome characteristics of common crop species.

Challenges: Map Assembly: Scenario 1

Duplicated and paralogous sequences, and transposable elements are difficult to assemble during the process of building a genome map (Fig. 22). In Fig. 22 colored shapes represent transposable elements or genes; genes X are a pair of paralogous genes. Short sequence reads are shown directly above where they would map to the reference.

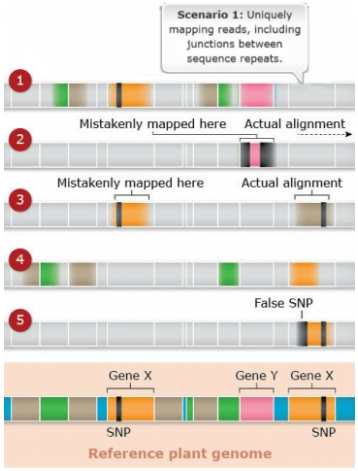


Fig. 22 The mapping of short sequence reads to a reference plant genome. Adapted from Morrell et al. (2012).

Challenges: Map Assembly: Scenario 2

Duplicated and paralogous sequences, and transposable elements are difficult to assemble during the process of building a genome map (Fig. 23). In Fig. 23 colored shapes represent transposable elements or genes; genes X are a pair of paralogous genes. Short sequence reads are shown directly above where they would map to the reference.

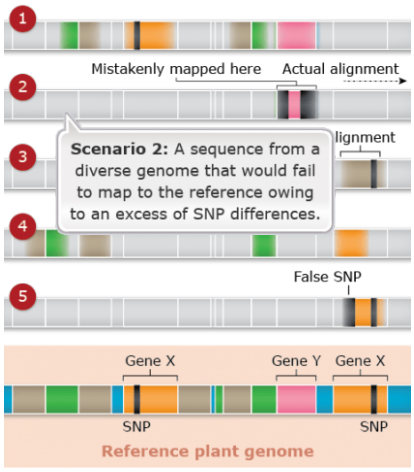


Fig. 23 The mapping of short sequence reads to a reference plant genome. Adapted from Morrell et al. (2012).

Challenges: Map Assembly: Scenario 3

Duplicated and paralogous sequences, and transposable elements are difficult to assemble during the process of building a genome map (Fig. 24). In Fig. 24 colored shapes represent transposable elements or genes; genes X are a pair of paralogous genes. Short sequence reads are shown directly above where they would map to the reference.

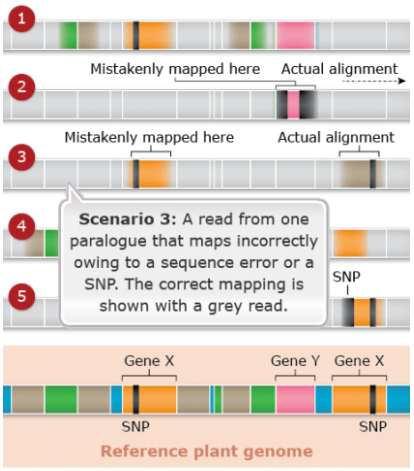


Fig. 24 The mapping of short sequence reads to a reference plant genome. Adapted from Morrell et al. (2012).

Challenges: Map Assembly: Scenario 4

Duplicated and paralogous sequences, and transposable elements are difficult to assemble during the process of building a genome map (Fig. 25). In Fig. 25 colored shapes represent transposable elements or genes; genes X are a pair of paralogous genes. Short sequence reads are shown directly above where they would map to the reference.

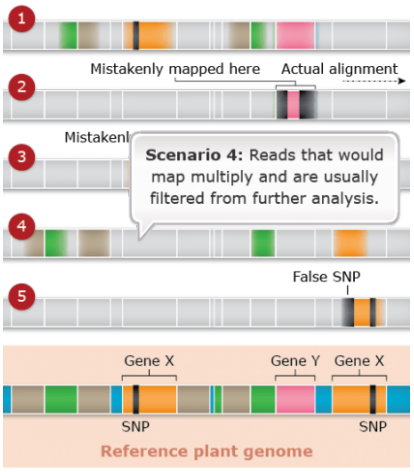


Fig. 25 The mapping of short sequence reads to a reference plant genome. Adapted from Morrell et al. (2012).

Challenges: Map Assembly: Scenario 5

Duplicated and paralogous sequences, and transposable elements are difficult to assemble during the process of building a genome map (Fig. 26). In Fig. 26 colored shapes represent transposable elements or genes; genes X are a pair of paralogous genes. Short sequence reads are shown directly above where they would map to the reference.

Challenges: Repeated

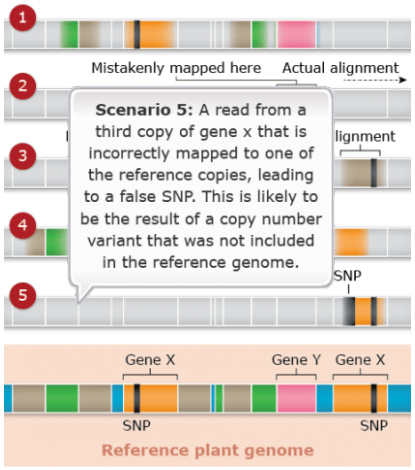


Fig. 26 The mapping of short sequence reads to a reference plant genome. Adapted from Morrell et al. (2012).

Sequences

High proportion of repeated sequences also makes it difficult to conduct reference genome-based SNP identification and genome-wide association studies. Therefore, regardless of the emerging high throughput sequencing technologies, it remains challenging to achieve sufficient genome coverage for assembling short read sequences and paralogous sequences. Consequently, fewer crop species with large genomes have been sequenced so far. Improvement in sequence read length by nextgen approaches will reduce this problem allowing detection of local patterns of LD for identifying paralogous reads in complex crop genomes.



Fig. 27 A pigeonpea plant in Ayotupas, West Timor, Indonesia. The pigeonpea genome is among those whose sequence has been published. Photo by Wibawo Djatmiko. Liscensed under CC BY-SA 3.0 via Wikimedia Commons.

Summary

Comparative genomics is a field of research focusing on determining the evolutionary relationships of genomes and link differences to functional consequences, or phenotypes. With progress in sequencing technology, an increased number of plant genomes have been sequenced making it possible to construct comparative maps and predict gene pairs of two species. To understand how genomes evolve, a genome map is constructed in one species and compared with maps from closely related species by the means of common markers. The majority of the comparative mapping studies are based on conservation of nucleotide sequences among closely related species. Comparative genomics is also useful for the identification of genes. Following prediction of gene location by comparative analysis, target genes may be isolated and characterized to determine their function. However, one of the greatest challenges in plant comparative genomics is the large size of plant genomes. Consequently, fewer crop species with large genomes have currently been sequenced.

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How to cite this module: Bhattacharyya, M, W. Suza, and T. Lübberstedt. (2023). Comparative Mapping and Genomics. In W. P. Suza, & K. R. Lamkey (Eds.), *Molecular Plant Breeding*. Iowa State University Digital Press.

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CHAPTER OVERVIEW

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25.1: Deep Time

History of life as revealed by the fossil record

With help from molecular phylogenies:

https://bio.libretexts.org/@go/page/74244

Eras	Periods	Epochs	Aquatic Life	Terrestrial Life
With approximate starting dates in millions of years ago in parentheses. Geologic features in green				
Cenozoic (66) The "Age of Mammals"	Quaternary (2.6)	Holocene		Humans in the new world
		Pleistocene	Periodic glaciation	First humans
			Continental drift continues	
	Neogene (23)	Pliocene	Atmospheric oxygen reaches today's level (21%)	Hominids
		Miocene		Adaptive radiation of birds, continued radiation of mammals
	Paleogene (66)	Oligocene	All modern groups present	
		Eocene		
		Paleocene		
Mesozoic (251) The "Age of Reptiles"	Cretaceous (146)	Still attached: N. America & N. Europe; Australia & Antarctica; Mass extinction of both aquatic and terrestrial life at the end		
			Modern bony fishes	Extinction of dinosaurs and pterosaurs; first snakes
			Extinction of ammonites, plesiosaurs, ichthyosaurs	Rise of angiosperms
		Africa & S. America begin to drift apart		
	Jurassic (200)		Plesiosaurs, ichthyosaurs abundant; first diatoms	*Archaeopteryx*; dinosaurs dominant but mammals (Eutheria) begin to diversify
			Ammonites again abundant	First lizards
			Skates, rays, and bony fishes abundant	Adaptive radiation of dinosaurs
			Pangaea splits into Laurasia and Gondwana;	

Eras	Periods	Epochs	Aquatic Life	Terrestrial Life			
			atmospheric oxygen drops to ~13%				
	Triassic (251)		Mass extinctions at the end.	Mass extinctions at the end. First mammals Adaptive radiation of reptiles: thecodonts, therapsids, turtles, crocodiles, first dinosaurs			
			Ammonites abundant at first				
			Rise of bony fishes				
	Paleozoic (542)		Periodic glaciation and arid climate; atmospheric oxygen reaches ~30%. Volcanic eruptions killed off 90% of marine species at end.				
		Permian (299)	Extinction of trilobites	Reptiles abundant. Cycads, conifers, ginkgos			
Pennsylvanian (320)		Warm, humid climate Together the Pennsylvanian and Mississippian make up the "Carboniferous"; also called the "Age of Amphibians"	Ammonites, bony fishes	First reptiles Coal swamps			
Mississippian (359)			Adaptive radiation of sharks	Forests of lycopsids, sphenopsids, and seed ferns Amphibians abundant Adaptive radiation of the insects (Hexapoda)			
			Atmospheric oxygen begins to rise as organic matter is buried, not respired				
Devonian (416) The "Age of Fishes"		Extensive inland seas	Cartilaginous and bony fishes abundant. Ammonites, nautiloids, ostracoderms, eurypterids	Ferns, lycopsids, and sphenopsids First gymnosperms First amphibians			
					Silurian (443)	Mild climate; inland seas	First bony fishes	First myriapods and chelicerates
Ordovician (485)		Mild climate, inland seas	Trilobites abundant	Fungi present First plants			

Eras	Periods	Epochs	Aquatic Life	Terrestrial Life
				(liverworts?) First insects
Cambrian (541)			First vertebrates (jawless fishes). Eurypterids, crustaceans mollusks, echinoderms, sponges, cnidarians, annelids, and tunicates present. Trilobites dominant.	No fossils of terrestrial eukaryotes, but phylogenetic trees suggest that lichens, mosses, perhaps even vascular plants were present.
		Periodic glaciation		
Proterozoic (2500)		Ediacaran (635)		Fossil evidence of multicellular algae, fungi, and bilaterian invertebrates
				Evidence of eukaryotes ~1.8 x10^9 years ago
Archaean (3600)			Evidence of archaea and bacteria ~3.5 x10^9 years ago	

The Geologic and Evolutionary Record

A remarkable feature of the table above is how often evolutionary changes coincided with geologic changes on the earth. But consider that changes in geology (e.g., mountain formation or lowering of the sea level) cause changes in climate, and together these alter the habitats available for life. Two types of geologic change seem to have had especially dramatic effects on life: **continental drift** and the **impact of asteroids**

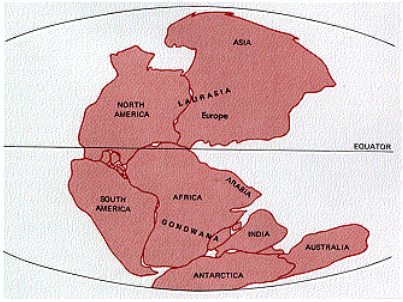


Figure 18.12.1 Pangaea

A body of evidence, both geological and biological, supports the conclusion that 200 million years ago, at the start of the **Mesozoic era**, all the continents were attached to one another in a single land mass, which has been named **Pangaea**. This drawing of Pangaea (adapted from data of R. S. Dietz and J. C. Holden) is based on a computer-generated fit of the continents as they would look if the sea level were lowered by 6000 feet (~1800 meters). During the **Triassic**, Pangaea began to break up, first into two major land masses:

- **Laurasia** in the Northern Hemisphere
- **Gondwana** in the Southern Hemisphere.

The present continents separated at intervals throughout the remainder of the Mesozoic and through the Cenozoic, eventually reaching the positions they have today. Let us examine some of the evidence.

Shape of the Continents

The east coast of South America and the west coast of Africa and are strikingly complementary. This is even more dramatic when one tries to fit the continents together using the boundaries of the continental slopes, e.g., 6000 feet (~1800 meters) down, rather than the shorelines.

Geology

- In both mineral content and age, the rocks in a region on the east coast of Brazil match precisely those found in Ghana on the west coast of Africa.
- The low mountain ranges and rock types in New England and eastern Canada appear to be continued in parts of Great Britain, France, and Scandinavia.
- India and the southern part of Africa both show evidence of periodic glaciation during Paleozoic times (even though both are now close to the equator). The pattern of glacial deposits in the two regions not only match each other but also glacial deposits found in South America, Australia, and Antarctica.

Fossils

- Fossil reptiles found in South Africa are also found in Brazil and Argentina.
- Fossil amphibians and reptiles found in Antarctica are also found in South Africa, India, and China.
- Most of the marsupials alive today are confined to South America and Australia. But if these two continents were connected by Antarctica in the Mesozoic, one might expect to find fossil marsupials there. In March 1982, this prediction was fulfilled with the discovery in Antarctica of the remains of **Polydolops**, a 9-ft (2.7 m) marsupial.

The Impact Hypothesis

The Cretaceous period, the last period of the Mesozoic, marked the end of the Age of Reptiles. It was followed by the Cenozoic era, the Age of Mammals. Although extinctions have occurred throughout the history of life, an extraordinary number of them occurred in a relatively brief period at the end of the Cretaceous. Why?

The Alvarez Theory

Louis Alvarez, his son Walter, and their colleagues proposed that a giant asteroid or comet striking the earth some 66 million years ago caused the massive die-off at the end of the Cretaceous. Presumably, the impact generated so much dust and gases that skies

were darkened all over the earth, photosynthesis declined, and worldwide temperatures dropped. The outcome was that as many as 75% of all species — including all dinosaurs — became extinct.

The key piece of evidence for the Alvarez hypothesis was the finding of thin deposits of clay containing the element iridium at the interface between the rocks of the Cretaceous and those of the Paleogene period (called the K-Pg boundary after the German word for Cretaceous). Iridium is a rare element on earth (although often discharged from volcanoes), but occurs in certain meteorites at concentrations thousands of times greater than in the earth's crust.

After languishing for many years, the Alvarez theory gained strong support from the discovery in the 1990s of the remains of a huge (180 km in diameter) crater in the Yucatan Peninsula that dated to 65 million years ago.

The abundance of sulfate-containing rock in the region suggests that the impact generated enormous amounts of sulfur dioxide (SO_2), which later returned to earth as a bath of acid rain. A smaller crater in Iowa, formed at the same time, many have contributed to the devastation. Perhaps during this period the earth passed through a swarm of asteroids or a comet and the repeated impacts made the earth uninhabitable for so many creatures of the Mesozoic.

Other Impacts

A mass extinction of non-dinosaur reptiles occurred earlier, at the end of the **Triassic**. It was followed by a great expansion in the diversity of dinosaurs. The recent discovery of a layer enriched in iridium in rocks formed at the boundary between the Triassic and Jurassic suggests that impact from an asteroid or comet may have been responsible then just as it was at the K-Pg boundary.

The largest extinction of all time occurred still earlier at the end of the Permian period. There is evidence off the coast of Australia that a huge impact there may have contributed to the extinctions at the Permian-Triassic (P-T) boundary.

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25.2: Origins of Life

To account for the origin of life on our earth requires solving several problems:

- How the organic molecules that define life, e.g. amino acids, nucleotides, were created.
- How these were assembled into macromolecules, e.g. proteins and nucleic acids, - a process requiring catalysts.
- How these were able to reproduce themselves.
- How these were assembled into a system delimited from its surroundings (i.e., a cell).

A number of theories address each of these problems. As for the first problem, four scenarios have been proposed. Organic molecules:

1. were synthesized from inorganic compounds in the atmosphere,
2. rained down on earth from outer space,
3. were synthesized at hydrothermal vents on the ocean floor,
4. were synthesized when comets or asteroids struck the early earth.

Scenario 1: Miller's Experiment

Stanley Miller, a graduate student in biochemistry, built the apparatus shown in Figure **25.2.1**. He filled it with water (H_2O), methane (CH_4), ammonia (NH_3) and hydrogen (H_2), but no oxygen. He hypothesized that this mixture resembled the atmosphere of the early earth. The mixture was kept circulating by continuously boiling and then condensing the water. The gases passed through a chamber containing two electrodes with a spark passing between them.

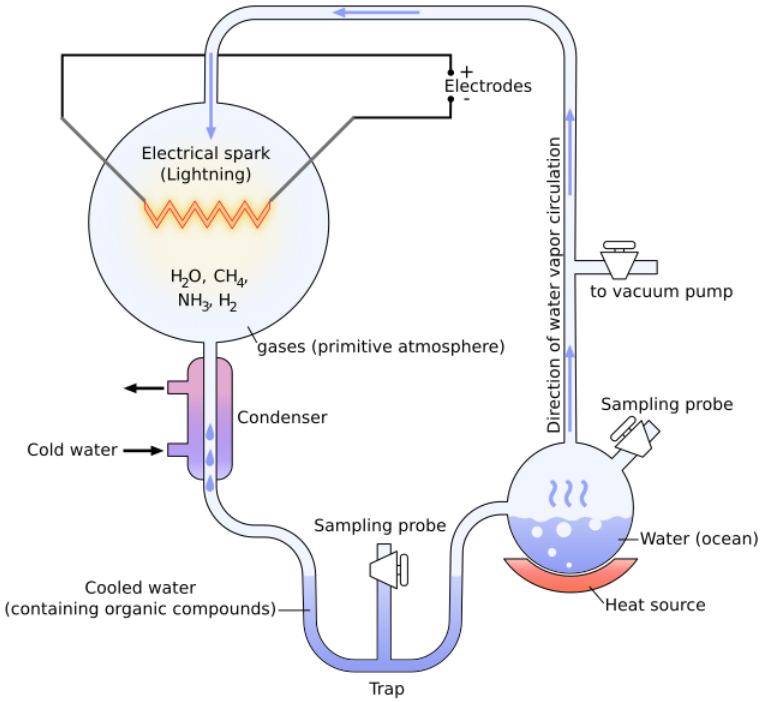


Figure **25.2.1**: Miller experiment. (CC BY-SA; Yassine Mrabet).

At the end of a week, Miller used paper chromatography to show that the flask now contained several amino acids as well as some other organic molecules. However, it is now thought that the atmosphere of the early earth was **not** rich in methane and ammonia - essential ingredients in Miller's experiments. In the years since Miller's work, many variants of his procedure have been tried. Virtually all the small molecules that are associated with life have been formed:

- 17 of the 20 amino acids used in protein synthesis, and all the purines and pyrimidines used in nucleic acid synthesis.
- But abiotic synthesis of **ribose** - and thus of **nucleotides** - has been much more difficult. However, success in synthesizing pyrimidine ribonucleotides under conditions that might have existed in the early earth was reported in the 14 May 2009 issue of

Nature.

- And in 2015, chemists in Cambridge England led by John Sutherland reported that they had been able to synthesize precursors of 12 of the 20 amino acids and two (of the four) ribonucleotides used by life as well as glycerol-1-phosphate, a precursor of lipids. They created all of these molecules using only hydrogen cyanide (HCN) and hydrogen sulfide (H_2S) irradiated with ultraviolet light in the presence of mineral catalysts.

Scenario 2: Molecules from Outer Space

Astronomers, using infrared spectroscopy, have identified a variety of organic molecules in interstellar space, including methane (CH_4), methanol (CH_3OH), formaldehyde (HCHO), cyanoacetylene (HC_3N) (which in spark-discharge experiments is a precursor to the pyrimidine **cytosine**), polycyclic aromatic hydrocarbonsas well as such inorganic building blocks as carbon dioxide (CO_2), carbon monoxide (CO), ammonia (NH_3), hydrogen sulfide (H_2S), and hydrogen cyanide (HCN).

There have been several reports of producing amino acids and other organic molecules in laboratories by taking a mixture of molecules known to be present in interstellar space such as ammonia (NH_3), carbon monoxide (CO), methanol (CH_3OH) and water (H_2O), hydrogen cyanide (HCN) and exposing it to a temperature close to that of space (near absolute zero) and intense ultraviolet (UV) radiation. Whether or not the molecules that formed terrestrial life arrived here from space, there is little doubt that **organic matter** continuously rains down on the earth (estimated at 30 tons per day).

Alternatively, organic molecules can be transport to Earth via meteorites as demonstrated with the Murchison Meteorite that that fell near Murchison, Australia on 28 September 1969. This meteorite turned out to contain a variety of organic molecules including: purines and pyrimidines, **polyols** - compounds with hydroxyl groups on a backbone of 3 to 6 carbons such as glycerol and glyceric acid (sugars are polyols) and the amino acids listed in Table **25.2.1**. The amino acids and their relative proportions were quite similar to the products formed in Miller's experiments.



Murchison meteorite at the The National Museum of Natural History (Washington). (CC SA-BY 3.0; :Basilicofresco).

Table **25.2.1**: Representative amino acids found in the Murchison meteorite. Six of the amino acids (blue) are found in all living things, but the others (yellow) are not normally found in living matter here on earth. The same amino acids are produced in discharge experiments like Miller's.

The question is if these molecules identified in the Murchison meteorite were simply terrestrial contaminants that got into the meteorite after it fell to earth? Probably not:

- Some of the samples were collected on the same day it fell and subsequently handled with great care to avoid contamination.

Glycine	Glutamic acid
Alanine	Isovaline
Valine	Norvaline
Proline	N-methylalanine
Aspartic acid	N-ethylglycine

- The polyols contained the isotopes carbon-13 and hydrogen-2 (deuterium) in greater amounts than found here on earth.
- The samples lacked certain amino acids that are found in all earthly proteins.
- Only **L** amino acids occur in earthly proteins, but the amino acids in the meteorite contain both **D** and **L** forms (although **L** forms were slightly more prevalent).

Scenario 3: Deep-Sea Hydrothermal Vents

Some deep-sea hydrothermal vents discharge copious amounts of hydrogen, hydrogen sulfide, and carbon dioxide at temperatures around 100°C. (These are not "black smokers".) These gases bubble up through chambers rich in iron sulfides (FeS, FeS_2). These can catalyze the formation of simple organic molecules like acetate. (And life today depends on enzymes that have Fe and S atoms in their active sites.)

Scenario 4: Laboratory Synthesis of Nucleobases Under Conditions Mimicking the Impact of Asteroids or Comets on the Early Earth

Researchers in the Czech Republic reported in 2014 that they had succeeded in the abiotic synthesis of adenine (A), guanine (G), cytosine (C), and uracil (U) — the four bases found in RNA (an RNA beginning?) and three of the four found in DNA. They achieved this by bombarding a mixture of formamide and clay with powerful laser pulses that mimicked the temperature and pressure expected when a large meteorite strikes the earth. Formamide is a simple substance, CH_3NO, thought to have been abundant on the early earth and containing the four elements fundamental to all life.

Assembling Polymers

Another problem is how **polymers** - the basis of life itself - could be assembled.

- In solution, hydrolysis of a growing polymer would soon limit the size it could reach.
- Abiotic synthesis produces a mixture of L and D enantiomers. Each inhibits the polymerization of the other. (So, for example, the presence of **D** amino acids inhibits the polymerization of **L** amino acids (the ones that make up proteins here on earth).

This has led to a theory that early polymers were assembled on solid, mineral surfaces that protected them from degradation, and in the laboratory polypeptides and polynucleotides (RNA molecules) containing about ~50 units have been synthesized on mineral (e.g., clay) surfaces.

An RNA Beginning?

All metabolism depends on enzymes and, until recently, every enzyme has turned out to be a protein. But proteins are synthesized from information encoded in DNA and translated into mRNA. So here is a chicken-and-egg dilemma. The synthesis of DNA and RNA requires proteins. So proteins cannot be made without nucleic acids and nucleic acids cannot be made without proteins. The discovery that certain RNA molecules have enzymatic activity provides a possible solution. These RNA molecules — called ribozymes — incorporate both the features required of life: storage of information and the ability to act as catalysts.

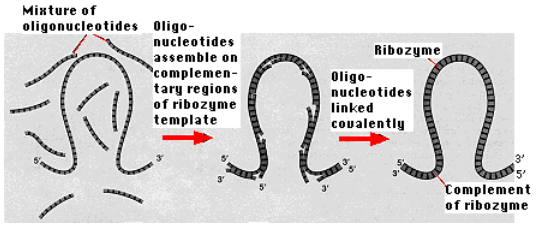


Figure 18.9.2 RNA. (The figure is based on the work of Green and Szostak, Science 258:1910, 1992.)

While no ribozyme in nature has yet been found that can replicate itself, ribozymes have been synthesized in the laboratory that can catalyze the assembly of short oligonucleotides into exact complements of themselves. The ribozyme serves as both the *template* on which short lengths of RNA ("oligonucleotides" are assembled following the rules of base pairing and the *catalyst* for covalently linking these oligonucleotides.

In principal, the minimal functions of life might have begun with RNA and only later did proteins take over the catalytic machinery of metabolism and DNA take over as the repository of the genetic code. Several other bits of evidence support this notion of an original "RNA world":

- Many of the cofactors that play so many roles in life are based on ribose; for example:
  - ATP
  - NAD
  - FAD
  - coenzyme A
  - cyclic AMP
  - GTP
- In the cell, all deoxyribonucleotides are synthesized from ribonucleotide precursors.
- Many bacteria control the transcription and/or translation of certain genes with RNA molecules, not protein molecules.

Reproduction?

Perhaps the earliest form of reproduction was a simple fission of the growing aggregate into two parts - each with identical metabolic and genetic systems intact.

The First Cell?

To function, the machinery of life must be separated from its surroundings - some form of extracellular fluid (ECF). This function is provided by the plasma membrane. Today's plasma membranes are made of a double layer of phospholipids. They are only permeable to small, uncharged molecules like H_2O, CO_2, and O_2. Specialized transmembrane transporters are needed for ions, hydrophilic, and charged organic molecules (e.g., amino acids and nucleotides) to pass into and out of the cell.

However, the same Szostak lab that produced the finding described above reported in the 3 July 2008 issue of **Nature** that fatty acids, fatty alcohols, and monoglycerides - all molecules that can be synthesized under prebiotic conditions - can also form lipid bilayers and these can spontaneously assemble into enclosed vesicles.

Unlike phospholipid vesicles, these

- admit from the external medium charged molecules like nucleotides
- admit from the external medium hydrophilic molecules like ribose
- grow by self-assembly
- are impermeable to, and thus retain, polymers like oligonucleotides.

These workers loaded their synthetic vesicles with a short single strand of deoxycytidine (dC) structured to provide a template for its replication. When the vesicles were placed in a medium containing (chemically modified) dG, these nucleotides entered the vesicles and assembled into a strand of Gs complementary to the template strand of Cs. Here, then, is a simple system that is a plausible model for the creation of the first cells from the primeval "soup" of organic molecules.

This transition is probably the easiest to understand.

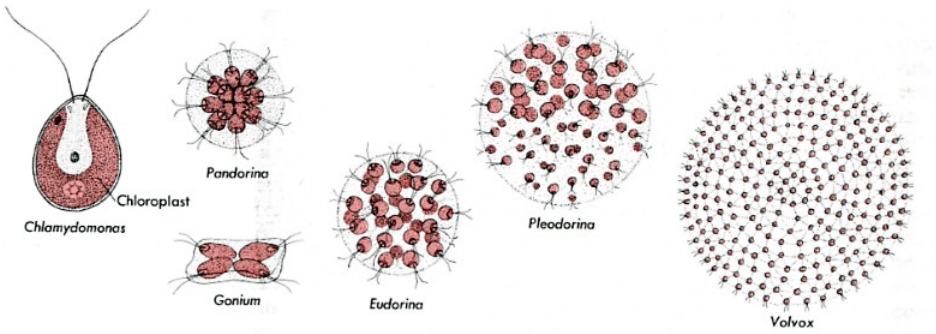


Figure 18.9.3 Unicellular to multicellular organisms

Several colonial flagellated green algae provide a clue. These species are called colonial because they are made up simply of clusters of independent cells. If a single cell of **Gonium**, **Pandorina**, or **Eudorina** is isolated from the rest of the colony, it will swim away looking quite like a **Chlamydomonas** cell. Then, as it undergoes mitosis, it will form a new colony with the characteristic number of cells in that colony.

(The figures are not drawn to scale. Their sizes range from Chlamydomonas which is about 10 µm in diameter - little larger than a human red blood cell - to Volvox whose sphere is some 350 µm in diameter - visible to the naked eye.)

The situation in **Pleodorina** and **Volvox** is different. In these organisms, some of the cells of the colony (most in Volvox) are not able to live independently. If a nonreproductive cell is isolated from a Volvox colony, it will fail to reproduce itself by mitosis and eventually will die. What has happened? In some way, as yet unclear, Volvox has crossed the line separating simple colonial organisms from truly multicellular ones. Unlike Gonium, Volvox cannot be considered simply a colony of individual cells. It is a single **organism** whose cells have lost their ability to live independently. If a sufficient number of them become damaged, the entire sphere of cells will die.

What has Volvox gained? In giving up their independence, the cells of Volvox have become specialists. No longer does every cell carry out all of life's functions (as in colonial forms); instead certain cells specialize to carry out certain functions while leaving other functions to other specialists. In Volvox this process goes no further than having certain cells specialize for reproduction while others, unable to reproduce themselves, fulfill the needs for photosynthesis and locomotion.

In more complex multicellular organisms, the degree of specialization is carried much further. Each cell has one or two precise functions to carry out. It depends on other cells to carry out all the other functions needed to maintain the life of the organism and thus its own.

The specialization and division of labor among cells is the outcome of their history of differentiation. One of the great problems in biology is how differentiation arises among cells, all of which having arisen by mitosis, share the same genes.

The genomes of both Chlamydomonas and Volvox have been sequenced. Although one is unicellular, the other multicellular, they have not only about the same number of protein-encoding genes (14,516 in Chlamydomonas, 14,520 in Volvox) but most of these are homologous. Volvox has only 58 genes that have no relatives in Chlamydomonas and even fewer unique mRNAs.

At one time, many of us would have expected that a multicellular organism like Volvox with its differentiated cells and complex life cycle would have had many more genes than a single-celled organism like Chlamydomonas. But that turns out not to be the case.

How to explain this apparent paradox? My guess is that just as we have seen in the evolution of animals, we are seeing here that the evolution of organismic complexity is not so much a matter of the evolution of **new genes** but rather the evolution of changes in the control elements (promoters and enhancers) that dictate how and where the basic tool kit of eukaryotic genes will be expressed .

The evidence is compelling that all these organisms are close relatives; that is, belong to the same clade. They illustrate how colonial forms could arise from unicellular ones and multicellular forms from colonial ones.

The Last Universal Common Ancestor (LUCA)?



The 3 kingdoms of contemporary life — archaea, bacteria, and eukaryotes — all share many similarities of their metabolic and genetic systems . Presumably these were present in an organism that was ancestral to these groups: the "LUCA". Although there are not enough data at present to describe LUCA, comparative genomics and proteomics reveal a closer relationship between archaea and eukaryotes than either shares with the bacteria. Except, of course, for the mitochondria and chloroplasts that eukaryotes gained from bacterial endosymbionts. Whether the endosymbionts were acquired before or after a lineage of archaea had acquired a nucleus - and thus started the lineage of eukaryotes - is still uncertain.

Creating Life?

When I headed off to college (in 1949), I wrote an essay speculating on the possibility that some day we would be able to create a living organism from nonliving ingredients. By the time I finished my formal studies in biology — having learned of the incredible complexity of even the simplest organism — I concluded that such a feat could never be accomplished.

Now I'm not so sure.

Several recent advances suggest that we may be getting close to creating life. (But note that these examples represent laboratory manipulations that do not necessarily reflect what may have happened when life first appeared.)

Examples:

- The ability to created membrane-enclosed vesicles that can take in small molecules and assemble them into polymers which remain within the "cell".
- The ability to assemble functional ribosomes — the structures that convert the information encoded in the genome into the proteins that run life — from their components.
- In 2008, scientists at the J. Craig Venter Institute (JCVI) reported (in **Science** 29 February 2008) that they had succeeded in synthesizing a complete bacterial chromosome — containing 582,970 base pairs — starting from single deoxynucleotides. The entire sequence of the genome of *Mycoplasma genitalium* was already known. Using this information, they synthesized some 10,000 short oligonucleotides (each about 50 bp long) representing the entire genitalium genome and then - step by step - assembled these into longer and longer fragments until finally they had made the entire circular DNA molecule that is the genome.

  Could this be placed in the cytoplasm of a living cell and run it?

  The same team showed in the previous year (see **Science** 3 August 2007) that they could insert an entire chromosome from one species of mycoplasma into the cytoplasm of a related species and, in due course, the recipient lost its own chromosome (perhaps destroyed by restriction enzymes encoded by the donor chromosome) and began expressing the phenotype of the donor. In short, they had changed one species into another. But the donor chromosome was made by the donor bacterium, not synthesized in the laboratory. However, there should be no serious obstacle to achieving the same genome transplantation with a chemically-synthesized chromosome.

  They've done it! The same team reported on 20 May 2010 in the online *Science* Express that they had successfully transplanted a completely synthetic genome — based on that of *Mycoplasma mycoides* — into the related species *Mycoplasma capricolum*. The recipient strain grew well and soon acquired the phenotype of the *M. mycoides* donor.

- In the 4 April 2014 issue of *Science* (Annaluru, N. *et al.*), a large group of researchers - including many undergraduates at Johns Hopkins University - reported that they had successfully replaced the natural chromosome 3 in *Saccharomyces cerevisiae* (which has 16 chromosomes) with a totally-synthetic chromosome.

  Their procedure:

  1. Chemically synthesize 69- to 79-nt oligonucleotides representing all the stretches of the known chromosome 9 sequence (which contains 316,617 base pairs) **except** for certain sequences such as transposons, many introns, and transfer RNA genes. In addition new, non-native, sequences such as loxP sites were included to aid future manipulations of the genome.
  2. Stitch these together into blocks of ~750 base pairs. This step was done *in vitro* by undergraduates enrolled in the "Build A Genome" class at Johns Hopkins.

3. Introduce these into yeast cells which ligated them into stretches of DNA containing 2–4 thousand base pairs.
4. Introduce these stepwise into yeast cells so that they replace the equivalent portions of the native chromosome.
5. The result: a strain of yeast that grows just as well with its new artificial chromosome (now containing only 272,871 base pairs) as it did before.

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SECTION OVERVIEW

25.3: Evidence for Early Life

25.3.1: Classification of Prokaryotes

25.3.2: The Origins of Archaea and Bacteria

25.3.3: Extremophiles and Biofilms

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25.3.1: Classification of Prokaryotes

Learning Objectives

- Discuss the origins of prokaryotic organisms in terms of the geologic timeline

Evolution of Prokaryotes

In the recent past, scientists grouped living things into five kingdoms (animals, plants, fungi, protists, and prokaryotes) based on several criteria such as: the absence or presence of a nucleus and other membrane-bound organelles, the absence or presence of cell walls, multicellularity, etc. In the late 20th century, the pioneering work of Carl Woese and others compared sequences of small-subunit ribosomal RNA (SSU rRNA) which resulted in a more fundamental way to group organisms on earth. Based on differences in the structure of cell membranes and in rRNA, Woese and his colleagues proposed that all life on earth evolved along three lineages, called domains. The domain Bacteria comprises all organisms in the kingdom Bacteria, the domain Archaea comprises the rest of the prokaryotes, and the domain Eukarya comprises all eukaryotes, including organisms in the kingdoms Animalia, Plantae, Fungi, and Protista.

The current model of the evolution of the first, living organisms is that these were some form of prokaryotes, which may have evolved out of protobionts. In general, the eukaryotes are thought to have evolved later in the history of life. However, some authors have questioned this conclusion, arguing that the current set of prokaryotic species may have evolved from more complex eukaryotic ancestors through a process of simplification. Others have argued that the three domains of life arose simultaneously, from a set of varied cells that formed a single gene pool.

Two of the three domains, Bacteria and Archaea, are prokaryotic. Based on fossil evidence, prokaryotes were the first inhabitants on Earth, appearing 3.5 to 3.8 billion years ago during the Precambrian Period. These organisms are abundant and ubiquitous; that is, they are present everywhere. In addition to inhabiting moderate environments, they are found in extreme conditions: from boiling springs to permanently frozen environments in Antarctica; from salty environments like the Dead Sea to environments under tremendous pressure, such as the depths of the ocean; and from areas without oxygen, such as a waste management plant, to radioactively-contaminated regions, such as Chernobyl. Prokaryotes reside in the human digestive system and on the skin, are responsible for certain illnesses, and serve an important role in the preparation of many foods.



Figure **25.3.1.1**: Prokaryotes in extreme environments: Certain prokaryotes can live in extreme environments such as the Morning Glory pool, a hot spring in Yellowstone National Park. The spring's vivid blue color is from the prokaryotes that thrive in its very hot waters.

Key Points

- All living things can be classified into three main groups called domains; these include the Archaea, the Bacteria, and the Eukarya.
- Prokaryotes arose during the Precambrian Period 3.5 to 3.8 billion years ago.
- Prokaryotic organisms can live in every type of environment on Earth, from very hot, to very cold, to super haline, to very acidic.
- The domains Bacteria and Archaea are the ones containing prokaryotic organisms.

- The Archaea are prokaryotes that inhabit extreme environments, such as inside of volcanoes, while Bacteria are more common organisms, such as *E. coli*.

Key Terms

- **prokaryote**: an organism whose cell (or cells) are characterized by the absence of a nucleus or any other membrane-bound organelles
- **domain**: in the three-domain system, the highest rank in the classification of organisms, above kingdom: Bacteria, Archaea, and Eukarya
- **archaea**: a taxonomic domain of single-celled organisms lacking nuclei, formerly called archaebacteria, but now known to differ fundamentally from bacteria

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25.3.2: The Origins of Archaea and Bacteria

Learning Objectives

- Distinguish bacteria from archaea in terms of their origins

Prokaryotes, the First Inhabitants of Earth

When and where did life begin? What were the conditions on earth when life began? Prokaryotes were the first forms of life on earth, existing for billions of years before plants and animals appeared. The earth and its moon are thought to be about 4.54 billion years old. This estimate is based on evidence from radiometric dating of meteorite material together with other substrate material from earth and the moon. Early earth had a very different atmosphere (contained less molecular oxygen) than it does today and was subjected to strong radiation; thus, the first organisms would have flourished where they were more protected, such as in ocean depths or beneath the surface of the earth. Also at this time, strong volcanic activity was common on Earth. It is probable that these first organisms, the first prokaryotes, were adapted to very high temperatures. Early earth was prone to geological upheaval and volcanic eruption, and was subject to bombardment by mutagenic radiation from the sun. The first organisms were prokaryotes that could withstand these harsh conditions.

Although probable prokaryotic cell fossils date to almost 3.5 billion years ago, most prokaryotes do not have distinctive morphologies; fossil shapes cannot be used to identify them as Archaea. Instead, chemical fossils of unique lipids are more informative because such compounds do not occur in other organisms. Some publications suggest that archaean or eukaryotic lipid remains are present in shales dating from 2.7 billion years ago. Such lipids have also been detected in Precambrian formations. The oldest such traces come from the Isua district of west Greenland, which include earth's oldest sediments, formed 3.8 billion years ago. The archaeal lineage may be the most ancient that exists on earth.

Within prokaryotes, archaeal cell structure is most similar to that of gram-positive bacteria, largely because both have a single lipid bilayer and usually contain a thick sacculus of varying chemical composition. In phylogenetic trees based upon different gene / protein sequences of prokaryotic homologs, the archaeal homologs are more closely related to those of Gram-positive bacteria. Archaea and gram-positive bacteria also share conserved indels in a number of important proteins, such as Hsp70 and glutamine synthetase.

It has been proposed that the archaea evolved from gram-positive bacteria in response to antibiotic selection pressure. This is suggested by the observation that archaea are resistant to a wide variety of antibiotics that are primarily produced by gram-positive bacteria and that these antibiotics primarily act on the genes that distinguish archaea from bacteria. The evolution of Archaea in response to antibiotic selection, or any other competitive selective pressure, could also explain their adaptation to extreme environments (such as high temperature or acidity) as the result of a search for unoccupied niches to escape from antibiotic-producing organisms.

Microbial Mats

Microbial mats or large biofilms may represent the earliest forms of life on earth; there is fossil evidence of their presence starting about 3.5 billion years ago. A microbial mat is a multi-layered sheet of prokaryotes that includes mostly bacteria, but also archaea. Microbial mats are a few centimeters thick, typically growing where different types of materials interface, mostly on moist surfaces. The various types of prokaryotes that comprise the mats use different metabolic pathways, which is the reason for their various colors. Prokaryotes in a microbial mat are held together by a glue-like sticky substance that they secrete called extracellular matrix.

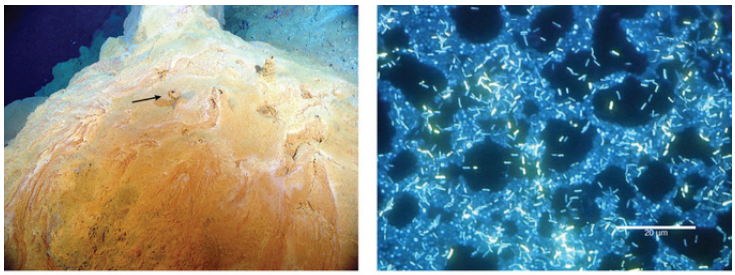


Figure **25.3.2.1**: Microbial mat: This (a) microbial mat, about one meter in diameter, grows over a hydrothermal vent in the Pacific Ocean in a region known as the "Pacific Ring of Fire." The mat helps retain microbial nutrients. Chimneys, such as the one indicated by the arrow, allow gases to escape. (b) In this micrograph, bacteria are visualized using fluorescence microscopy.

The first microbial mats likely obtained their energy from chemicals found near hydrothermal vents. A hydrothermal vent is a breakage or fissure in the earth's surface that releases geothermally-heated water. With the evolution of photosynthesis about 3 billion years ago, some prokaryotes in microbial mats came to use a more widely-available energy source, sunlight, whereas others were still dependent on chemicals from hydrothermal vents for energy and food.

Stromatolites

Fossilized microbial mats represent the earliest record of life on earth. A stromatolite is a sedimentary structure formed when minerals are precipitated out of water by prokaryotes in a microbial mat. Stromatolites form layered rocks made of carbonate or silicate. Although most stromatolites are artifacts from the past, there are places on earth where stromatolites are still forming. For example, growing stromatolites have been found in the Anza-Borrego Desert State Park in San Diego County, California.



Figure **25.3.2.1**: Stromatolites: (a) These living stromatolites are located in Shark Bay, Australia. (b) These fossilized stromatolites, found in Glacier National Park, Montana, are nearly 1.5 billion years old.

Key Points

- The first prokaryotes were adapted to the extreme conditions of early earth.
- It has been proposed that archaea evolved from gram-positive bacteria as a response to antibiotic selection pressures.
- Microbial mats and stromatolites represent some of the earliest prokaryotic formations that have been found.

Key Terms

- **stromatolite**: a laminated, columnar, rock-like structure built over geologic time by microorganisms such as cyanobacteria
- **gram-positive**: that is stained violet by Gram's method due to the presence of a peptidoglycan cell wall
- **sacculus**: a small sac
- **indel**: either an insertion or deletion mutation in the genetic code

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25.3.3: Extremophiles and Biofilms

Learning Objectives

- Discuss the distinguishing features of extremophiles and the environments that produce biofilms

Microbes Are Adaptable: Life in Moderate and Extreme Environments

Some organisms have developed strategies that allow them to survive harsh conditions. Prokaryotes thrive in a vast array of environments; some grow in conditions that would seem very normal to us, whereas others are able to thrive and grow under conditions that would kill a plant or animal. Almost all prokaryotes have a cell wall: a protective structure that allows them to survive in both hyper- and hypo-osmotic conditions. Some soil bacteria are able to form endospores that resist heat and drought, thereby allowing the organism to survive until favorable conditions recur. These adaptations, along with others, allow bacteria to be the most abundant life form in all terrestrial and aquatic ecosystems.

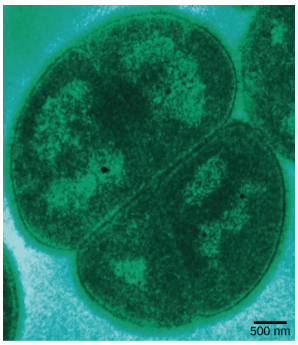


Figure **25.3.3.1**: Bacteria and radiation tolerance: Deinococcus radiodurans, visualized in this false color transmission electron micrograph, is a prokaryote that can tolerate very high doses of ionizing radiation. It has developed DNA repair mechanisms that allow it to reconstruct its chromosome even if it has been broken into hundreds of pieces by radiation or heat.

Other bacteria and archaea are adapted to grow under extreme conditions and are called extremophiles, meaning “lovers of extremes.” Extremophiles have been found in all kinds of environments: the depth of the oceans, hot springs, the Arctic and the Antarctic, in very dry places, deep inside earth, in harsh chemical environments, and in high radiation environments, just to mention a few. These organisms give us a better understanding of prokaryotic diversity and raise the possibility of finding new prokaryotic species that may lead to the discovery of new therapeutic drugs or have industrial applications. Because they have specialized adaptations that allow them to live in extreme conditions, many extremophiles cannot survive in moderate environments. There are many different groups of extremophiles. They are identified based on the conditions in which they grow best. Several habitats are extreme in multiple ways. For example, a soda lake is both salty and alkaline, so organisms that live in a soda lake must be both alkaliphiles and halophiles. Other extremophiles, like radioresistant organisms, do not prefer an extreme environment (in this case, one with high levels of radiation), but have adapted to survive in it.

Prokaryotes in the Dead Sea

One example of a very harsh environment is the Dead Sea, a hypersaline basin that is located between Jordan and Israel. Hypersaline environments are essentially concentrated seawater. In the Dead Sea, the sodium concentration is 10 times higher than that of seawater. The water also contains high levels of magnesium (about 40 times higher than in seawater) that would be toxic to most living things. Iron, calcium, and magnesium, elements that form divalent ions (Fe^{2+}, Ca^{2+}, and Mg^{2+}), produce what is commonly referred to as “hard” water. Taken together, the high concentration of divalent cations, the acidic pH (6.0), and the intense solar radiation flux make the Dead Sea a unique, and uniquely hostile, ecosystem.



Figure 25.3.3.1: Halophile habitats: (a) The Dead Sea is hypersaline. Nevertheless, salt-tolerant bacteria thrive in this sea. (b) These halobacteria cells can form salt-tolerant bacterial mats.

The Ecology of Biofilms

Until a couple of decades ago, microbiologists used to think of prokaryotes as isolated entities living apart. This model, however, does not reflect the true ecology of prokaryotes, most of which prefer to live in communities where they can interact. A biofilm is a microbial community held together in a gummy-textured matrix that consists primarily of polysaccharides secreted by the organisms, together with some proteins and nucleic acids. Biofilms grow attached to surfaces. Some of the best-studied biofilms are composed of prokaryotes, although fungal biofilms have also been described, as well as some composed of a mixture of fungi and bacteria.

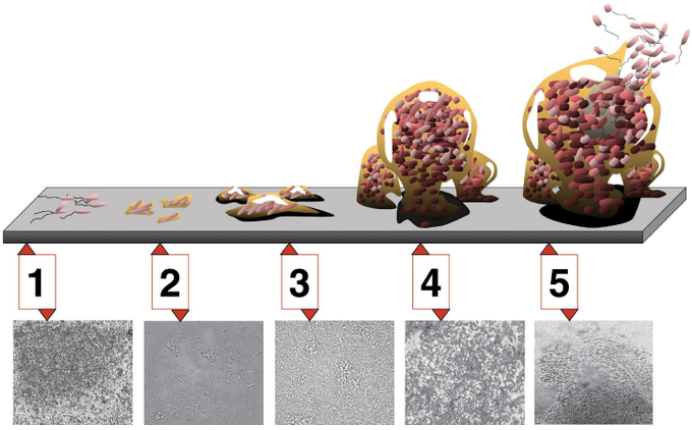


Figure 25.3.3.1: Biofilm Development: Five stages of biofilm development are shown. During stage 1, initial attachment, bacteria adhere to a solid surface via weak van der Waals interactions. During stage 2, irreversible attachment, hairlike appendages called pili permanently anchor the bacteria to the surface. During stage 3, maturation I, the biofilm grows through cell division and recruitment of other bacteria. An extracellular matrix composed primarily of polysaccharides holds the biofilm together. During stage 4, maturation II, the biofilm continues to grow and takes on a more complex shape. During stage 5, dispersal, the biofilm matrix is partly broken down, allowing some bacteria to escape and colonize another surface. Micrographs of a Pseudomonas aeruginosa biofilm in each of the stages of development are shown.

Biofilms are present almost everywhere: they can cause the clogging of pipes and readily colonize surfaces in industrial settings. In recent, large-scale outbreaks of bacterial contamination of food, biofilms have played a major role. They also colonize household surfaces, such as kitchen counters, cutting boards, sinks, and toilets, as well as places on the human body, such as the surfaces of our teeth.

Interactions among the organisms that populate a biofilm, together with their protective exopolysaccharidic (EPS) environment, make these communities more robust than free-living, or planktonic, prokaryotes. The sticky substance that holds bacteria together also excludes most antibiotics and disinfectants, making biofilm bacteria hardier than their planktonic counterparts. Overall, biofilms are very difficult to destroy because they are resistant to many common forms of sterilization.

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Key Points

- Prokaryotes live in all environments, no matter how extreme they may be.
- Bacteria that prefer very salty environments are called halophiles, while those that live in very acidic environments are called acidophiles.
- An example of a habitat that halophiles can colonize is the Dead Sea, a body of water that is 10 times saltier than regular ocean water.
- A biofilm is a microbial community held together in a gummy-textured matrix that consists primarily of polysaccharides secreted by the organisms.
- Biofilms can be found clogging pipes, on kitchen counters, or even on the surface of one’s teeth.

Key Terms

- **extremophile**: an organism that lives under extreme conditions of temperature, salinity, etc; commercially important as a source of enzymes that operate under similar conditions
- **halophile**: an organism that lives and thrives in an environment of high salinity, often requiring such an environment; a form of extremophile
- **alkaliphile**: any organism that lives and thrives in an alkaline environment, such as a soda lake; a form of extremophile

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SECTION OVERVIEW

25.4: Earth's Changing System

Skills to Develop

- Describe how the present-day theory of evolution was developed
- Define adaptation
- Explain convergent and divergent evolution
- Describe homologous and vestigial structures
- Discuss misconceptions about the theory of evolution

Evolution by natural selection describes a mechanism for how species change over time. That species change had been suggested and debated well before Darwin began to explore this idea. The view that species were static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks who expressed evolutionary ideas. In the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc Comte de Buffon who observed that various geographic regions have different plant and animal populations, even when the environments are similar. It was also accepted that there were extinct species.

During this time, James Hutton, a Scottish naturalist, proposed that geological change occurred gradually by the accumulation of small changes from processes operating like they are today over long periods of time. This contrasted with the predominant view that the geology of the planet was a consequence of catastrophic events occurring during a relatively brief past. Hutton's view was popularized in the nineteenth century by the geologist Charles Lyell who became a friend to Darwin. Lyell's ideas were influential on Darwin's thinking: Lyell's notion of the greater age of Earth gave more time for gradual change in species, and the process of change provided an analogy for gradual change in species. In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a mechanism for evolutionary change. This mechanism is now referred to as an inheritance of acquired characteristics by which modifications in an individual are caused by its environment, or the use or disuse of a structure during its lifetime, could be inherited by its offspring and thus bring about change in a species. While this mechanism for evolutionary change was discredited, Lamarck's ideas were an important influence on evolutionary thought.

Charles Darwin and Natural Selection

In the mid-nineteenth century, the actual mechanism for evolution was independently conceived of and described by two naturalists: Charles Darwin and Alfred Russel Wallace. Importantly, each naturalist spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world on *H.M.S. Beagle*, including stops in South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, like Wallace's later journeys to the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands west of Ecuador. On these islands, Darwin observed species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with a unique beak shape (Figure **25.4.1**). The species on the islands had a graded series of beak sizes and shapes with very small differences between the most similar. He observed that these finches closely resembled another finch species on the mainland of South America. Darwin imagined that the island species might be species modified from one of the original mainland species. Upon further study, he realized that the varied beaks of each finch helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks for breaking seeds, and insect-eating finches had spear-like beaks for stabbing their prey.

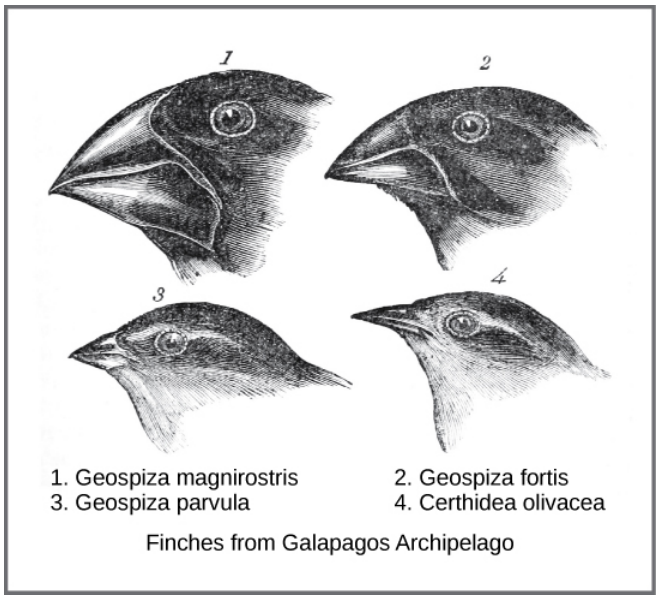


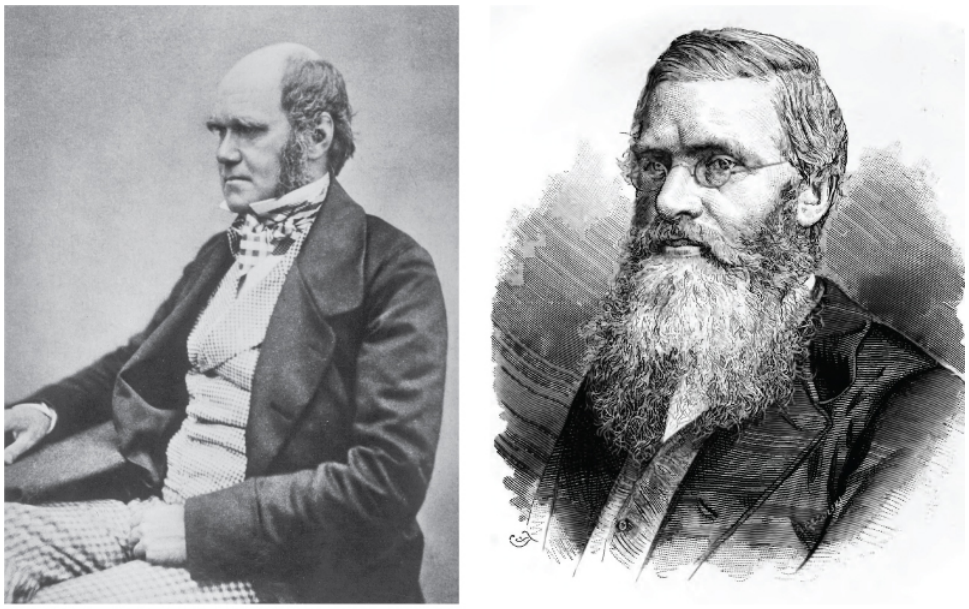
Figure **25.4.1**: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources.

Wallace and Darwin both observed similar patterns in other organisms and they independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. Natural selection, also known as "survival of the fittest," is the more prolific reproduction of individuals with favorable traits that survive environmental change because of those traits; this leads to evolutionary change.

For example, a population of giant tortoises found in the Galapagos Archipelago was observed by Darwin to have longer necks than those that lived on other islands with dry lowlands. These tortoises were "selected" because they could reach more leaves and access more food than those with short necks. In times of drought when fewer leaves would be available, those that could reach more leaves had a better chance to eat and survive than those that couldn't reach the food source. Consequently, long-necked tortoises would be more likely to be reproductively successful and pass the long-necked trait to their offspring. Over time, only long-necked tortoises would be present in the population.

Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, most characteristics of organisms are inherited, or passed from parent to offspring. Although no one, including Darwin and Wallace, knew how this happened at the time, it was a common understanding. Second, more offspring are produced than are able to survive, so resources for survival and reproduction are limited. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is competition for those resources in each generation. Both Darwin and Wallace's understanding of this principle came from reading an essay by the economist Thomas Malthus who discussed this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Darwin and Wallace reasoned that offspring with inherited characteristics which allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called descent with modification. Ultimately, natural selection leads to greater adaptation of the population to its local environment; it is the only mechanism known for adaptive evolution.

Papers by Darwin and Wallace (Figure **25.4.2**) presenting the idea of natural selection were read together in 1858 before the Linnean Society in London. The following year Darwin's book, *On the Origin of Species*, was published. His book outlined in considerable detail his arguments for evolution by natural selection.



(a) (b)

Figure 25.4.2: Both (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Demonstrations of evolution by natural selection are time consuming and difficult to obtain. One of the best examples has been demonstrated in the very birds that helped to inspire Darwin's theory: the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of natural selection. The Grants found changes from one generation to the next in the distribution of beak shapes with the medium ground finch on the Galápagos island of Daphne Major. The birds have inherited variation in the bill shape with some birds having wide deep bills and others having thinner bills. During a period in which rainfall was higher than normal because of an El Niño, the large hard seeds that large-billed birds ate were reduced in number; however, there was an abundance of the small soft seeds which the small-billed birds ate. Therefore, survival and reproduction were much better in the following years for the small-billed birds. In the years following this El Niño, the Grants measured beak sizes in the population and found that the average bill size was smaller. Since bill size is an inherited trait, parents with smaller bills had more offspring and the size of bills had evolved to be smaller. As conditions improved in 1987 and larger seeds became more available, the trend toward smaller average bill size ceased.

Career Connection: Field Biologist

Many people hike, explore caves, scuba dive, or climb mountains for recreation. People often participate in these activities hoping to see wildlife. Experiencing the outdoors can be incredibly enjoyable and invigorating. What if your job was to be outside in the wilderness? Field biologists by definition work outdoors in the "field." The term field in this case refers to any location outdoors, even under water. A field biologist typically focuses research on a certain species, group of organisms, or a single habitat (Figure 25.4.3).



Figure **25.4.3**: A field biologist tranquilizes a polar bear for study. (credit: Karen Rhode)

One objective of many field biologists includes discovering new species that have never been recorded. Not only do such findings expand our understanding of the natural world, but they also lead to important innovations in fields such as medicine and agriculture. Plant and microbial species, in particular, can reveal new medicinal and nutritive knowledge. Other organisms can play key roles in ecosystems or be considered rare and in need of protection. When discovered, these important species can be used as evidence for environmental regulations and laws.

Processes and Patterns of Evolution

Natural selection can only take place if there is variation, or differences, among individuals in a population. Importantly, these differences must have some genetic basis; otherwise, the selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons such as an individual being taller because of better nutrition rather than different genes.

Genetic diversity in a population comes from two main mechanisms: mutation and sexual reproduction. Mutation, a change in DNA, is the ultimate source of new alleles, or new genetic variation in any population. The genetic changes caused by mutation can have one of three outcomes on the phenotype. A mutation affects the phenotype of the organism in a way that gives it reduced fitness—lower likelihood of survival or fewer offspring. A mutation may produce a phenotype with a beneficial effect on fitness. And, many mutations will also have no effect on the fitness of the phenotype; these are called neutral mutations. Mutations may also have a whole range of effect sizes on the fitness of the organism that expresses them in their phenotype, from a small effect to a great effect. Sexual reproduction also leads to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each of the offspring.

A heritable trait that helps the survival and reproduction of an organism in its present environment is called an adaptation. Scientists describe groups of organisms becoming adapted to their environment when a change in the range of genetic variation occurs over time that increases or maintains the “fit” of the population to its environment. The webbed feet of platypuses are an adaptation for swimming. The snow leopards’ thick fur is an adaptation for living in the cold. The cheetahs’ fast speed is an adaptation for catching prey.

Whether or not a trait is favorable depends on the environmental conditions at the time. The same traits are not always selected because environmental conditions can change. For example, consider a species of plant that grew in a moist climate and did not need to conserve water. Large leaves were selected because they allowed the plant to obtain more energy from the sun. Large leaves require more water to maintain than small leaves, and the moist environment provided favorable conditions to support large leaves. After thousands of years, the climate changed, and the area no longer had excess water. The direction of natural selection shifted so that plants with small leaves were selected because those populations were able to conserve water to survive the new environmental conditions.

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. When two species evolve in diverse directions from a common point, it is called divergent evolution. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments and adaptation to different kinds of pollinators (Figure **25.4.4**).



(a) (b)

Figure **25.4.4**: Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star (*Liatrus spicata*) and the (b) purple coneflower (*Echinacea purpurea*) vary in appearance, yet both share a similar basic morphology. (credit a: modification of work by Drew Avery; credit b: modification of work by Cory Zanker)

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called convergent evolution, where similar traits evolve independently in species that do not share a recent common ancestry. The two species came to the same function, flying, but did so separately from each other.

These physical changes occur over enormous spans of time and help explain how evolution occurs. Natural selection acts on individual organisms, which in turn can shape an entire species. Although natural selection may work in a single generation on an individual, it can take thousands or even millions of years for the genotype of an entire species to evolve. It is over these large time spans that life on earth has changed and continues to change.

Evidence of Evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, to identifying patterns in nature that were consistent with evolution, and since Darwin, our understanding has become clearer and broader.

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today, and fossils show a progression of evolution. Scientists determine the age of fossils and categorize them from all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years (Figure **25.4.5**). For example, scientists have recovered highly detailed records showing the evolution of humans and horses (Figure **25.4.5**). The whale flipper shares a similar morphology to appendages of birds and mammals (Figure **25.4.6**) indicating that these species share a common ancestor.



(a) (b)

Figure **25.4.5**: In this (a) display, fossil hominids are arranged from oldest (bottom) to newest (top). As hominids evolved, the shape of the skull changed. An artist's rendition of (b) extinct species of the genus *Equus* reveals that these ancient species resembled the modern horse (*Equus ferus*) but varied in size.

Anatomy and Embryology

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction (Figure **25.4.6**) resulting from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout. Scientists call these synonymous parts homologous structures.

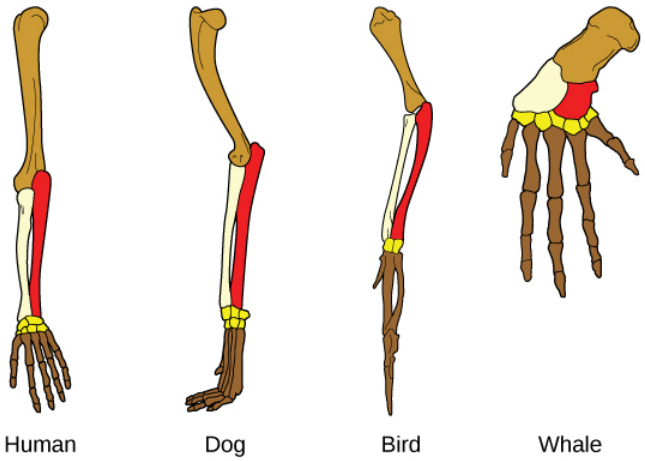


Figure **25.4.6**: The similar construction of these appendages indicates that these organisms share a common ancestor.

Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past common ancestor. These unused structures without function are called vestigial structures. Other examples of vestigial structures are wings on flightless birds, leaves on some cacti, and hind leg bones in whales.

Link to Learning

Visit this interactive site to guess which bones structures are homologous and which are analogous, and see examples of evolutionary adaptations to illustrate these concepts.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan, living in the arctic region have been selected for seasonal white phenotypes

during winter to blend with the snow and ice (Figure **25.4.7**). These similarities occur not because of common ancestry, but because of similar selection pressures—the benefits of not being seen by predators.



(a) (b)

Figure **25.4.7**: The white winter coat of the (a) arctic fox and the (b) ptarmigan's plumage are adaptations to their environments. (credit a: modification of work by Keith Morehouse)

Embryology, the study of the development of the anatomy of an organism to its adult form, also provides evidence of relatedness between now widely divergent groups of organisms. Mutational tweaking in the embryo can have such magnified consequences in the adult that embryo formation tends to be conserved. As a result, structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits and tails at some point in their early development. These disappear in the adults of terrestrial groups but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by the time of birth.

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of members of the plant family Proteaceae in Australia, southern Africa, and South America is best explained by their presence prior to the southern supercontinent Gondwana breaking up.

The great diversification of marsupials in Australia and the absence of other mammals reflect Australia's long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents species from migrating. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all unique to their one point of origin, yet they display distant relationships to ancestral species on mainlands.

Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material and in the near universality of the genetic code and the machinery of DNA replication and expression. Fundamental divisions in life between the three domains are reflected in major structural differences in otherwise conservative structures such as the components of ribosomes and the structures of membranes.

In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences—exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events that allow the free modification of one copy by mutation, selection, or drift (changes in a population's gene pool resulting from chance), while the second copy continues to produce a functional protein.

Misconceptions of Evolution

Although the theory of evolution generated some controversy when it was first proposed, it was almost universally accepted by biologists, particularly younger biologists, within 20 years after publication of *On the Origin of Species*. Nevertheless, the theory of evolution is a difficult concept and misconceptions about how it works abound

Link to Learning

This site addresses some of the main misconceptions associated with the theory of evolution.

Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word "theory" with the way scientists use the word. In science, a "theory" is understood to be a body of thoroughly tested and verified explanations for a set of observations of the natural world. Scientists have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes understood facts about the world. In the same way, the theory of evolution describes facts about the living world. As such, a theory in science has survived significant efforts to discredit it by scientists. In contrast, a "theory" in common vernacular is a word meaning a guess or suggested explanation; this meaning is more akin to the scientific concept of "hypothesis." When critics of evolution say evolution is "just a theory," they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mischaracterization.

Individuals Evolve

Evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, obviously, but this is called development and involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking about the evolution of a characteristic, it is probably best to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium-ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time and then measures the average bill size in the population several years later, this average value will be different as a result of evolution. Although some individuals may survive from the first time to the second, they will still have the same bill size; however, there will be many new individuals that contribute to the shift in average bill size.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics believe that it cannot explain the origin of life. The theory does not try to explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies the origin of species. It does not shed light on the beginnings of life including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, and presumably it just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA either within a cell or pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the

expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Organisms Evolve on Purpose

Statements such as “organisms evolve in response to a change in an environment” are quite common, but such statements can lead to two types of misunderstandings. First, the statement must not be understood to mean that individual organisms evolve. The statement is shorthand for “a population evolves in response to a changing environment.” However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and therefore producing proportionately more offspring than other phenotypes. This results in change in the population if the characteristics are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic.

In a larger sense, evolution is not goal directed. Species do not become “better” over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species, despite the commonness of this kind of language in popular discourse. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at some point in the future. This holds equally well for a species of insect as it does the human species.

Summary

Evolution is the process of adaptation through mutation which allows more desirable characteristics to be passed to the next generation. Over time, organisms evolve more characteristics that are beneficial to their survival. For living organisms to adapt and change to environmental pressures, genetic variation must be present. With genetic variation, individuals have differences in form and function that allow some to survive certain conditions better than others. These organisms pass their favorable traits to their offspring. Eventually, environments change, and what was once a desirable, advantageous trait may become an undesirable trait and organisms may further evolve. Evolution may be convergent with similar traits evolving in multiple species or divergent with diverse traits evolving in multiple species that came from a common ancestor. Evidence of evolution can be observed by means of DNA code and the fossil record, and also by the existence of homologous and vestigial structures.

Glossary

adaptation
: heritable trait or behavior in an organism that aids in its survival and reproduction in its present environment

convergent evolution
: process by which groups of organisms independently evolve to similar forms

divergent evolution
: process by which groups of organisms evolve in diverse directions from a common point

homologous structures
: parallel structures in diverse organisms that have a common ancestor

natural selection

reproduction of individuals with favorable genetic traits that survive environmental change because of those traits, leading to evolutionary change

variation

genetic differences among individuals in a population

vestigial structure

physical structure present in an organism but that has no apparent function and appears to be from a functional structure in a distant ancestor

25.4.1: Eukaryotic Origins

25.4.2: Climate and the Effects of Global Climate Change

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25.4.1: Eukaryotic Origins

Skills to Develop

- List the unifying characteristics of eukaryotes
- Describe what scientists know about the origins of eukaryotes based on the last common ancestor
- Explain endosymbiotic theory

Living things fall into three large groups: Archaea, Bacteria, and Eukarya. The first two have prokaryotic cells, and the third contains all eukaryotes. A relatively sparse fossil record is available to help discern what the first members of each of these lineages looked like, so it is possible that all the events that led to the last common ancestor of extant eukaryotes will remain unknown. However, comparative biology of extant organisms and the limited fossil record provide some insight into the history of Eukarya.

The earliest fossils found appear to be Bacteria, most likely cyanobacteria. They are about 3.5 billion years old and are recognizable because of their relatively complex structure and, for prokaryotes, relatively large cells. Most other prokaryotes have small cells, 1 or 2 µm in size, and would be difficult to pick out as fossils. Most living eukaryotes have cells measuring 10 µm or greater. Structures this size, which might be fossils, appear in the geological record about 2.1 billion years ago.

Characteristics of Eukaryotes

Data from these fossils have led comparative biologists to the conclusion that living eukaryotes are all descendants of a single common ancestor. Mapping the characteristics found in all major groups of eukaryotes reveals that the following characteristics must have been present in the last common ancestor, because these characteristics are present in at least some of the members of each major lineage.

1. Cells with nuclei surrounded by a nuclear envelope with nuclear pores. This is the single characteristic that is both necessary and sufficient to define an organism as a eukaryote. All extant eukaryotes have cells with nuclei.
2. Mitochondria. Some extant eukaryotes have very reduced remnants of mitochondria in their cells, whereas other members of their lineages have “typical” mitochondria.
3. A cytoskeleton containing the structural and motility components called actin microfilaments and microtubules. All extant eukaryotes have these cytoskeletal elements.
4. Flagella and cilia, organelles associated with cell motility. Some extant eukaryotes lack flagella and/or cilia, but they are descended from ancestors that possessed them.
5. Chromosomes, each consisting of a linear DNA molecule coiled around basic (alkaline) proteins called histones. The few eukaryotes with chromosomes lacking histones clearly evolved from ancestors that had them.
6. Mitosis, a process of nuclear division wherein replicated chromosomes are divided and separated using elements of the cytoskeleton. Mitosis is universally present in eukaryotes.
7. Sex, a process of genetic recombination unique to eukaryotes in which diploid nuclei at one stage of the life cycle undergo meiosis to yield haploid nuclei and subsequent karyogamy, a stage where two haploid nuclei fuse together to create a diploid zygote nucleus.
8. Members of all major lineages have cell walls, and it might be reasonable to conclude that the last common ancestor could make cell walls during some stage of its life cycle. However, not enough is known about eukaryotes’ cell walls and their development to know how much homology exists among them. If the last common ancestor could make cell walls, it is clear that this ability must have been lost in many groups.

Endosymbiosis and the Evolution of Eukaryotes

In order to understand eukaryotic organisms fully, it is necessary to understand that all extant eukaryotes are descendants of a chimeric organism that was a composite of a host cell and the cell(s) of an alpha-proteobacterium that “took up residence” inside it. This major theme in the origin of eukaryotes is known as endosymbiosis, one cell engulfing another such that the engulfed cell survives and both cells benefit. Over many generations, a symbiotic relationship can result in two organisms that depend on each other so completely that neither could survive on its own. Endosymbiotic events likely contributed to the origin of the last common

ancestor of today's eukaryotes and to later diversification in certain lineages of eukaryotes (Figure **25.4.1.4**). Before explaining this further, it is necessary to consider metabolism in prokaryotes.

Prokaryotic Metabolism

Many important metabolic processes arose in prokaryotes, and some of these, such as nitrogen fixation, are never found in eukaryotes. The process of aerobic respiration is found in all major lineages of eukaryotes, and it is localized in the mitochondria. Aerobic respiration is also found in many lineages of prokaryotes, but it is not present in all of them, and many forms of evidence suggest that such anaerobic prokaryotes never carried out aerobic respiration nor did their ancestors.

While today's atmosphere is about one-fifth molecular oxygen (O_2), geological evidence shows that it originally lacked O_2. Without oxygen, aerobic respiration would not be expected, and living things would have relied on fermentation instead. At some point before, about 3.5 billion years ago, some prokaryotes began using energy from sunlight to power anabolic processes that reduce carbon dioxide to form organic compounds. That is, they evolved the ability to photosynthesize. Hydrogen, derived from various sources, was captured using light-powered reactions to reduce fixed carbon dioxide in the Calvin cycle. The group of Gram-negative bacteria that gave rise to cyanobacteria used water as the hydrogen source and released O_2 as a waste product.

Eventually, the amount of photosynthetic oxygen built up in some environments to levels that posed a risk to living organisms, since it can damage many organic compounds. Various metabolic processes evolved that protected organisms from oxygen, one of which, aerobic respiration, also generated high levels of ATP. It became widely present among prokaryotes, including in a group we now call alpha-proteobacteria. Organisms that did not acquire aerobic respiration had to remain in oxygen-free environments. Originally, oxygen-rich environments were likely localized around places where cyanobacteria were active, but by about 2 billion years ago, geological evidence shows that oxygen was building up to higher concentrations in the atmosphere. Oxygen levels similar to today's levels only arose within the last 700 million years.

Recall that the first fossils that we believe to be eukaryotes date to about 2 billion years old, so they appeared as oxygen levels were increasing. Also, recall that all extant eukaryotes descended from an ancestor with mitochondria. These organelles were first observed by light microscopists in the late 1800s, where they appeared to be somewhat worm-shaped structures that seemed to be moving around in the cell. Some early observers suggested that they might be bacteria living inside host cells, but these hypotheses remained unknown or rejected in most scientific communities.

Endosymbiotic Theory

As cell biology developed in the twentieth century, it became clear that mitochondria were the organelles responsible for producing ATP using aerobic respiration. In the 1960s, American biologist Lynn Margulis developed endosymbiotic theory, which states that eukaryotes may have been a product of one cell engulfing another, one living within another, and evolving over time until the separate cells were no longer recognizable as such. In 1967, Margulis introduced new work on the theory and substantiated her findings through microbiological evidence. Although Margulis' work initially was met with resistance, this once-revolutionary hypothesis is now widely (but not completely) accepted, with work progressing on uncovering the steps involved in this evolutionary process and the key players involved. Much still remains to be discovered about the origins of the cells that now make up the cells in all living eukaryotes.

Broadly, it has become clear that many of our nuclear genes and the molecular machinery responsible for replication and expression appear closely related to those in Archaea. On the other hand, the metabolic organelles and genes responsible for many energy-harvesting processes had their origins in bacteria. Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of discovery in biology. For instance, it is not known whether the endosymbiotic event that led to mitochondria occurred before or after the host cell had a nucleus. Such organisms would be among the extinct precursors of the last common ancestor of eukaryotes.

Mitochondria

One of the major features distinguishing prokaryotes from eukaryotes is the presence of mitochondria. Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption. Each mitochondrion measures 1 to 10 or greater micrometers in length and exists in the cell as an organelle that can be ovoid to worm-shaped to intricately branched (Figure **25.4.1.1**). Mitochondria arise from the division of existing mitochondria; they may fuse

together; and they may be moved around inside the cell by interactions with the cytoskeleton. However, mitochondria cannot survive outside the cell. As the atmosphere was oxygenated by photosynthesis, and as successful aerobic prokaryotes evolved, evidence suggests that an ancestral cell with some membrane compartmentalization engulfed a free-living aerobic prokaryote, specifically an alpha-proteobacterium, thereby giving the host cell the ability to use oxygen to release energy stored in nutrients. Alpha-proteobacteria are a large group of bacteria that includes species symbiotic with plants, disease organisms that can infect humans via ticks, and many free-living species that use light for energy. Several lines of evidence support that mitochondria are derived from this endosymbiotic event. Most mitochondria are shaped like alpha-proteobacteria and are surrounded by two membranes, which would result when one membrane-bound organism was engulfed into a vacuole by another membrane-bound organism. The mitochondrial inner membrane is extensive and involves substantial infoldings called cristae that resemble the textured, outer surface of alpha-proteobacteria. The matrix and inner membrane are rich with the enzymes necessary for aerobic respiration.

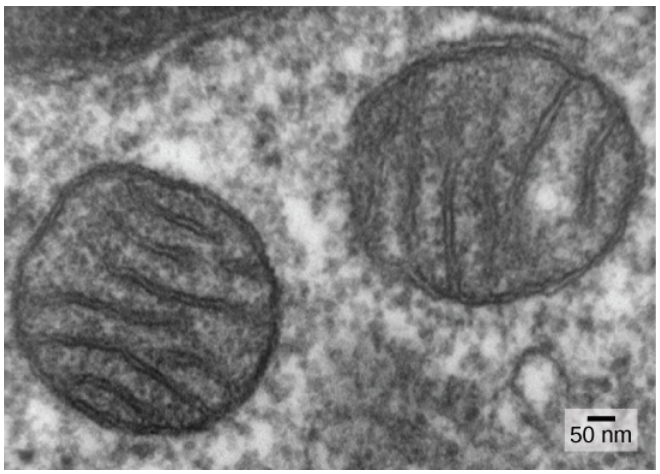


Figure 25.4.1.1: In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section. (credit: Louise Howard)

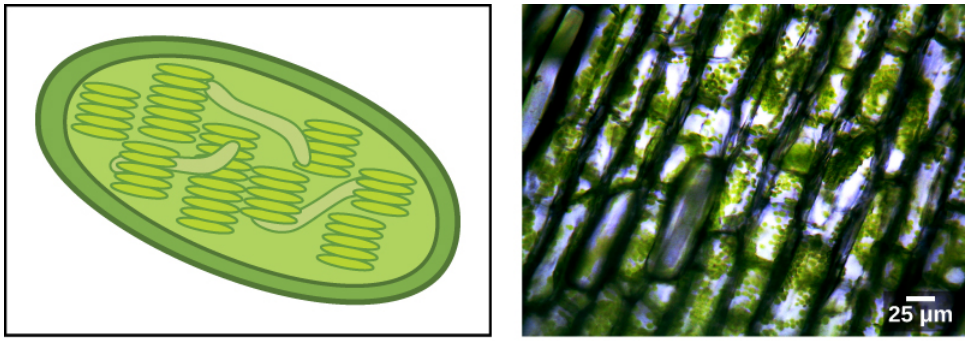
Mitochondria divide independently by a process that resembles binary fission in prokaryotes. Specifically, mitochondria are not formed from scratch (de novo) by the eukaryotic cell; they reproduce within it and are distributed with the cytoplasm when a cell divides or two cells fuse. Therefore, although these organelles are highly integrated into the eukaryotic cell, they still reproduce as if they are independent organisms within the cell. However, their reproduction is synchronized with the activity and division of the cell. Mitochondria have their own (usually) circular DNA chromosome that is stabilized by attachments to the inner membrane and carries genes similar to genes expressed by alpha-proteobacteria. Mitochondria also have special ribosomes and transfer RNAs that resemble these components in prokaryotes. These features all support that mitochondria were once free-living prokaryotes.

Mitochondria that carry out aerobic respiration have their own genomes, with genes similar to those in alpha-proteobacteria. However, many of the genes for respiratory proteins are located in the nucleus. When these genes are compared to those of other organisms, they appear to be of alpha-proteobacterial origin. Additionally, in some eukaryotic groups, such genes are found in the mitochondria, whereas in other groups, they are found in the nucleus. This has been interpreted as evidence that genes have been transferred from the endosymbiont chromosome to the host genome. This loss of genes by the endosymbiont is probably one explanation why mitochondria cannot live without a host.

Some living eukaryotes are anaerobic and cannot survive in the presence of too much oxygen. Some appear to lack organelles that could be recognized as mitochondria. In the 1970s to the early 1990s, many biologists suggested that some of these eukaryotes were descended from ancestors whose lineages had diverged from the lineage of mitochondrion-containing eukaryotes before endosymbiosis occurred. However, later findings suggest that reduced organelles are found in most, if not all, anaerobic eukaryotes, and that all eukaryotes appear to carry some genes in their nuclei that are of mitochondrial origin. In addition to the aerobic generation of ATP, mitochondria have several other metabolic functions. One of these functions is to generate clusters of iron and sulfur that are important cofactors of many enzymes. Such functions are often associated with the reduced mitochondrion-derived organelles of anaerobic eukaryotes. Therefore, most biologists accept that the last common ancestor of eukaryotes had mitochondria.

Plastids

Some groups of eukaryotes are photosynthetic. Their cells contain, in addition to the standard eukaryotic organelles, another kind of organelle called a plastid. When such cells are carrying out photosynthesis, their plastids are rich in the pigment chlorophyll *a* and a range of other pigments, called accessory pigments, which are involved in harvesting energy from light. Photosynthetic plastids are called chloroplasts (Figure **25.4.1.2**).



(a) (b)

Figure **25.4.1.2**: (a) This chloroplast cross-section illustrates its elaborate inner membrane organization. Stacks of thylakoid membranes compartmentalize photosynthetic enzymes and provide scaffolding for chloroplast DNA. (b) In this micrograph of *Elodea* sp., the chloroplasts can be seen as small green spheres. (credit b: modification of work by Brandon Zierer; scale-bar data from Matt Russell)

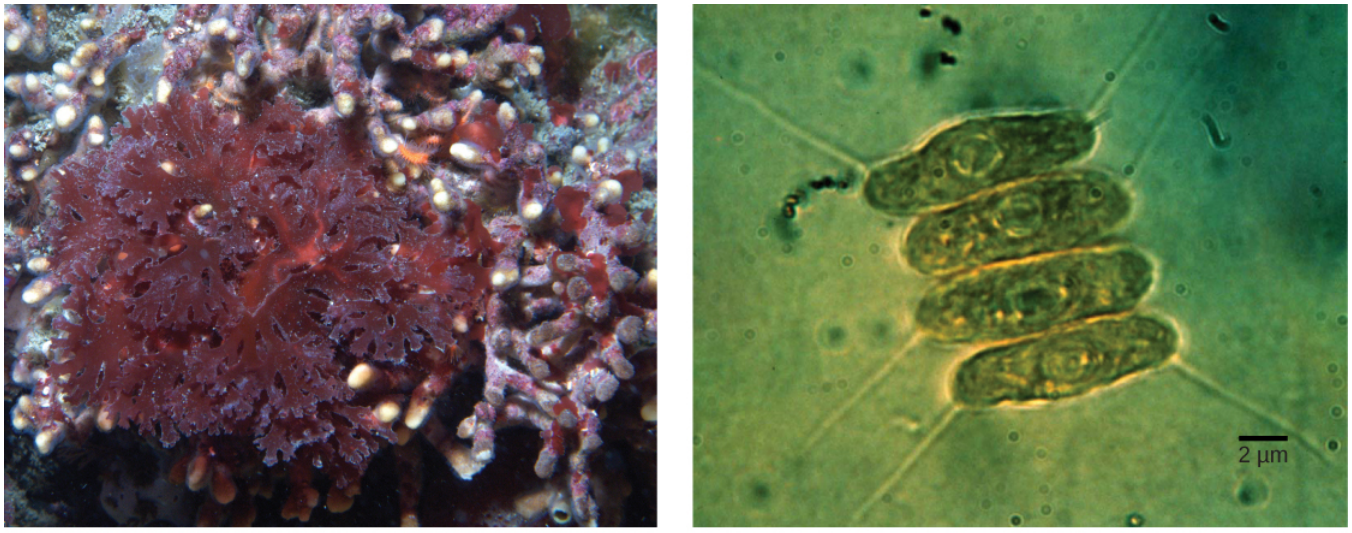
Like mitochondria, plastids appear to have an endosymbiotic origin. This hypothesis was also championed by Lynn Margulis. Plastids are derived from cyanobacteria that lived inside the cells of an ancestral, aerobic, heterotrophic eukaryote. This is called primary endosymbiosis, and plastids of primary origin are surrounded by two membranes. The best evidence is that this has happened twice in the history of eukaryotes. In one case, the common ancestor of the major lineage/supergroup Archaeplastida took on a cyanobacterial endosymbiont; in the other, the ancestor of the small amoeboid rhizarian taxon, *Paulinella*, took on a different cyanobacterial endosymbiont. Almost all photosynthetic eukaryotes are descended from the first event, and only a couple of species are derived from the other.

Cyanobacteria are a group of Gram-negative bacteria with all the conventional structures of the group. However, unlike most prokaryotes, they have extensive, internal membrane-bound sacs called thylakoids. Chlorophyll is a component of these membranes, as are many of the proteins of the light reactions of photosynthesis. Cyanobacteria also have the peptidoglycan wall and lipopolysaccharide layer associated with Gram-negative bacteria.

Chloroplasts of primary origin have thylakoids, a circular DNA chromosome, and ribosomes similar to those of cyanobacteria. Each chloroplast is surrounded by two membranes. In the group of Archaeplastida called the glaucophytes and in *Paulinella*, a thin peptidoglycan layer is present between the outer and inner plastid membranes. All other plastids lack this relictual cyanobacterial wall. The outer membrane surrounding the plastid is thought to be derived from the vacuole in the host, and the inner membrane is thought to be derived from the plasma membrane of the symbiont.

There is also, as with the case of mitochondria, strong evidence that many of the genes of the endosymbiont were transferred to the nucleus. Plastids, like mitochondria, cannot live independently outside the host. In addition, like mitochondria, plastids are derived from the division of other plastids and never built from scratch. Researchers have suggested that the endosymbiotic event that led to Archaeplastida occurred 1 to 1.5 billion years ago, at least 5 hundred million years after the fossil record suggests that eukaryotes were present.

Not all plastids in eukaryotes are derived directly from primary endosymbiosis. Some of the major groups of algae became photosynthetic by secondary endosymbiosis, that is, by taking in either green algae or red algae (both from Archaeplastida) as endosymbionts (Figure **25.4.1.3**). Numerous microscopic and genetic studies have supported this conclusion. Secondary plastids are surrounded by three or more membranes, and some secondary plastids even have clear remnants of the nucleus of endosymbiotic alga. Others have not “kept” any remnants. There are cases where tertiary or higher-order endosymbiotic events are the best explanations for plastids in some eukaryotes.



(a) (b)

Figure **25.4.1.3**: (a) Red algae and (b) green algae (visualized by light microscopy) share similar DNA sequences with photosynthetic cyanobacteria. Scientists speculate that, in a process called endosymbiosis, an ancestral prokaryote engulfed a photosynthetic cyanobacterium that evolved into modern-day chloroplasts. (credit a: modification of work by Ed Bierman; credit b: modification of work by G. Fahnenstiel, NOAA; scale-bar data from Matt Russell)

Art Connection

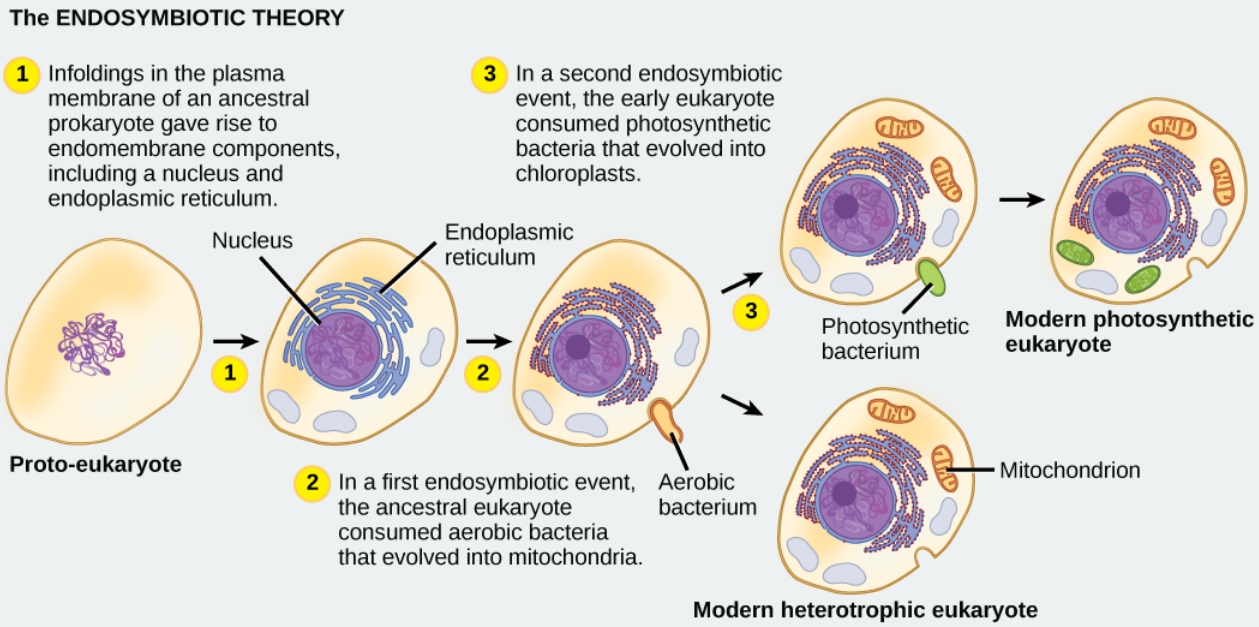


Figure **25.4.1.4**: The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote, and, in some cases, a photosynthetic prokaryote, to form mitochondria and chloroplasts, respectively.

What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Evolution Connection: Secondary Endosymbiosis in Chlorarachniophytes

Endosymbiosis involves one cell engulfing another to produce, over time, a coevolved relationship in which neither cell could survive alone. The chloroplasts of red and green algae, for instance, are derived from the engulfment of a photosynthetic cyanobacterium by an early prokaryote.

This leads to the question of the possibility of a cell containing an endosymbiont to itself become engulfed, resulting in a secondary endosymbiosis. Molecular and morphological evidence suggest that the chlorarachniophyte protists are derived from a secondary endosymbiotic event. Chlorarachniophytes are rare algae indigenous to tropical seas and sand that can be classified into the rhizarian supergroup. Chlorarachniophytes extend thin cytoplasmic strands, interconnecting themselves with other chlorarachniophytes, in a cytoplasmic network. These protists are thought to have originated when a eukaryote engulfed a green alga, the latter of which had already established an endosymbiotic relationship with a photosynthetic cyanobacterium (Figure **25.4.1.5**).

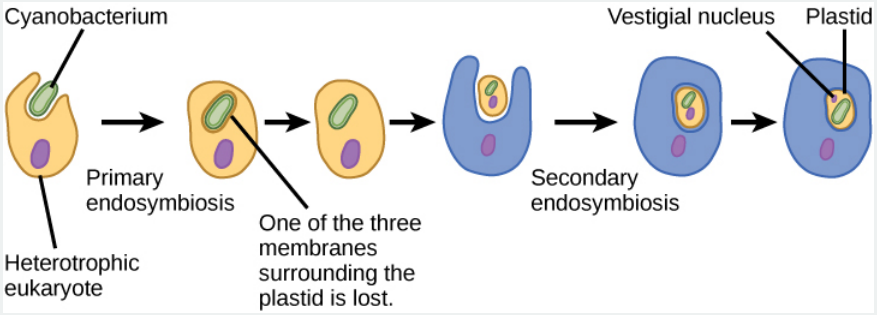


Figure **25.4.1.5**: The hypothesized process of endosymbiotic events leading to the evolution of chlorarachniophytes is shown. In a primary endosymbiotic event, a heterotrophic eukaryote consumed a cyanobacterium. In a secondary endosymbiotic event, the cell resulting from primary endosymbiosis was consumed by a second cell. The resulting organelle became a plastid in modern chlorarachniophytes.

Several lines of evidence support that chlorarachniophytes evolved from secondary endosymbiosis. The chloroplasts contained within the green algal endosymbionts still are capable of photosynthesis, making chlorarachniophytes photosynthetic. The green algal endosymbiont also exhibits a stunted vestigial nucleus. In fact, it appears that chlorarachniophytes are the products of an evolutionarily recent secondary endosymbiotic event. The plastids of chlorarachniophytes are surrounded by four membranes: The first two correspond to the inner and outer membranes of the photosynthetic cyanobacterium, the third corresponds to the green alga, and the fourth corresponds to the vacuole that surrounded the green alga when it was engulfed by the chlorarachniophyte ancestor. In other lineages that involved secondary endosymbiosis, only three membranes can be identified around plastids. This is currently rectified as a sequential loss of a membrane during the course of evolution.

The process of secondary endosymbiosis is not unique to chlorarachniophytes. In fact, secondary endosymbiosis of green algae also led to euglenid protists, whereas secondary endosymbiosis of red algae led to the evolution of dinoflagellates, apicomplexans, and stramenopiles.

Summary

The oldest fossil evidence of eukaryotes is about 2 billion years old. Fossils older than this all appear to be prokaryotes. It is probable that today's eukaryotes are descended from an ancestor that had a prokaryotic organization. The last common ancestor of today's Eukarya had several characteristics, including cells with nuclei that divided mitotically and contained linear chromosomes where the DNA was associated with histones, a cytoskeleton and endomembrane system, and the ability to make cilia/flagella during at least part of its life cycle. It was aerobic because it had mitochondria that were the result of an aerobic alpha-proteobacterium that lived inside a host cell. Whether this host had a nucleus at the time of the initial symbiosis remains unknown. The last common ancestor may have had a cell wall for at least part of its life cycle, but more data are needed to confirm this hypothesis. Today's eukaryotes are very diverse in their shapes, organization, life cycles, and number of cells per individual.

Art Connections

Figure **25.4.1.4**: What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Answer

All eukaryotic cells have mitochondria, but not all eukaryotic cells have chloroplasts.

Glossary

endosymbiosis
: engulfment of one cell within another such that the engulfed cell survives, and both cells benefit; the process responsible for the evolution of mitochondria and chloroplasts in eukaryotes

endosymbiotic theory
: theory that states that eukaryotes may have been a product of one cell engulfing another, one living within another, and evolving over time until the separate cells were no longer recognizable as such

plastid
: one of a group of related organelles in plant cells that are involved in the storage of starches, fats, proteins, and pigments

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25.4.2: Climate and the Effects of Global Climate Change

Skills to Develop

- Define global climate change
- Summarize the effects of the Industrial Revolution on global atmospheric carbon dioxide concentration
- Describe three natural factors affecting long-term global climate
- List two or more greenhouse gases and describe their role in the greenhouse effect

All biomes are universally affected by global conditions, such as climate, that ultimately shape each biome's environment. Scientists who study climate have noted a series of marked changes that have gradually become increasingly evident during the last sixty years. Global climate change is the term used to describe altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide.

Climate and Weather

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather.

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. In contrast, weather refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held on because it is difficult to accurately predict the weather on a specific day. Climate can be considered "average" weather.

Global Climate Change

Climate change can be understood by approaching three areas of study:

- current and past global climate change
- causes of past and present-day global climate change
- ancient and current results of climate change

It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. It is common for reports and discussions about global climate change to confuse the data showing that Earth's climate is changing with the factors that drive this climate change.

Evidence for Global Climate Change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on historical evidence of Earth's past climate.

Antarctic ice cores are a key example of such evidence. These ice cores are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure **25.4.2.1**a). The 0 °C on this graph refers to the long-term average. Temperatures that are greater than 0 °C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0

°C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the graph in Figure **25.4.2.1**b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles; note the relationship between carbon dioxide concentration and temperature. Figure **25.4.2.1**b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

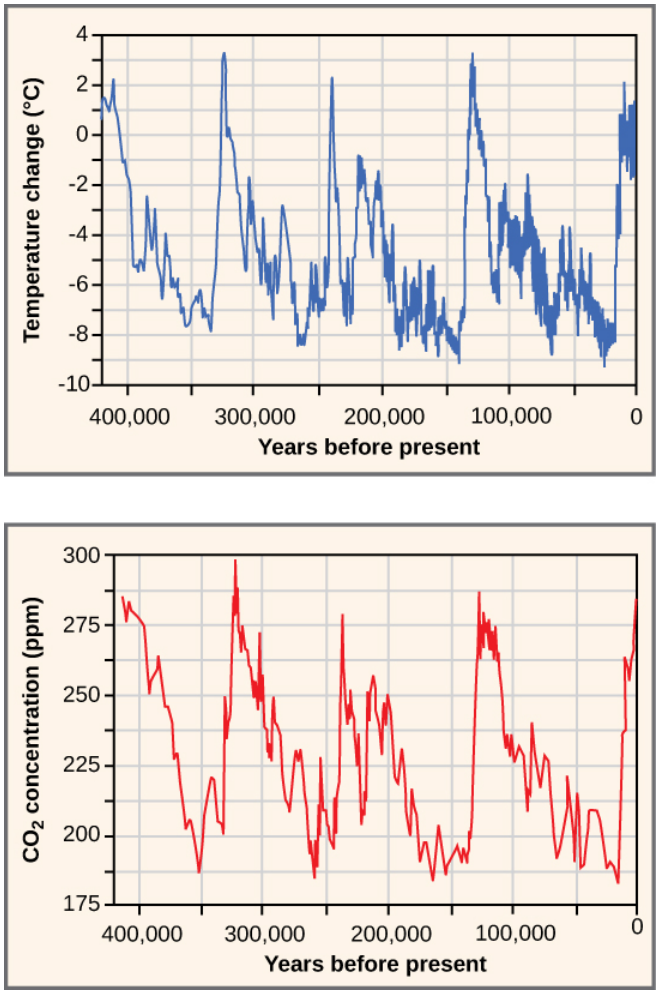


Figure **25.4.2.1:** Ice at the Russian Vostok station in East Antarctica was laid down over the course of 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern day were determined from the amount of deuterium (an isotope of hydrogen) present.

Figure **25.4.2.1**a does not show the last 2,000 years with enough detail to compare the changes of Earth's temperature during the last 400,000 years with the temperature change that has occurred in the more recent past. Two significant temperature anomalies, or irregularities, have occurred in the last 2000 years. These are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era. The Medieval Climate Anomaly occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Because of this warming, the Vikings were able to colonize Greenland.

The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is

a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The Industrial Revolution, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and the United States. New technologies were invented and provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a fossil fuel is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure **25.4.2.2**).

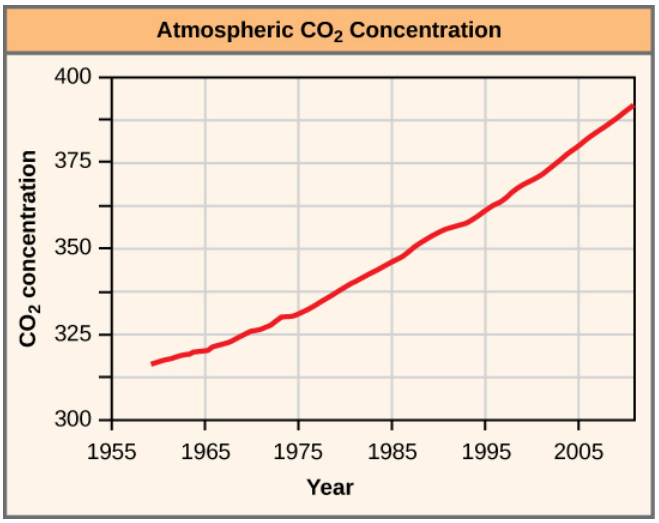


Figure **25.4.2.2**: The atmospheric concentration of CO_2 has risen steadily since the beginning of industrialization.

Current and Past Drivers of Global Climate Change

Since it is not possible to go back in time to directly observe and measure climate, scientists use indirect evidence to determine the drivers, or factors, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change: before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases. The first of these is the Milankovitch cycles. The Milankovitch cycles describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. Solar intensity is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanos in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to haze-effect cooling, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

Greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as greenhouse gases trap the heat in the atmosphere, as do the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of

the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's surface, and then a portion of that energy is re-radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface. Greenhouse gases absorb and emit radiation and are an important factor in the greenhouse effect: the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises, global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2011, the atmospheric carbon dioxide concentration was 392 ppm. However, the planet would not be inhabitable by current life forms if water vapor did not produce its drastic greenhouse warming effect.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm. Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas (Figure **25.4.2.3**). Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH_4) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Another source of methane is the melting of clathrates. Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.



Figure **25.4.2.3**: The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (credit: “Pöllö”/Wikimedia Commons)

Documented Results of Climate Change: Past and Present

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena such as retreating glaciers and melting polar ice cause a continual rise in sea level. Meanwhile, changes in climate can negatively affect organisms.

Geological Climate Change

Global warming has been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth’s geologic history. Scientists estimate that approximately 70 percent of the terrestrial plant and animal species and 84 percent of marine species became extinct, vanishing forever near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

Link to Learning



Watch this NASA video to discover the mixed effects of global warming on plant growth. While scientists found that warmer temperatures in the 1980s and 1990s caused an increase in plant productivity, this advantage has since been counteracted by more frequent droughts.

Present Climate Change

A number of global events have occurred that may be attributed to climate change during our lifetimes. Glacier National Park in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the Grinnell Glacier (Figure **25.4.2.4**) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km^3 of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.



Figure **25.4.2.4:** The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: modification of work by USGS)

This loss of ice is leading to increases in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, including the temperature of the water (the density of water is related to its temperature) and the amount of water found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the geographic distribution and phenology of

plants and animals. (Phenology is the study of the effects of climatic conditions on the timing of periodic lifecycle events, such as flowering in plants or migration in birds.) Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

Summary

The Earth has gone through periodic cycles of increases and decreases in temperature. During the past 2000 years, the Medieval Climate Anomaly was a warmer period, while the Little Ice Age was unusually cool. Both of these irregularities can be explained by natural causes of changes in climate, and, although the temperature changes were small, they had significant effects. Natural drivers of climate change include Milankovitch cycles, changes in solar activity, and volcanic eruptions. None of these factors, however, leads to rapid increases in global temperature or sustained increases in carbon dioxide. The burning of fossil fuels is an important source of greenhouse gases, which plays a major role in the greenhouse effect. Long ago, global warming resulted in the Permian extinction: a large-scale extinction event that is documented in the fossil record. Currently, modern-day climate change is associated with the increased melting of glaciers and polar ice sheets, resulting in a gradual increase in sea level. Plants and animals can also be affected by global climate change when the timing of seasonal events, such as flowering or pollination, is affected by global warming.

Glossary

clathrates
: frozen chunks of ice and methane found at the bottom of the ocean

climate
: long-term, predictable atmospheric conditions present in a specific area

global climate change
: altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide

greenhouse effect
: warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere

greenhouse gases
: atmospheric gases such as carbon dioxide and methane that absorb and emit radiation, thus trapping heat in Earth’s atmosphere

haze-effect cooling
: effect of the gases and solids from a volcanic eruption on global climate

Milankovitch cycles
: cyclic changes in the Earth's orbit that may affect climate

solar intensity
: amount of solar power energy the sun emits in a given amount of time

weather
: conditions of the atmosphere during a short period of time

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SECTION OVERVIEW

25.5: Ever-Changing Life on Earth

Skills to Develop

- Describe how the present-day theory of evolution was developed
- Define adaptation
- Explain convergent and divergent evolution
- Describe homologous and vestigial structures
- Discuss misconceptions about the theory of evolution

Evolution by natural selection describes a mechanism for how species change over time. That species change had been suggested and debated well before Darwin began to explore this idea. The view that species were static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks who expressed evolutionary ideas. In the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc Comte de Buffon who observed that various geographic regions have different plant and animal populations, even when the environments are similar. It was also accepted that there were extinct species.

During this time, James Hutton, a Scottish naturalist, proposed that geological change occurred gradually by the accumulation of small changes from processes operating like they are today over long periods of time. This contrasted with the predominant view that the geology of the planet was a consequence of catastrophic events occurring during a relatively brief past. Hutton's view was popularized in the nineteenth century by the geologist Charles Lyell who became a friend to Darwin. Lyell's ideas were influential on Darwin's thinking: Lyell's notion of the greater age of Earth gave more time for gradual change in species, and the process of change provided an analogy for gradual change in species. In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a mechanism for evolutionary change. This mechanism is now referred to as an inheritance of acquired characteristics by which modifications in an individual are caused by its environment, or the use or disuse of a structure during its lifetime, could be inherited by its offspring and thus bring about change in a species. While this mechanism for evolutionary change was discredited, Lamarck's ideas were an important influence on evolutionary thought.

Charles Darwin and Natural Selection

In the mid-nineteenth century, the actual mechanism for evolution was independently conceived of and described by two naturalists: Charles Darwin and Alfred Russel Wallace. Importantly, each naturalist spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world on *H.M.S. Beagle*, including stops in South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, like Wallace's later journeys to the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands west of Ecuador. On these islands, Darwin observed species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with a unique beak shape (Figure **25.5.1**). The species on the islands had a graded series of beak sizes and shapes with very small differences between the most similar. He observed that these finches closely resembled another finch species on the mainland of South America. Darwin imagined that the island species might be species modified from one of the original mainland species. Upon further study, he realized that the varied beaks of each finch helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks for breaking seeds, and insect-eating finches had spear-like beaks for stabbing their prey.

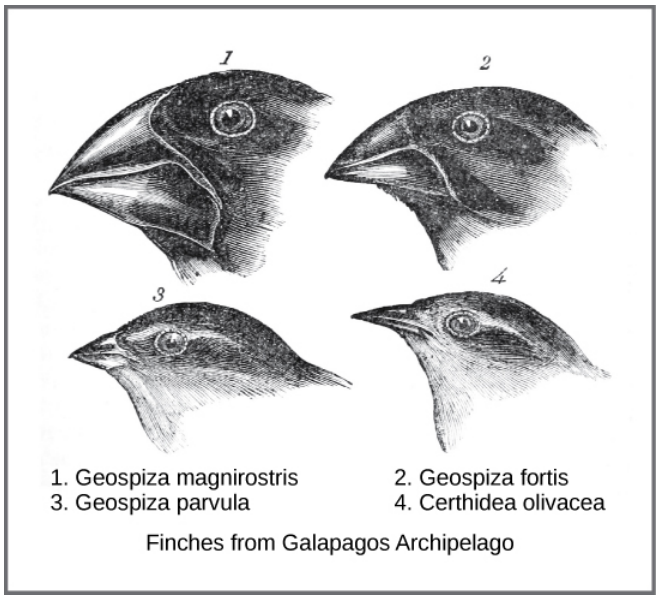


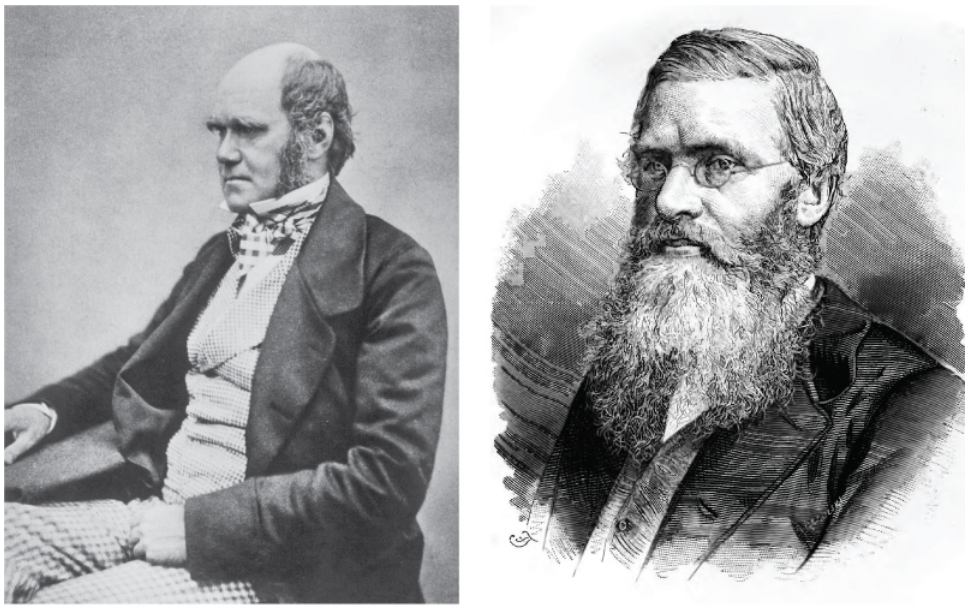
Figure **25.5.1**: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources.

Wallace and Darwin both observed similar patterns in other organisms and they independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. Natural selection, also known as "survival of the fittest," is the more prolific reproduction of individuals with favorable traits that survive environmental change because of those traits; this leads to evolutionary change.

For example, a population of giant tortoises found in the Galapagos Archipelago was observed by Darwin to have longer necks than those that lived on other islands with dry lowlands. These tortoises were "selected" because they could reach more leaves and access more food than those with short necks. In times of drought when fewer leaves would be available, those that could reach more leaves had a better chance to eat and survive than those that couldn't reach the food source. Consequently, long-necked tortoises would be more likely to be reproductively successful and pass the long-necked trait to their offspring. Over time, only long-necked tortoises would be present in the population.

Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, most characteristics of organisms are inherited, or passed from parent to offspring. Although no one, including Darwin and Wallace, knew how this happened at the time, it was a common understanding. Second, more offspring are produced than are able to survive, so resources for survival and reproduction are limited. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is competition for those resources in each generation. Both Darwin and Wallace's understanding of this principle came from reading an essay by the economist Thomas Malthus who discussed this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Darwin and Wallace reasoned that offspring with inherited characteristics which allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called descent with modification. Ultimately, natural selection leads to greater adaptation of the population to its local environment; it is the only mechanism known for adaptive evolution.

Papers by Darwin and Wallace (Figure **25.5.2**) presenting the idea of natural selection were read together in 1858 before the Linnean Society in London. The following year Darwin's book, *On the Origin of Species*, was published. His book outlined in considerable detail his arguments for evolution by natural selection.



(a) (b)

Figure **25.5.2**: Both (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Demonstrations of evolution by natural selection are time consuming and difficult to obtain. One of the best examples has been demonstrated in the very birds that helped to inspire Darwin's theory: the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of natural selection. The Grants found changes from one generation to the next in the distribution of beak shapes with the medium ground finch on the Galápagos island of Daphne Major. The birds have inherited variation in the bill shape with some birds having wide deep bills and others having thinner bills. During a period in which rainfall was higher than normal because of an El Niño, the large hard seeds that large-billed birds ate were reduced in number; however, there was an abundance of the small soft seeds which the small-billed birds ate. Therefore, survival and reproduction were much better in the following years for the small-billed birds. In the years following this El Niño, the Grants measured beak sizes in the population and found that the average bill size was smaller. Since bill size is an inherited trait, parents with smaller bills had more offspring and the size of bills had evolved to be smaller. As conditions improved in 1987 and larger seeds became more available, the trend toward smaller average bill size ceased.

Career Connection: Field Biologist

Many people hike, explore caves, scuba dive, or climb mountains for recreation. People often participate in these activities hoping to see wildlife. Experiencing the outdoors can be incredibly enjoyable and invigorating. What if your job was to be outside in the wilderness? Field biologists by definition work outdoors in the "field." The term field in this case refers to any location outdoors, even under water. A field biologist typically focuses research on a certain species, group of organisms, or a single habitat (Figure **25.5.3**).



Figure **25.5.3**: A field biologist tranquilizes a polar bear for study. (credit: Karen Rhode)

One objective of many field biologists includes discovering new species that have never been recorded. Not only do such findings expand our understanding of the natural world, but they also lead to important innovations in fields such as medicine and agriculture. Plant and microbial species, in particular, can reveal new medicinal and nutritive knowledge. Other organisms can play key roles in ecosystems or be considered rare and in need of protection. When discovered, these important species can be used as evidence for environmental regulations and laws.

Processes and Patterns of Evolution

Natural selection can only take place if there is variation, or differences, among individuals in a population. Importantly, these differences must have some genetic basis; otherwise, the selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons such as an individual being taller because of better nutrition rather than different genes.

Genetic diversity in a population comes from two main mechanisms: mutation and sexual reproduction. Mutation, a change in DNA, is the ultimate source of new alleles, or new genetic variation in any population. The genetic changes caused by mutation can have one of three outcomes on the phenotype. A mutation affects the phenotype of the organism in a way that gives it reduced fitness—lower likelihood of survival or fewer offspring. A mutation may produce a phenotype with a beneficial effect on fitness. And, many mutations will also have no effect on the fitness of the phenotype; these are called neutral mutations. Mutations may also have a whole range of effect sizes on the fitness of the organism that expresses them in their phenotype, from a small effect to a great effect. Sexual reproduction also leads to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each of the offspring.

A heritable trait that helps the survival and reproduction of an organism in its present environment is called an adaptation. Scientists describe groups of organisms becoming adapted to their environment when a change in the range of genetic variation occurs over time that increases or maintains the “fit” of the population to its environment. The webbed feet of platypuses are an adaptation for swimming. The snow leopards’ thick fur is an adaptation for living in the cold. The cheetahs’ fast speed is an adaptation for catching prey.

Whether or not a trait is favorable depends on the environmental conditions at the time. The same traits are not always selected because environmental conditions can change. For example, consider a species of plant that grew in a moist climate and did not need to conserve water. Large leaves were selected because they allowed the plant to obtain more energy from the sun. Large leaves require more water to maintain than small leaves, and the moist environment provided favorable conditions to support large leaves. After thousands of years, the climate changed, and the area no longer had excess water. The direction of natural selection shifted so that plants with small leaves were selected because those populations were able to conserve water to survive the new environmental conditions.

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. When two species evolve in diverse directions from a common point, it is called divergent evolution. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments and adaptation to different kinds of pollinators (Figure **25.5.4**).



(a) (b)

Figure **25.5.4**: Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star (*Liatrus spicata*) and the (b) purple coneflower (*Echinacea purpurea*) vary in appearance, yet both share a similar basic morphology. (credit a: modification of work by Drew Avery; credit b: modification of work by Cory Zanker)

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called convergent evolution, where similar traits evolve independently in species that do not share a recent common ancestry. The two species came to the same function, flying, but did so separately from each other.

These physical changes occur over enormous spans of time and help explain how evolution occurs. Natural selection acts on individual organisms, which in turn can shape an entire species. Although natural selection may work in a single generation on an individual, it can take thousands or even millions of years for the genotype of an entire species to evolve. It is over these large time spans that life on earth has changed and continues to change.

Evidence of Evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, to identifying patterns in nature that were consistent with evolution, and since Darwin, our understanding has become clearer and broader.

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today, and fossils show a progression of evolution. Scientists determine the age of fossils and categorize them from all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years (Figure **25.5.5**). For example, scientists have recovered highly detailed records showing the evolution of humans and horses (Figure **25.5.5**). The whale flipper shares a similar morphology to appendages of birds and mammals (Figure **25.5.6**) indicating that these species share a common ancestor.



(a) (b)

Figure **25.5.5**: In this (a) display, fossil hominids are arranged from oldest (bottom) to newest (top). As hominids evolved, the shape of the skull changed. An artist's rendition of (b) extinct species of the genus *Equus* reveals that these ancient species resembled the modern horse (*Equus ferus*) but varied in size.

Anatomy and Embryology

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction (Figure **25.5.6**) resulting from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout. Scientists call these synonymous parts homologous structures.

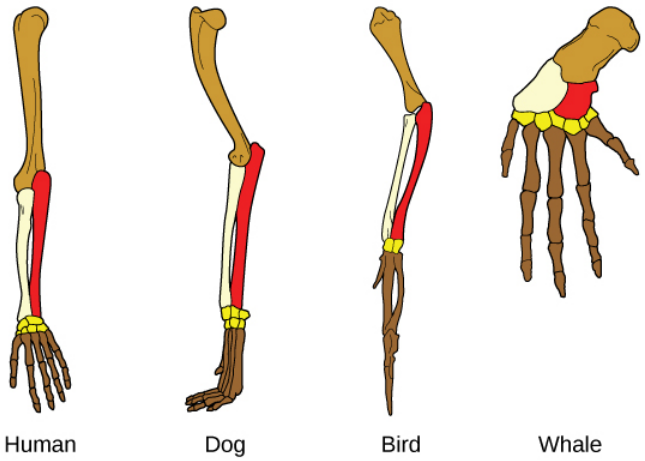


Figure **25.5.6**: The similar construction of these appendages indicates that these organisms share a common ancestor.

Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past common ancestor. These unused structures without function are called vestigial structures. Other examples of vestigial structures are wings on flightless birds, leaves on some cacti, and hind leg bones in whales.

Link to Learning

Visit this interactive site to guess which bones structures are homologous and which are analogous, and see examples of evolutionary adaptations to illustrate these concepts.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan, living in the arctic region have been selected for seasonal white phenotypes

during winter to blend with the snow and ice (Figure **25.5.7**). These similarities occur not because of common ancestry, but because of similar selection pressures—the benefits of not being seen by predators.



(a) (b)

Figure **25.5.7**: The white winter coat of the (a) arctic fox and the (b) ptarmigan's plumage are adaptations to their environments. (credit a: modification of work by Keith Morehouse)

Embryology, the study of the development of the anatomy of an organism to its adult form, also provides evidence of relatedness between now widely divergent groups of organisms. Mutational tweaking in the embryo can have such magnified consequences in the adult that embryo formation tends to be conserved. As a result, structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits and tails at some point in their early development. These disappear in the adults of terrestrial groups but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by the time of birth.

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of members of the plant family Proteaceae in Australia, southern Africa, and South America is best explained by their presence prior to the southern supercontinent Gondwana breaking up.

The great diversification of marsupials in Australia and the absence of other mammals reflect Australia's long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents species from migrating. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all unique to their one point of origin, yet they display distant relationships to ancestral species on mainlands.

Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material and in the near universality of the genetic code and the machinery of DNA replication and expression. Fundamental divisions in life between the three domains are reflected in major structural differences in otherwise conservative structures such as the components of ribosomes and the structures of membranes.

In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences—exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events that allow the free modification of one copy by mutation, selection, or drift (changes in a population's gene pool resulting from chance), while the second copy continues to produce a functional protein.

Misconceptions of Evolution

Although the theory of evolution generated some controversy when it was first proposed, it was almost universally accepted by biologists, particularly younger biologists, within 20 years after publication of *On the Origin of Species*. Nevertheless, the theory of evolution is a difficult concept and misconceptions about how it works abound

Link to Learning

This site addresses some of the main misconceptions associated with the theory of evolution.

Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word "theory" with the way scientists use the word. In science, a "theory" is understood to be a body of thoroughly tested and verified explanations for a set of observations of the natural world. Scientists have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes understood facts about the world. In the same way, the theory of evolution describes facts about the living world. As such, a theory in science has survived significant efforts to discredit it by scientists. In contrast, a "theory" in common vernacular is a word meaning a guess or suggested explanation; this meaning is more akin to the scientific concept of "hypothesis." When critics of evolution say evolution is "just a theory," they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mischaracterization.

Individuals Evolve

Evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, obviously, but this is called development and involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking about the evolution of a characteristic, it is probably best to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium-ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time and then measures the average bill size in the population several years later, this average value will be different as a result of evolution. Although some individuals may survive from the first time to the second, they will still have the same bill size; however, there will be many new individuals that contribute to the shift in average bill size.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics believe that it cannot explain the origin of life. The theory does not try to explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies the origin of species. It does not shed light on the beginnings of life including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, and presumably it just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA either within a cell or pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the

expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Organisms Evolve on Purpose

Statements such as “organisms evolve in response to a change in an environment” are quite common, but such statements can lead to two types of misunderstandings. First, the statement must not be understood to mean that individual organisms evolve. The statement is shorthand for “a population evolves in response to a changing environment.” However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and therefore producing proportionately more offspring than other phenotypes. This results in change in the population if the characteristics are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic.

In a larger sense, evolution is not goal directed. Species do not become “better” over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species, despite the commonness of this kind of language in popular discourse. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at some point in the future. This holds equally well for a species of insect as it does the human species.

Summary

Evolution is the process of adaptation through mutation which allows more desirable characteristics to be passed to the next generation. Over time, organisms evolve more characteristics that are beneficial to their survival. For living organisms to adapt and change to environmental pressures, genetic variation must be present. With genetic variation, individuals have differences in form and function that allow some to survive certain conditions better than others. These organisms pass their favorable traits to their offspring. Eventually, environments change, and what was once a desirable, advantageous trait may become an undesirable trait and organisms may further evolve. Evolution may be convergent with similar traits evolving in multiple species or divergent with diverse traits evolving in multiple species that came from a common ancestor. Evidence of evolution can be observed by means of DNA code and the fossil record, and also by the existence of homologous and vestigial structures.

Glossary

adaptation
: heritable trait or behavior in an organism that aids in its survival and reproduction in its present environment

convergent evolution
: process by which groups of organisms independently evolve to similar forms

divergent evolution
: process by which groups of organisms evolve in diverse directions from a common point

homologous structures
: parallel structures in diverse organisms that have a common ancestor

natural selection

reproduction of individuals with favorable genetic traits that survive environmental change because of those traits, leading to evolutionary change

variation
genetic differences among individuals in a population

vestigial structure
physical structure present in an organism but that has no apparent function and appears to be from a functional structure in a distant ancestor

25.5.1: Eukaryotic Origins

25.5.2: The Evolutionary History of the Animal Kingdom

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25.5.1: Eukaryotic Origins

Skills to Develop

- List the unifying characteristics of eukaryotes
- Describe what scientists know about the origins of eukaryotes based on the last common ancestor
- Explain endosymbiotic theory

Living things fall into three large groups: Archaea, Bacteria, and Eukarya. The first two have prokaryotic cells, and the third contains all eukaryotes. A relatively sparse fossil record is available to help discern what the first members of each of these lineages looked like, so it is possible that all the events that led to the last common ancestor of extant eukaryotes will remain unknown. However, comparative biology of extant organisms and the limited fossil record provide some insight into the history of Eukarya.

The earliest fossils found appear to be Bacteria, most likely cyanobacteria. They are about 3.5 billion years old and are recognizable because of their relatively complex structure and, for prokaryotes, relatively large cells. Most other prokaryotes have small cells, 1 or 2 µm in size, and would be difficult to pick out as fossils. Most living eukaryotes have cells measuring 10 µm or greater. Structures this size, which might be fossils, appear in the geological record about 2.1 billion years ago.

Characteristics of Eukaryotes

Data from these fossils have led comparative biologists to the conclusion that living eukaryotes are all descendants of a single common ancestor. Mapping the characteristics found in all major groups of eukaryotes reveals that the following characteristics must have been present in the last common ancestor, because these characteristics are present in at least some of the members of each major lineage.

1. Cells with nuclei surrounded by a nuclear envelope with nuclear pores. This is the single characteristic that is both necessary and sufficient to define an organism as a eukaryote. All extant eukaryotes have cells with nuclei.
2. Mitochondria. Some extant eukaryotes have very reduced remnants of mitochondria in their cells, whereas other members of their lineages have “typical” mitochondria.
3. A cytoskeleton containing the structural and motility components called actin microfilaments and microtubules. All extant eukaryotes have these cytoskeletal elements.
4. Flagella and cilia, organelles associated with cell motility. Some extant eukaryotes lack flagella and/or cilia, but they are descended from ancestors that possessed them.
5. Chromosomes, each consisting of a linear DNA molecule coiled around basic (alkaline) proteins called histones. The few eukaryotes with chromosomes lacking histones clearly evolved from ancestors that had them.
6. Mitosis, a process of nuclear division wherein replicated chromosomes are divided and separated using elements of the cytoskeleton. Mitosis is universally present in eukaryotes.
7. Sex, a process of genetic recombination unique to eukaryotes in which diploid nuclei at one stage of the life cycle undergo meiosis to yield haploid nuclei and subsequent karyogamy, a stage where two haploid nuclei fuse together to create a diploid zygote nucleus.
8. Members of all major lineages have cell walls, and it might be reasonable to conclude that the last common ancestor could make cell walls during some stage of its life cycle. However, not enough is known about eukaryotes’ cell walls and their development to know how much homology exists among them. If the last common ancestor could make cell walls, it is clear that this ability must have been lost in many groups.

Endosymbiosis and the Evolution of Eukaryotes

In order to understand eukaryotic organisms fully, it is necessary to understand that all extant eukaryotes are descendants of a chimeric organism that was a composite of a host cell and the cell(s) of an alpha-proteobacterium that “took up residence” inside it. This major theme in the origin of eukaryotes is known as endosymbiosis, one cell engulfing another such that the engulfed cell survives and both cells benefit. Over many generations, a symbiotic relationship can result in two organisms that depend on each other so completely that neither could survive on its own. Endosymbiotic events likely contributed to the origin of the last common

ancestor of today's eukaryotes and to later diversification in certain lineages of eukaryotes (Figure **25.5.1.4**). Before explaining this further, it is necessary to consider metabolism in prokaryotes.

Prokaryotic Metabolism

Many important metabolic processes arose in prokaryotes, and some of these, such as nitrogen fixation, are never found in eukaryotes. The process of aerobic respiration is found in all major lineages of eukaryotes, and it is localized in the mitochondria. Aerobic respiration is also found in many lineages of prokaryotes, but it is not present in all of them, and many forms of evidence suggest that such anaerobic prokaryotes never carried out aerobic respiration nor did their ancestors.

While today's atmosphere is about one-fifth molecular oxygen (O_2), geological evidence shows that it originally lacked O_2. Without oxygen, aerobic respiration would not be expected, and living things would have relied on fermentation instead. At some point before, about 3.5 billion years ago, some prokaryotes began using energy from sunlight to power anabolic processes that reduce carbon dioxide to form organic compounds. That is, they evolved the ability to photosynthesize. Hydrogen, derived from various sources, was captured using light-powered reactions to reduce fixed carbon dioxide in the Calvin cycle. The group of Gram-negative bacteria that gave rise to cyanobacteria used water as the hydrogen source and released O_2 as a waste product.

Eventually, the amount of photosynthetic oxygen built up in some environments to levels that posed a risk to living organisms, since it can damage many organic compounds. Various metabolic processes evolved that protected organisms from oxygen, one of which, aerobic respiration, also generated high levels of ATP. It became widely present among prokaryotes, including in a group we now call alpha-proteobacteria. Organisms that did not acquire aerobic respiration had to remain in oxygen-free environments. Originally, oxygen-rich environments were likely localized around places where cyanobacteria were active, but by about 2 billion years ago, geological evidence shows that oxygen was building up to higher concentrations in the atmosphere. Oxygen levels similar to today's levels only arose within the last 700 million years.

Recall that the first fossils that we believe to be eukaryotes date to about 2 billion years old, so they appeared as oxygen levels were increasing. Also, recall that all extant eukaryotes descended from an ancestor with mitochondria. These organelles were first observed by light microscopists in the late 1800s, where they appeared to be somewhat worm-shaped structures that seemed to be moving around in the cell. Some early observers suggested that they might be bacteria living inside host cells, but these hypotheses remained unknown or rejected in most scientific communities.

Endosymbiotic Theory

As cell biology developed in the twentieth century, it became clear that mitochondria were the organelles responsible for producing ATP using aerobic respiration. In the 1960s, American biologist Lynn Margulis developed endosymbiotic theory, which states that eukaryotes may have been a product of one cell engulfing another, one living within another, and evolving over time until the separate cells were no longer recognizable as such. In 1967, Margulis introduced new work on the theory and substantiated her findings through microbiological evidence. Although Margulis' work initially was met with resistance, this once-revolutionary hypothesis is now widely (but not completely) accepted, with work progressing on uncovering the steps involved in this evolutionary process and the key players involved. Much still remains to be discovered about the origins of the cells that now make up the cells in all living eukaryotes.

Broadly, it has become clear that many of our nuclear genes and the molecular machinery responsible for replication and expression appear closely related to those in Archaea. On the other hand, the metabolic organelles and genes responsible for many energy-harvesting processes had their origins in bacteria. Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of discovery in biology. For instance, it is not known whether the endosymbiotic event that led to mitochondria occurred before or after the host cell had a nucleus. Such organisms would be among the extinct precursors of the last common ancestor of eukaryotes.

Mitochondria

One of the major features distinguishing prokaryotes from eukaryotes is the presence of mitochondria. Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption. Each mitochondrion measures 1 to 10 or greater micrometers in length and exists in the cell as an organelle that can be ovoid to worm-shaped to intricately branched (Figure **25.5.1.1**). Mitochondria arise from the division of existing mitochondria; they may fuse

together; and they may be moved around inside the cell by interactions with the cytoskeleton. However, mitochondria cannot survive outside the cell. As the atmosphere was oxygenated by photosynthesis, and as successful aerobic prokaryotes evolved, evidence suggests that an ancestral cell with some membrane compartmentalization engulfed a free-living aerobic prokaryote, specifically an alpha-proteobacterium, thereby giving the host cell the ability to use oxygen to release energy stored in nutrients. Alpha-proteobacteria are a large group of bacteria that includes species symbiotic with plants, disease organisms that can infect humans via ticks, and many free-living species that use light for energy. Several lines of evidence support that mitochondria are derived from this endosymbiotic event. Most mitochondria are shaped like alpha-proteobacteria and are surrounded by two membranes, which would result when one membrane-bound organism was engulfed into a vacuole by another membrane-bound organism. The mitochondrial inner membrane is extensive and involves substantial infoldings called cristae that resemble the textured, outer surface of alpha-proteobacteria. The matrix and inner membrane are rich with the enzymes necessary for aerobic respiration.

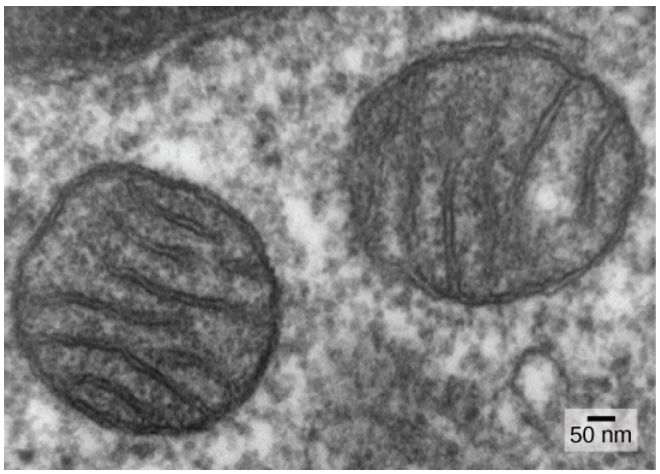


Figure **25.5.1.1**: In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section. (credit: Louise Howard)

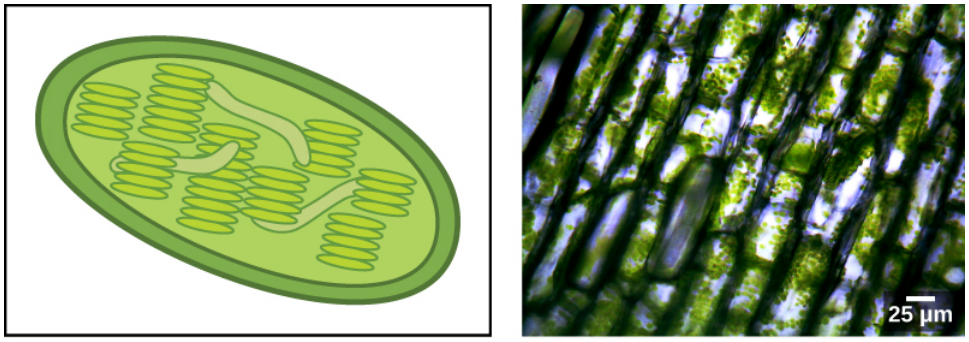
Mitochondria divide independently by a process that resembles binary fission in prokaryotes. Specifically, mitochondria are not formed from scratch (de novo) by the eukaryotic cell; they reproduce within it and are distributed with the cytoplasm when a cell divides or two cells fuse. Therefore, although these organelles are highly integrated into the eukaryotic cell, they still reproduce as if they are independent organisms within the cell. However, their reproduction is synchronized with the activity and division of the cell. Mitochondria have their own (usually) circular DNA chromosome that is stabilized by attachments to the inner membrane and carries genes similar to genes expressed by alpha-proteobacteria. Mitochondria also have special ribosomes and transfer RNAs that resemble these components in prokaryotes. These features all support that mitochondria were once free-living prokaryotes.

Mitochondria that carry out aerobic respiration have their own genomes, with genes similar to those in alpha-proteobacteria. However, many of the genes for respiratory proteins are located in the nucleus. When these genes are compared to those of other organisms, they appear to be of alpha-proteobacterial origin. Additionally, in some eukaryotic groups, such genes are found in the mitochondria, whereas in other groups, they are found in the nucleus. This has been interpreted as evidence that genes have been transferred from the endosymbiont chromosome to the host genome. This loss of genes by the endosymbiont is probably one explanation why mitochondria cannot live without a host.

Some living eukaryotes are anaerobic and cannot survive in the presence of too much oxygen. Some appear to lack organelles that could be recognized as mitochondria. In the 1970s to the early 1990s, many biologists suggested that some of these eukaryotes were descended from ancestors whose lineages had diverged from the lineage of mitochondrion-containing eukaryotes before endosymbiosis occurred. However, later findings suggest that reduced organelles are found in most, if not all, anaerobic eukaryotes, and that all eukaryotes appear to carry some genes in their nuclei that are of mitochondrial origin. In addition to the aerobic generation of ATP, mitochondria have several other metabolic functions. One of these functions is to generate clusters of iron and sulfur that are important cofactors of many enzymes. Such functions are often associated with the reduced mitochondrion-derived organelles of anaerobic eukaryotes. Therefore, most biologists accept that the last common ancestor of eukaryotes had mitochondria.

Plastids

Some groups of eukaryotes are photosynthetic. Their cells contain, in addition to the standard eukaryotic organelles, another kind of organelle called a plastid. When such cells are carrying out photosynthesis, their plastids are rich in the pigment chlorophyll *a* and a range of other pigments, called accessory pigments, which are involved in harvesting energy from light. Photosynthetic plastids are called chloroplasts (Figure **25.5.1.2**).



(a) (b)

Figure **25.5.1.2**: (a) This chloroplast cross-section illustrates its elaborate inner membrane organization. Stacks of thylakoid membranes compartmentalize photosynthetic enzymes and provide scaffolding for chloroplast DNA. (b) In this micrograph of *Elodea* sp., the chloroplasts can be seen as small green spheres. (credit b: modification of work by Brandon Zierer; scale-bar data from Matt Russell)

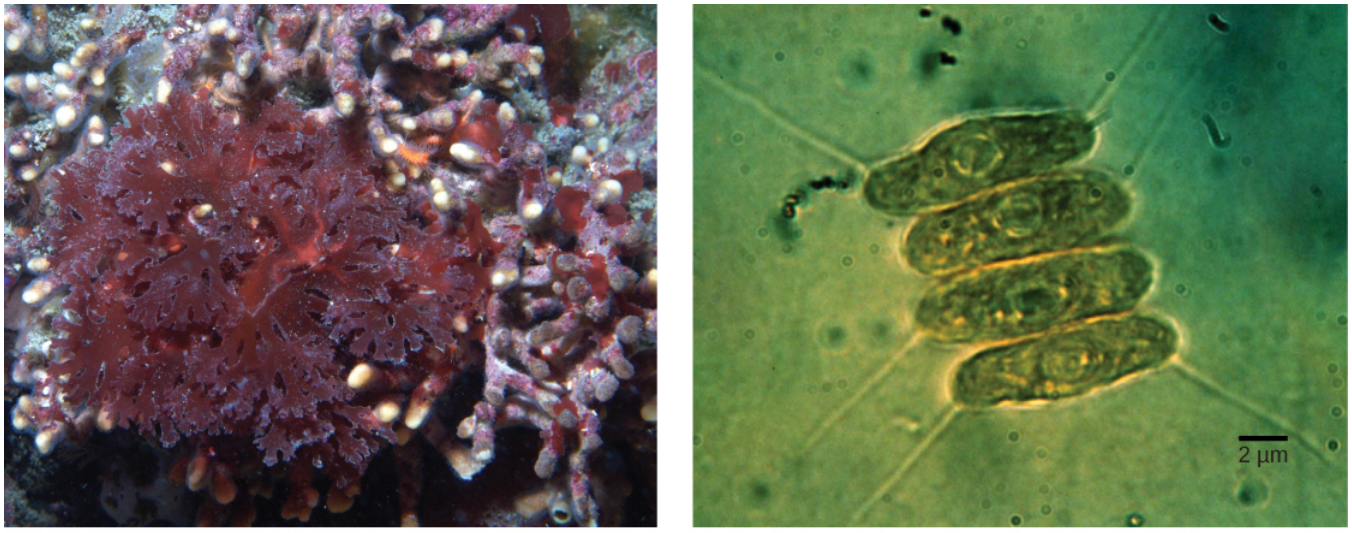
Like mitochondria, plastids appear to have an endosymbiotic origin. This hypothesis was also championed by Lynn Margulis. Plastids are derived from cyanobacteria that lived inside the cells of an ancestral, aerobic, heterotrophic eukaryote. This is called primary endosymbiosis, and plastids of primary origin are surrounded by two membranes. The best evidence is that this has happened twice in the history of eukaryotes. In one case, the common ancestor of the major lineage/supergroup Archaeplastida took on a cyanobacterial endosymbiont; in the other, the ancestor of the small amoeboid rhizarian taxon, *Paulinella*, took on a different cyanobacterial endosymbiont. Almost all photosynthetic eukaryotes are descended from the first event, and only a couple of species are derived from the other.

Cyanobacteria are a group of Gram-negative bacteria with all the conventional structures of the group. However, unlike most prokaryotes, they have extensive, internal membrane-bound sacs called thylakoids. Chlorophyll is a component of these membranes, as are many of the proteins of the light reactions of photosynthesis. Cyanobacteria also have the peptidoglycan wall and lipopolysaccharide layer associated with Gram-negative bacteria.

Chloroplasts of primary origin have thylakoids, a circular DNA chromosome, and ribosomes similar to those of cyanobacteria. Each chloroplast is surrounded by two membranes. In the group of Archaeplastida called the glaucophytes and in *Paulinella*, a thin peptidoglycan layer is present between the outer and inner plastid membranes. All other plastids lack this relictual cyanobacterial wall. The outer membrane surrounding the plastid is thought to be derived from the vacuole in the host, and the inner membrane is thought to be derived from the plasma membrane of the symbiont.

There is also, as with the case of mitochondria, strong evidence that many of the genes of the endosymbiont were transferred to the nucleus. Plastids, like mitochondria, cannot live independently outside the host. In addition, like mitochondria, plastids are derived from the division of other plastids and never built from scratch. Researchers have suggested that the endosymbiotic event that led to Archaeplastida occurred 1 to 1.5 billion years ago, at least 5 hundred million years after the fossil record suggests that eukaryotes were present.

Not all plastids in eukaryotes are derived directly from primary endosymbiosis. Some of the major groups of algae became photosynthetic by secondary endosymbiosis, that is, by taking in either green algae or red algae (both from Archaeplastida) as endosymbionts (Figure **25.5.1.3**). Numerous microscopic and genetic studies have supported this conclusion. Secondary plastids are surrounded by three or more membranes, and some secondary plastids even have clear remnants of the nucleus of endosymbiotic alga. Others have not “kept” any remnants. There are cases where tertiary or higher-order endosymbiotic events are the best explanations for plastids in some eukaryotes.



(a) (b)

Figure **25.5.1.3**: (a) Red algae and (b) green algae (visualized by light microscopy) share similar DNA sequences with photosynthetic cyanobacteria. Scientists speculate that, in a process called endosymbiosis, an ancestral prokaryote engulfed a photosynthetic cyanobacterium that evolved into modern-day chloroplasts. (credit a: modification of work by Ed Bierman; credit b: modification of work by G. Fahnenstiel, NOAA; scale-bar data from Matt Russell)

Art Connection

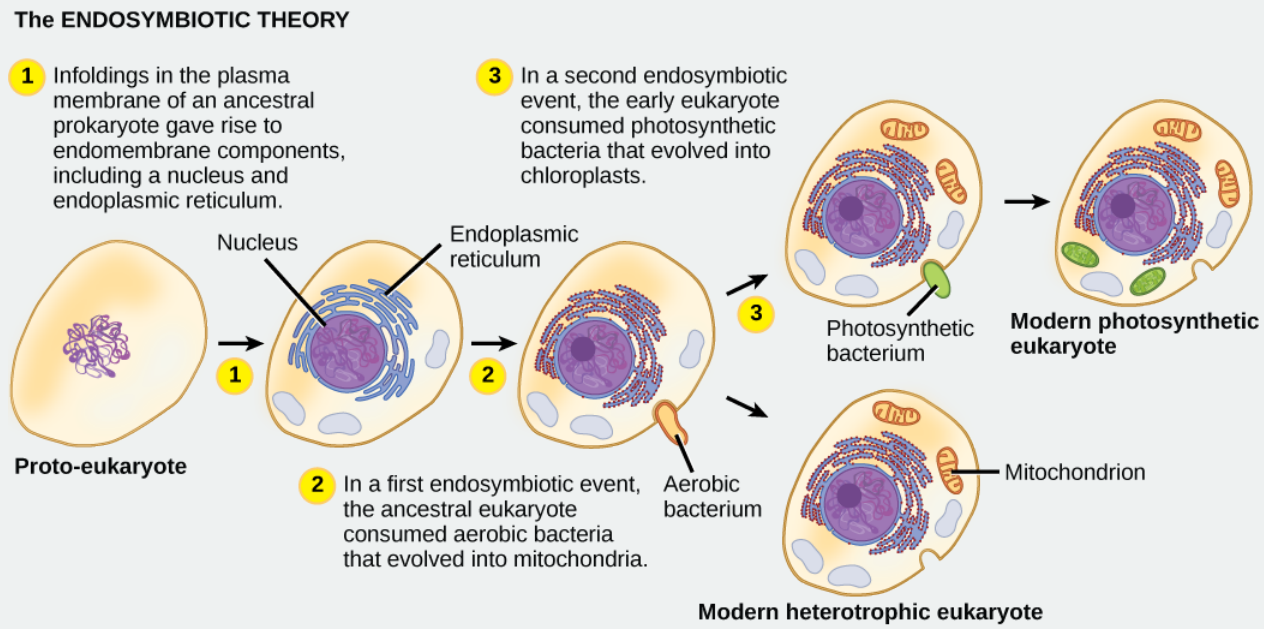


Figure **25.5.1.4**: The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote, and, in some cases, a photosynthetic prokaryote, to form mitochondria and chloroplasts, respectively.

What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Evolution Connection: Secondary Endosymbiosis in Chlorarachniophytes

Endosymbiosis involves one cell engulfing another to produce, over time, a coevolved relationship in which neither cell could survive alone. The chloroplasts of red and green algae, for instance, are derived from the engulfment of a photosynthetic cyanobacterium by an early prokaryote.

This leads to the question of the possibility of a cell containing an endosymbiont to itself become engulfed, resulting in a secondary endosymbiosis. Molecular and morphological evidence suggest that the chlorarachniophyte protists are derived from a secondary endosymbiotic event. Chlorarachniophytes are rare algae indigenous to tropical seas and sand that can be classified into the rhizarian supergroup. Chlorarachniophytes extend thin cytoplasmic strands, interconnecting themselves with other chlorarachniophytes, in a cytoplasmic network. These protists are thought to have originated when a eukaryote engulfed a green alga, the latter of which had already established an endosymbiotic relationship with a photosynthetic cyanobacterium (Figure **25.5.1.5**).

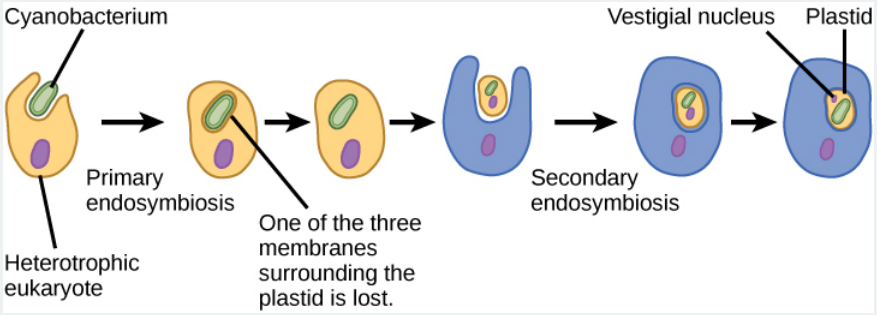


Figure **25.5.1.5**: The hypothesized process of endosymbiotic events leading to the evolution of chlorarachniophytes is shown. In a primary endosymbiotic event, a heterotrophic eukaryote consumed a cyanobacterium. In a secondary endosymbiotic event, the cell resulting from primary endosymbiosis was consumed by a second cell. The resulting organelle became a plastid in modern chlorarachniophytes.

Several lines of evidence support that chlorarachniophytes evolved from secondary endosymbiosis. The chloroplasts contained within the green algal endosymbionts still are capable of photosynthesis, making chlorarachniophytes photosynthetic. The green algal endosymbiont also exhibits a stunted vestigial nucleus. In fact, it appears that chlorarachniophytes are the products of an evolutionarily recent secondary endosymbiotic event. The plastids of chlorarachniophytes are surrounded by four membranes: The first two correspond to the inner and outer membranes of the photosynthetic cyanobacterium, the third corresponds to the green alga, and the fourth corresponds to the vacuole that surrounded the green alga when it was engulfed by the chlorarachniophyte ancestor. In other lineages that involved secondary endosymbiosis, only three membranes can be identified around plastids. This is currently rectified as a sequential loss of a membrane during the course of evolution.

The process of secondary endosymbiosis is not unique to chlorarachniophytes. In fact, secondary endosymbiosis of green algae also led to euglenid protists, whereas secondary endosymbiosis of red algae led to the evolution of dinoflagellates, apicomplexans, and stramenopiles.

Summary

The oldest fossil evidence of eukaryotes is about 2 billion years old. Fossils older than this all appear to be prokaryotes. It is probable that today's eukaryotes are descended from an ancestor that had a prokaryotic organization. The last common ancestor of today's Eukarya had several characteristics, including cells with nuclei that divided mitotically and contained linear chromosomes where the DNA was associated with histones, a cytoskeleton and endomembrane system, and the ability to make cilia/flagella during at least part of its life cycle. It was aerobic because it had mitochondria that were the result of an aerobic alpha-proteobacterium that lived inside a host cell. Whether this host had a nucleus at the time of the initial symbiosis remains unknown. The last common ancestor may have had a cell wall for at least part of its life cycle, but more data are needed to confirm this hypothesis. Today's eukaryotes are very diverse in their shapes, organization, life cycles, and number of cells per individual.

Art Connections

Figure **25.5.1.4**: What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Answer

All eukaryotic cells have mitochondria, but not all eukaryotic cells have chloroplasts.

Glossary

endosymbiosis
: engulfment of one cell within another such that the engulfed cell survives, and both cells benefit; the process responsible for the evolution of mitochondria and chloroplasts in eukaryotes

endosymbiotic theory
: theory that states that eukaryotes may have been a product of one cell engulfing another, one living within another, and evolving over time until the separate cells were no longer recognizable as such

plastid
: one of a group of related organelles in plant cells that are involved in the storage of starches, fats, proteins, and pigments

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25.5.2: The Evolutionary History of the Animal Kingdom

Skills to Develop

- Describe the features that characterized the earliest animals and when they appeared on earth
- Explain the significance of the Cambrian period for animal evolution and the changes in animal diversity that took place during that time
- Describe some of the unresolved questions surrounding the Cambrian explosion
- Discuss the implications of mass animal extinctions that have occurred in evolutionary history

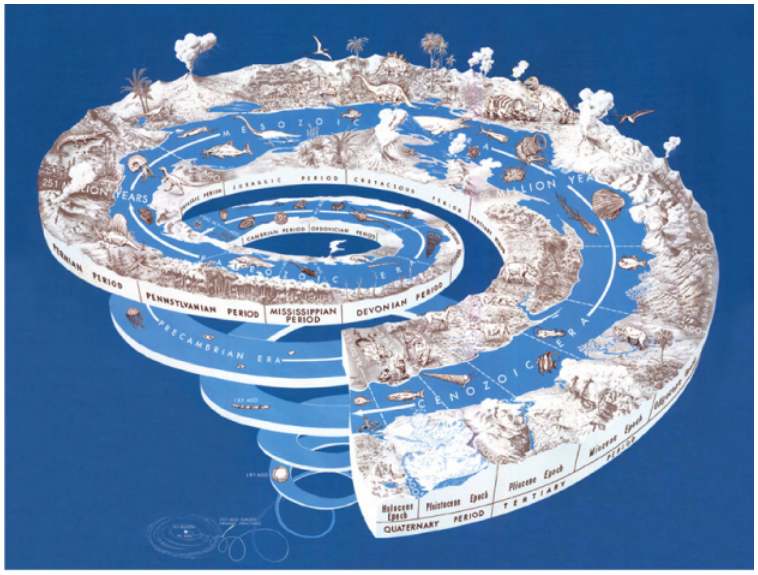
Many questions regarding the origins and evolutionary history of the animal kingdom continue to be researched and debated, as new fossil and molecular evidence change prevailing theories. Some of these questions include the following: How long have animals existed on Earth? What were the earliest members of the animal kingdom, and what organism was their common ancestor? While animal diversity increased during the Cambrian period of the Paleozoic era, 530 million years ago, modern fossil evidence suggests that primitive animal species existed much earlier.

Pre-Cambrian Animal Life

The time before the Cambrian period is known as the Ediacaran period (from about 635 million years ago to 543 million years ago), the final period of the late Proterozoic Neoproterozoic Era (Figure **25.5.2.1**). It is believed that early animal life, termed Ediacaran biota, evolved from protists at this time. Some protest species called choanoflagellates closely resemble the choanocyte cells in the simplest animals, sponges. In addition to their morphological similarity, molecular analyses have revealed similar sequence homologies in their DNA.

EON	ERA	PERIOD	MILLIONS OF YEARS AGO
Phanerozoic	Cenozoic	Quaternary	1.6
		Tertiary	66
	Mesozoic	Cretaceous	138
		Jurassic	205
		Triassic	240
	Paleozoic	Permian	290
		Pennsylvanian	330
		Mississippian	360
		Devonian	410
		Silurian	435
		Ordovician	500
		Cambrian	540
Proterozoic	Late Proterozoic Middle Proterozoic Early Proterozoic	Ediacaran 635-543 MYA	2500
Archean	Late Archean Middle Archean Early Archean		3800?
Pre-Archean			

(a)



(b)

Figure **25.5.2.1**: (a) Earth's history is divided into eons, eras, and periods. Note that the Ediacaran period starts in the Proterozoic eon and ends in the Cambrian period of the Phanerozoic eon. (b) Stages on the geological time scale are represented as a spiral. (credit: modification of work by USGS)

The earliest life comprising Ediacaran biota was long believed to include only tiny, sessile, soft-bodied sea creatures. However, recently there has been increasing scientific evidence suggesting that more varied and complex animal species lived during this time, and possibly even before the Ediacaran period.

Fossils believed to represent the oldest animals with hard body parts were recently discovered in South Australia. These sponge-like fossils, named *Coronacollina acula*, date back as far as 560 million years, and are believed to show the existence of hard body parts and spicules that extended 20–40 cm from the main body (estimated about 5 cm long). Other fossils from the Ediacaran period are shown in Figure **25.5.2.2**.



(a) (b)

Figure **25.5.2.2**: Fossils of (a) *Cyclomedusa* and (b) *Dickinsonia* date to 650 million years ago, during the Ediacaran period. (credit: modification of work by "Smith609"/Wikimedia Commons)

Another recent fossil discovery may represent the earliest animal species ever found. While the validity of this claim is still under investigation, these primitive fossils appear to be small, one-centimeter long, sponge-like creatures. These fossils from South Australia date back 650 million years, actually placing the putative animal before the great ice age extinction event that marked the transition between the Cryogenian period and the Ediacaran period. Until this discovery, most scientists believed that there was no animal life prior to the Ediacaran period. Many scientists now believe that animals may in fact have evolved during the Cryogenian period.

The Cambrian Explosion of Animal Life

The Cambrian period, occurring between approximately 542–488 million years ago, marks the most rapid evolution of new animal phyla and animal diversity in Earth's history. It is believed that most of the animal phyla in existence today had their origins during this time, often referred to as the Cambrian explosion (Figure 27.4.3). Echinoderms, mollusks, worms, arthropods, and chordates arose during this period. One of the most dominant species during the Cambrian period was the trilobite, an arthropod that was among the first animals to exhibit a sense of vision (Figure **25.5.2.4**).



Figure **25.5.2.3**: An artist's rendition depicts some organisms from the Cambrian period.

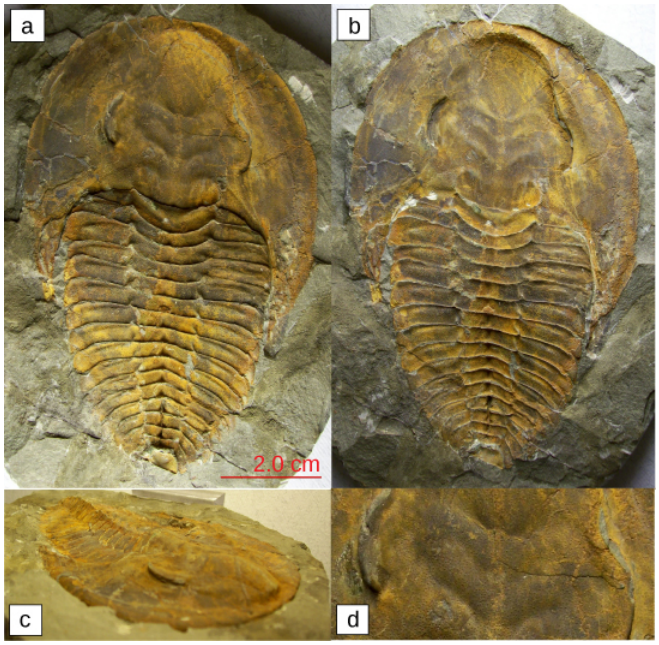


Figure **25.5.2.4**: These fossils (a–d) belong to trilobites, extinct arthropods that appeared in the early Cambrian period, 525 million years ago, and disappeared from the fossil record during a mass extinction at the end of the Permian period, about 250 million years ago.

The cause of the Cambrian explosion is still debated. There are many theories that attempt to answer this question. Environmental changes may have created a more suitable environment for animal life. Examples of these changes include rising atmospheric oxygen levels and large increases in oceanic calcium concentrations that preceded the Cambrian period (Figure **25.5.2.5**). Some scientists believe that an expansive, continental shelf with numerous shallow lagoons or pools provided the necessary living space for larger numbers of different types of animals to co-exist. There is also support for theories that argue that ecological relationships between species, such as changes in the food web, competition for food and space, and predator-prey relationships, were primed to promote a sudden massive coevolution of species. Yet other theories claim genetic and developmental reasons for the Cambrian explosion. The morphological flexibility and complexity of animal development afforded by the evolution of *Hox* control genes may have provided the necessary opportunities for increases in possible animal morphologies at the time of the Cambrian period. Theories that attempt to explain why the Cambrian explosion happened must be able to provide valid reasons for the massive animal diversification, as well as explain why it happened *when* it did. There is evidence that both supports and refutes each of the theories described above, and the answer may very well be a combination of these and other theories.

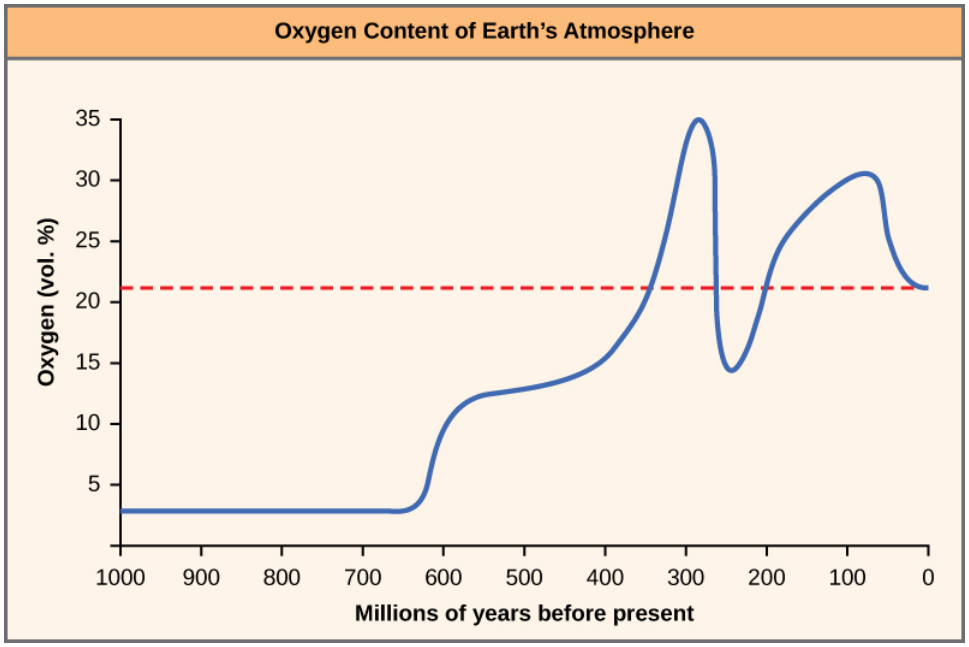


Figure **25.5.2.5**: The oxygen concentration in Earth's atmosphere rose sharply around 300 million years ago.

However, unresolved questions about the animal diversification that took place during the Cambrian period remain. For example, we do not understand how the evolution of so many species occurred in such a short period of time. Was there really an "explosion" of life at this particular time? Some scientists question the validity of the this idea, because there is increasing evidence to suggest that more animal life existed prior to the Cambrian period and that other similar species' so-called explosions (or radiations) occurred later in history as well. Furthermore, the vast diversification of animal species that appears to have begun during the Cambrian period continued well into the following Ordovician period. Despite some of these arguments, most scientists agree that the Cambrian period marked a time of impressively rapid animal evolution and diversification that is unmatched elsewhere during history.

Link to Learning



View an animation of what ocean life may have been like during the Cambrian explosion.

Post-Cambrian Evolution and Mass Extinctions

The periods that followed the Cambrian during the Paleozoic Era are marked by further animal evolution and the emergence of many new orders, families, and species. As animal phyla continued to diversify, new species adapted to new ecological niches. During the Ordovician period, which followed the Cambrian period, plant life first appeared on land. This change allowed formerly

aquatic animal species to invade land, feeding directly on plants or decaying vegetation. Continual changes in temperature and moisture throughout the remainder of the Paleozoic Era due to continental plate movements encouraged the development of new adaptations to terrestrial existence in animals, such as limbed appendages in amphibians and epidermal scales in reptiles.

Changes in the environment often create new niches (living spaces) that contribute to rapid speciation and increased diversity. On the other hand, cataclysmic events, such as volcanic eruptions and meteor strikes that obliterate life, can result in devastating losses of diversity. Such periods of mass extinction (Figure **25.5.2.6**) have occurred repeatedly in the evolutionary record of life, erasing some genetic lines while creating room for others to evolve into the empty niches left behind. The end of the Permian period (and the Paleozoic Era) was marked by the largest mass extinction event in Earth's history, a loss of roughly 95 percent of the extant species at that time. Some of the dominant phyla in the world's oceans, such as the trilobites, disappeared completely. On land, the disappearance of some dominant species of Permian reptiles made it possible for a new line of reptiles to emerge, the dinosaurs. The warm and stable climatic conditions of the ensuing Mesozoic Era promoted an explosive diversification of dinosaurs into every conceivable niche in land, air, and water. Plants, too, radiated into new landscapes and empty niches, creating complex communities of producers and consumers, some of which became very large on the abundant food available.

Another mass extinction event occurred at the end of the Cretaceous period, bringing the Mesozoic Era to an end. Skies darkened and temperatures fell as a large meteor impact and tons of volcanic ash blocked incoming sunlight. Plants died, herbivores and carnivores starved, and the mostly cold-blooded dinosaurs ceded their dominance of the landscape to more warm-blooded mammals. In the following Cenozoic Era, mammals radiated into terrestrial and aquatic niches once occupied by dinosaurs, and birds, the warm-blooded offshoots of one line of the ruling reptiles, became aerial specialists. The appearance and dominance of flowering plants in the Cenozoic Era created new niches for insects, as well as for birds and mammals. Changes in animal species diversity during the late Cretaceous and early Cenozoic were also promoted by a dramatic shift in Earth's geography, as continental plates slid over the crust into their current positions, leaving some animal groups isolated on islands and continents, or separated by mountain ranges or inland seas from other competitors. Early in the Cenozoic, new ecosystems appeared, with the evolution of grasses and coral reefs. Late in the Cenozoic, further extinctions followed by speciation occurred during ice ages that covered high latitudes with ice and then retreated, leaving new open spaces for colonization.

Link to Learning

Watch the following video to learn more about the mass extinctions.

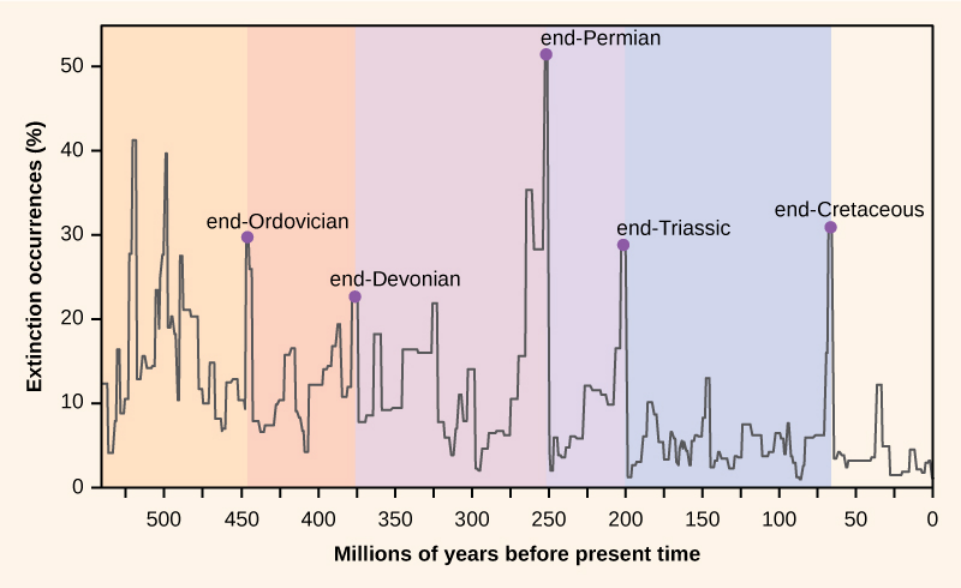


Figure **25.5.2.6**: Mass extinctions have occurred repeatedly over geological time.

Career Connection: Paleontologist

Natural history museums contain the fossil casts of extinct animals and information about how these animals evolved, lived, and died. Paleontogists are scientists who study prehistoric life. They use fossils to observe and explain how life evolved on Earth and how species interacted with each other and with the environment. A paleontologist needs to be knowledgeable in biology, ecology, chemistry, geology, and many other scientific disciplines. A paleontologist's work may involve field studies: searching for and studying fossils. In addition to digging for and finding fossils, paleontologists also prepare fossils for further study and analysis. Although dinosaurs are probably the first animals that come to mind when thinking about paleontology, paleontologists study everything from plant life, fungi, and fish to sea animals and birds.

An undergraduate degree in earth science or biology is a good place to start toward the career path of becoming a paleontologist. Most often, a graduate degree is necessary. Additionally, work experience in a museum or in a paleontology lab is useful.

Summary

The most rapid diversification and evolution of animal species in all of history occurred during the Cambrian period of the Paleozoic Era, a phenomenon known as the Cambrian explosion. Until recently, scientists believed that there were only very few tiny and simplistic animal species in existence before this period. However, recent fossil discoveries have revealed that additional, larger, and more complex animals existed during the Ediacaran period, and even possibly earlier, during the Cryogenian period. Still, the Cambrian period undoubtedly witnessed the emergence of the majority of animal phyla that we know today, although many questions remain unresolved about this historical phenomenon.

The remainder of the Paleozoic Era is marked by the growing appearance of new classes, families, and species, and the early colonization of land by certain marine animals. The evolutionary history of animals is also marked by numerous major extinction events, each of which wiped out a majority of extant species. Some species of most animal phyla survived these extinctions, allowing the phyla to persist and continue to evolve into species that we see today.

Glossary

Cambrian explosion
: time during the Cambrian period (542–488 million years ago) when most of the animal phyla in existence today evolved

Cryogenian period
: geologic period (850–630 million years ago) characterized by a very cold global climate

Ediacaran period

geological period (630–542 million years ago) when the oldest definite multicellular organisms with tissues evolved

mass extinction

event that wipes out the majority of species within a relatively short geological time period

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CHAPTER OVERVIEW

26: Viruses

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26.1: The Nature of Viruses

Skills to Develop

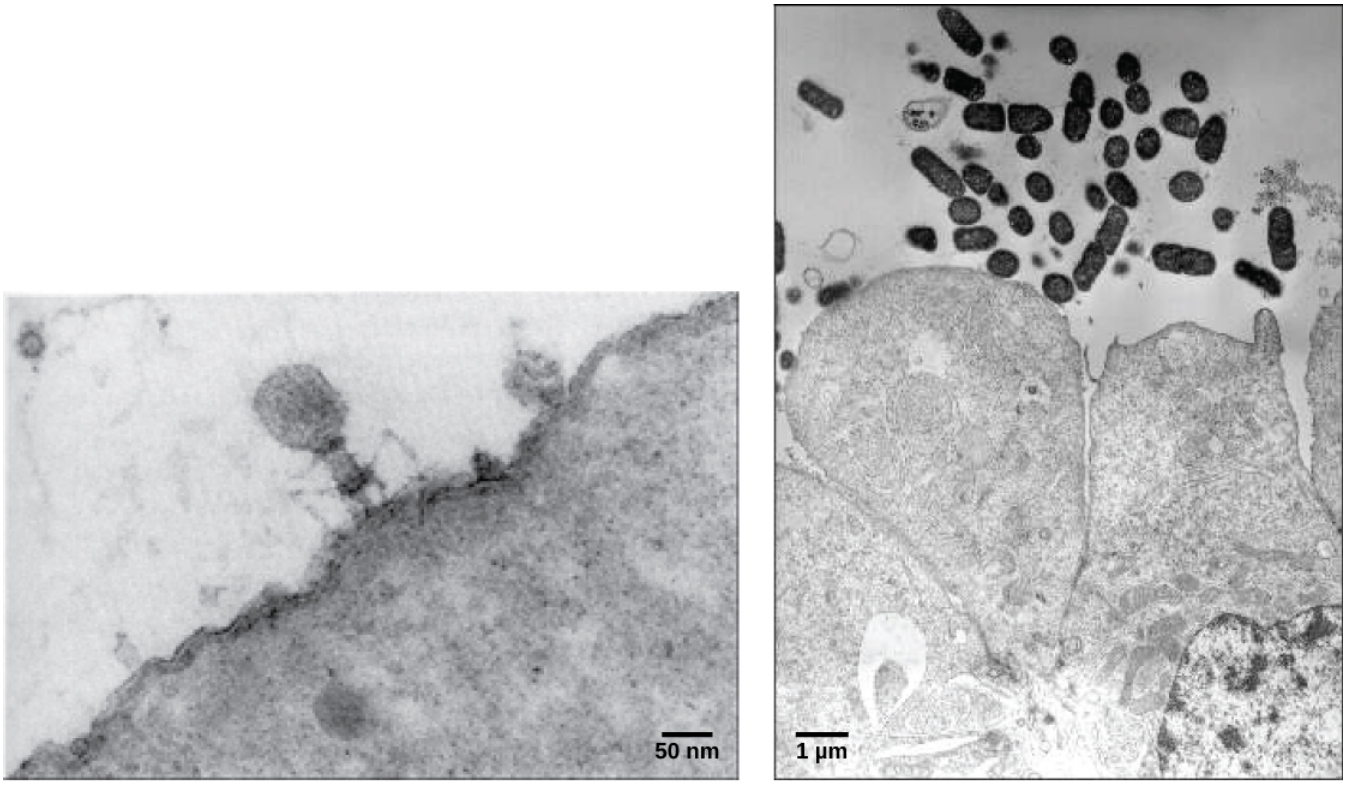
- Describe how viruses were first discovered and how they are detected
- Discuss three hypotheses about how viruses evolved
- Recognize the basic shapes of viruses
- Understand past and emerging classification systems for viruses

Viruses are diverse entities. They vary in their structure, their replication methods, and in their target hosts. Nearly all forms of life—from bacteria and archaea to eukaryotes such as plants, animals, and fungi—have viruses that infect them. While most biological diversity can be understood through evolutionary history, such as how species have adapted to conditions and environments, much about virus origins and evolution remains unknown.

Discovery and Detection

Viruses were first discovered after the development of a porcelain filter, called the Chamberland-Pasteur filter, which could remove all bacteria visible in the microscope from any liquid sample. In 1886, Adolph Meyer demonstrated that a disease of tobacco plants, tobacco mosaic disease, could be transferred from a diseased plant to a healthy one via liquid plant extracts. In 1892, Dmitri Ivanowski showed that this disease could be transmitted in this way even after the Chamberland-Pasteur filter had removed all viable bacteria from the extract. Still, it was many years before it was proven that these "filterable" infectious agents were not simply very small bacteria but were a new type of very small, disease-causing particle.

Virions, single virus particles, are very small, about 20–250 nanometers in diameter. These individual virus particles are the infectious form of a virus outside the host cell. Unlike bacteria (which are about 100-times larger), we cannot see viruses with a light microscope, with the exception of some large virions of the poxvirus family. It was not until the development of the electron microscope in the late 1930s that scientists got their first good view of the structure of the tobacco mosaic virus (TMV) (Figure **26.1.1**) and other viruses (Figure **26.1.1**). The surface structure of virions can be observed by both scanning and transmission electron microscopy, whereas the internal structures of the virus can only be observed in images from a transmission electron microscope. The use of these technologies has allowed for the discovery of many viruses of all types of living organisms. They were initially grouped by shared morphology. Later, groups of viruses were classified by the type of nucleic acid they contained, DNA or RNA, and whether their nucleic acid was single- or double-stranded. More recently, molecular analysis of viral replicative cycles has further refined their classification.



(a) (b)

Figure 26.1.1: In these transmission electron micrographs, (a) a virus is dwarfed by the bacterial cell it infects, while (b) these *E. coli* cells are dwarfed by cultured colon cells. (credit a: modification of work by U.S. Dept. of Energy, Office of Science, LBL, PBD; credit b: modification of work by J.P. Nataro and S. Sears, unpub. data, CDC; scale-bar data from Matt Russell)

Evolution of Viruses

Although biologists have accumulated a significant amount of knowledge about how present-day viruses evolve, much less is known about how viruses originated in the first place. When exploring the evolutionary history of most organisms, scientists can look at fossil records and similar historic evidence. However, viruses do not fossilize, so researchers must conjecture by investigating how today's viruses evolve and by using biochemical and genetic information to create speculative virus histories.

While most findings agree that viruses don't have a single common ancestor, scholars have yet to find a single hypothesis about virus origins that is fully accepted in the field. One such hypothesis, called devolution or the regressive hypothesis, proposes to explain the origin of viruses by suggesting that viruses evolved from free-living cells. However, many components of how this process might have occurred are a mystery. A second hypothesis (called escapist or the progressive hypothesis) accounts for viruses having either an RNA or a DNA genome and suggests that viruses originated from RNA and DNA molecules that escaped from a host cell. A third hypothesis posits a system of self-replication similar to that of other self-replicating molecules, likely evolving alongside the cells they rely on as hosts; studies of some plant pathogens support this hypothesis.

As technology advances, scientists may develop and refine further hypotheses to explain the origin of viruses. The emerging field called virus molecular systematics attempts to do just that through comparisons of sequenced genetic material. These researchers hope to one day better understand the origin of viruses, a discovery that could lead to advances in the treatments for the ailments they produce.

Viral Morphology

Viruses are acellular, meaning they are biological entities that do not have a cellular structure. They therefore lack most of the components of cells, such as organelles, ribosomes, and the plasma membrane. A virion consists of a nucleic acid core, an outer protein coating or capsid, and sometimes an outer envelope made of protein and phospholipid membranes derived from the host cell. Viruses may also contain additional proteins, such as enzymes. The most obvious difference between members of viral

families is their morphology, which is quite diverse. An interesting feature of viral complexity is that the complexity of the host does not correlate with the complexity of the virion. Some of the most complex virion structures are observed in bacteriophages, viruses that infect the simplest living organisms, bacteria.

Morphology

Viruses come in many shapes and sizes, but these are consistent and distinct for each viral family. All virions have a nucleic acid genome covered by a protective layer of proteins, called a capsid. The capsid is made up of protein subunits called capsomeres. Some viral capsids are simple polyhedral “spheres,” whereas others are quite complex in structure.

In general, the shapes of viruses are classified into four groups: filamentous, isometric (or icosahedral), enveloped, and head and tail. Filamentous viruses are long and cylindrical. Many plant viruses are filamentous, including TMV. Isometric viruses have shapes that are roughly spherical, such as poliovirus or herpesviruses. Enveloped viruses have membranes surrounding capsids. Animal viruses, such as HIV, are frequently enveloped. Head and tail viruses infect bacteria and have a head that is similar to icosahedral viruses and a tail shape like filamentous viruses.

Many viruses use some sort of glycoprotein to attach to their host cells via molecules on the cell called viral receptors (Figure **26.1.2**). For these viruses, attachment is a requirement for later penetration of the cell membrane, so they can complete their replication inside the cell. The receptors that viruses use are molecules that are normally found on cell surfaces and have their own physiological functions. Viruses have simply evolved to make use of these molecules for their own replication. For example, HIV uses the CD4 molecule on T lymphocytes as one of its receptors. CD4 is a type of molecule called a cell adhesion molecule, which functions to keep different types of immune cells in close proximity to each other during the generation of a T lymphocyte immune response.

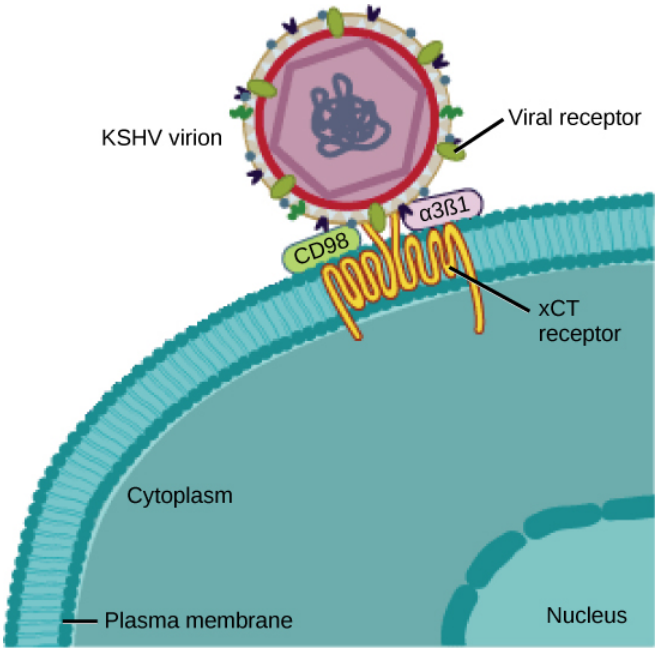


Figure **26.1.2**: The KSHV virus binds the xCT receptor on the surface of human cells. xCT receptors protect cells against stress. Stressed cells express more xCT receptors than non-stressed cells. The KSHV virion causes cells to become stressed, thereby increasing expression of the receptor to which it binds. (credit: modification of work by NIAID, NIH)

Among the most complex virions known, the T4 bacteriophage, which infects the *Escherichia coli* bacterium, has a tail structure that the virus uses to attach to host cells and a head structure that houses its DNA.

Adenovirus, a non-enveloped animal virus that causes respiratory illnesses in humans, uses glycoprotein spikes protruding from its capsomeres to attach to host cells. Non-enveloped viruses also include those that cause polio (poliovirus), plantar warts (papillomavirus), and hepatitis A (hepatitis A virus).

Enveloped virions like HIV, the causative agent in AIDS, consist of nucleic acid (RNA in the case of HIV) and capsid proteins surrounded by a phospholipid bilayer envelope and its associated proteins. Glycoproteins embedded in the viral envelope are used

to attach to host cells. Other envelope proteins are the matrix proteins that stabilize the envelope and often play a role in the assembly of progeny virions. Chicken pox, influenza, and mumps are examples of diseases caused by viruses with envelopes. Because of the fragility of the envelope, non-enveloped viruses are more resistant to changes in temperature, pH, and some disinfectants than enveloped viruses.

Overall, the shape of the virion and the presence or absence of an envelope tell us little about what disease the virus may cause or what species it might infect, but they are still useful means to begin viral classification (Figure **26.1.3**).

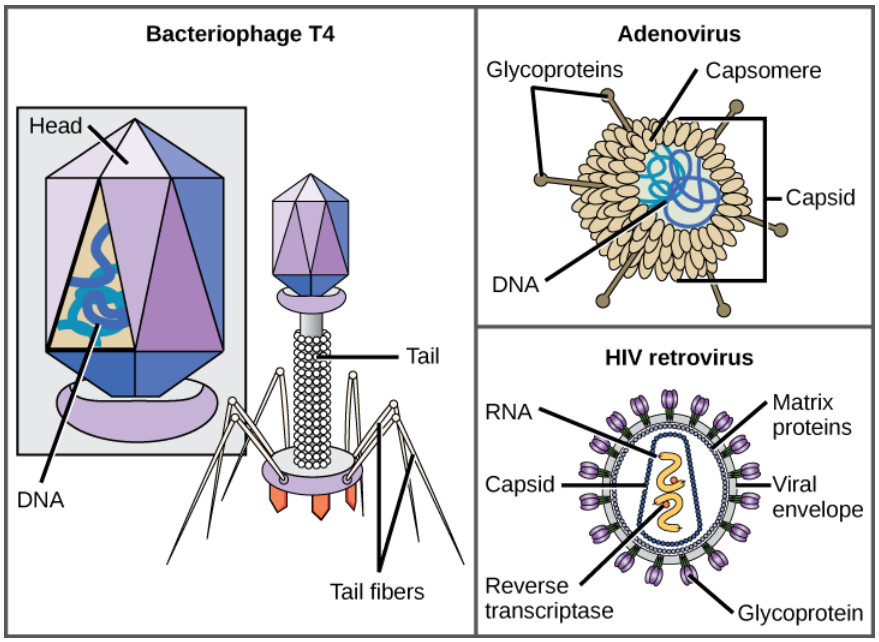


Figure **26.1.3**: Viruses can be either complex in shape or relatively simple. This figure shows three relatively complex virions: the bacteriophage T4, with its DNA-containing head group and tail fibers that attach to host cells; adenovirus, which uses spikes from its capsid to bind to host cells; and HIV, which uses glycoproteins embedded in its envelope to bind to host cells. Notice that HIV has proteins called matrix proteins, internal to the envelope, which help stabilize virion shape. (credit "bacteriophage, adenovirus": modification of work by NCBI, NIH; credit "HIV retrovirus": modification of work by NIAID, NIH)

Exercise 26.1.1

Which of the following statements about virus structure is true?

A. All viruses are encased in a viral membrane.
B. The capsomere is made up of small protein subunits called capsids.
C. DNA is the genetic material in all viruses.
D. Glycoproteins help the virus attach to the host cell.

Answer

D

Types of Nucleic Acid

Unlike nearly all living organisms that use DNA as their genetic material, viruses may use either DNA or RNA as theirs. The virus core contains the genome or total genetic content of the virus. Viral genomes tend to be small, containing only those genes that encode proteins that the virus cannot get from the host cell. This genetic material may be single- or double-stranded. It may also be linear or circular. While most viruses contain a single nucleic acid, others have genomes that have several, which are called segments.

In DNA viruses, the viral DNA directs the host cell's replication proteins to synthesize new copies of the viral genome and to transcribe and translate that genome into viral proteins. DNA viruses cause human diseases, such as chickenpox, hepatitis B, and some venereal diseases, like herpes and genital warts.

RNA viruses contain only RNA as their genetic material. To replicate their genomes in the host cell, the RNA viruses encode enzymes that can replicate RNA into DNA, which cannot be done by the host cell. These RNA polymerase enzymes are more likely to make copying errors than DNA polymerases, and therefore often make mistakes during transcription. For this reason, mutations in RNA viruses occur more frequently than in DNA viruses. This causes them to change and adapt more rapidly to their host. Human diseases caused by RNA viruses include hepatitis C, measles, and rabies.

Virus Classification

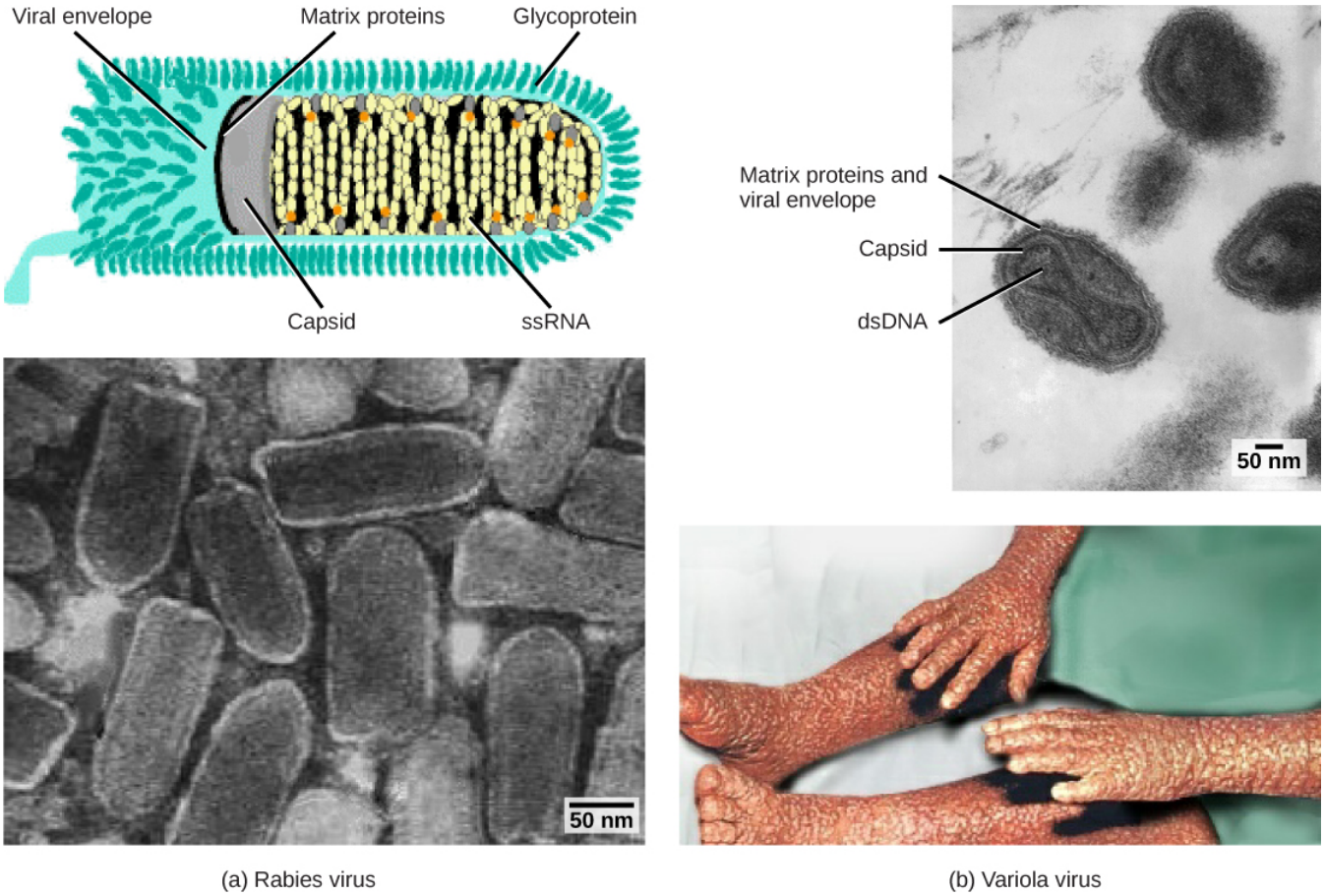
To understand the features shared among different groups of viruses, a classification scheme is necessary. As most viruses are not thought to have evolved from a common ancestor, however, the methods that scientists use to classify living things are not very useful. Biologists have used several classification systems in the past, based on the morphology and genetics of the different viruses. However, these earlier classification methods grouped viruses differently, based on which features of the virus they were using to classify them. The most commonly used classification method today is called the Baltimore classification scheme and is based on how messenger RNA (mRNA) is generated in each particular type of virus.

Past Systems of Classification

Viruses are classified in several ways: by factors such as their core content (Table **26.1.1** and Figure **26.1.2**), the structure of their capsids, and whether they have an outer envelope. The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures.

Table **26.1.1**: Virus Classification by Genome Structure and Core

Core Classifications	Examples
• RNA • DNA	• Rabies virus, retroviruses • Herpesviruses, smallpox virus
• Single-stranded • Double-stranded	• Rabies virus, retroviruses • Herpesviruses, smallpox virus
• Linear • Circular	• Rabies virus, retroviruses, herpesviruses, smallpox virus • Papillomaviruses, many bacteriophages
• Non-segmented: genome consists of a single segment of genetic material • Segmented: genome is divided into multiple segments	• Parainfluenza viruses • Influenza viruses



(a) Rabies virus

(b) Variola virus

Figure **26.1.4**: Viruses are classified based on their core genetic material and capsid design. (a) Rabies virus has a single-stranded RNA (ssRNA) core and an enveloped helical capsid, whereas (b) variola virus, the causative agent of smallpox, has a double-stranded DNA (dsDNA) core and a complex capsid. Rabies transmission occurs when saliva from an infected mammal enters a wound. The virus travels through neurons in the peripheral nervous system to the central nervous system where it impairs brain function, and then travels to other tissues. The virus can infect any mammal, and most die within weeks of infection. Smallpox is a human virus transmitted by inhalation of the variola virus, localized in the skin, mouth, and throat, which causes a characteristic rash. Before its eradication in 1979, infection resulted in a 30–35 percent mortality rate. (credit "rabies diagram": modification of work by CDC; "rabies micrograph": modification of work by Dr. Fred Murphy, CDC; credit "small pox micrograph": modification of work by Dr. Fred Murphy, Sylvia Whitfield, CDC; credit "smallpox photo": modification of work by CDC; scale-bar data from Matt Russell)

Viruses can also be classified by the design of their capsids (Figure **26.1.3** and Figure **26.1.4**). Capsids are classified as naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex (Figure **26.1.5** and Figure **26.1.6**). The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures (Table **26.1.2**).

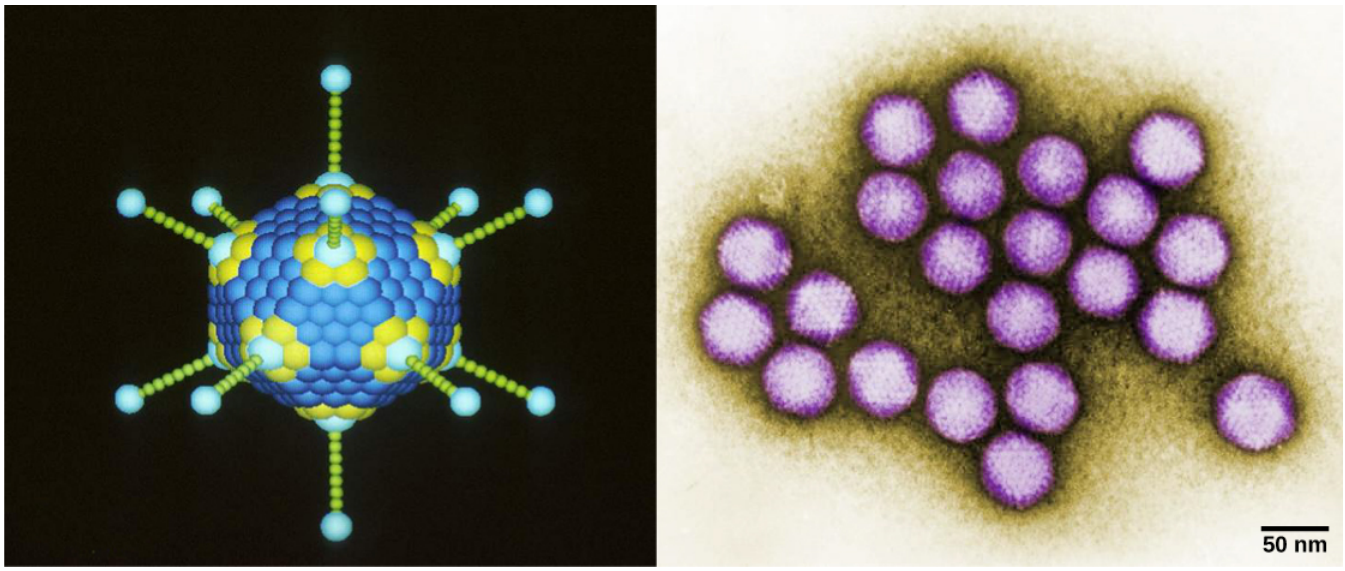


Figure **26.1.5**: Adenovirus (left) is depicted with a double-stranded DNA genome enclosed in an icosahedral capsid that is 90–100 nm across. The virus, shown clustered in the micrograph (right), is transmitted orally and causes a variety of illnesses in vertebrates, including human eye and respiratory infections. (credit "adenovirus": modification of work by Dr. Richard Feldmann, National Cancer Institute; credit "micrograph": modification of work by Dr. G. William Gary, Jr., CDC; scale-bar data from Matt Russell)

Table **26.1.2**: Virus Classification by Capsid Structure

Capsid Classification	Examples
Naked icosahedral	Hepatitis A virus, polioviruses
Enveloped icosahedral	Epstein-Barr virus, herpes simplex virus, rubella virus, yellow fever virus, HIV-1
Enveloped helical	Influenza viruses, mumps virus, measles virus, rabies virus
Naked helical	Tobacco mosaic virus
Complex with many proteins; some have combinations of icosahedral and helical capsid structures	Herpesviruses, smallpox virus, hepatitis B virus, T4 bacteriophage

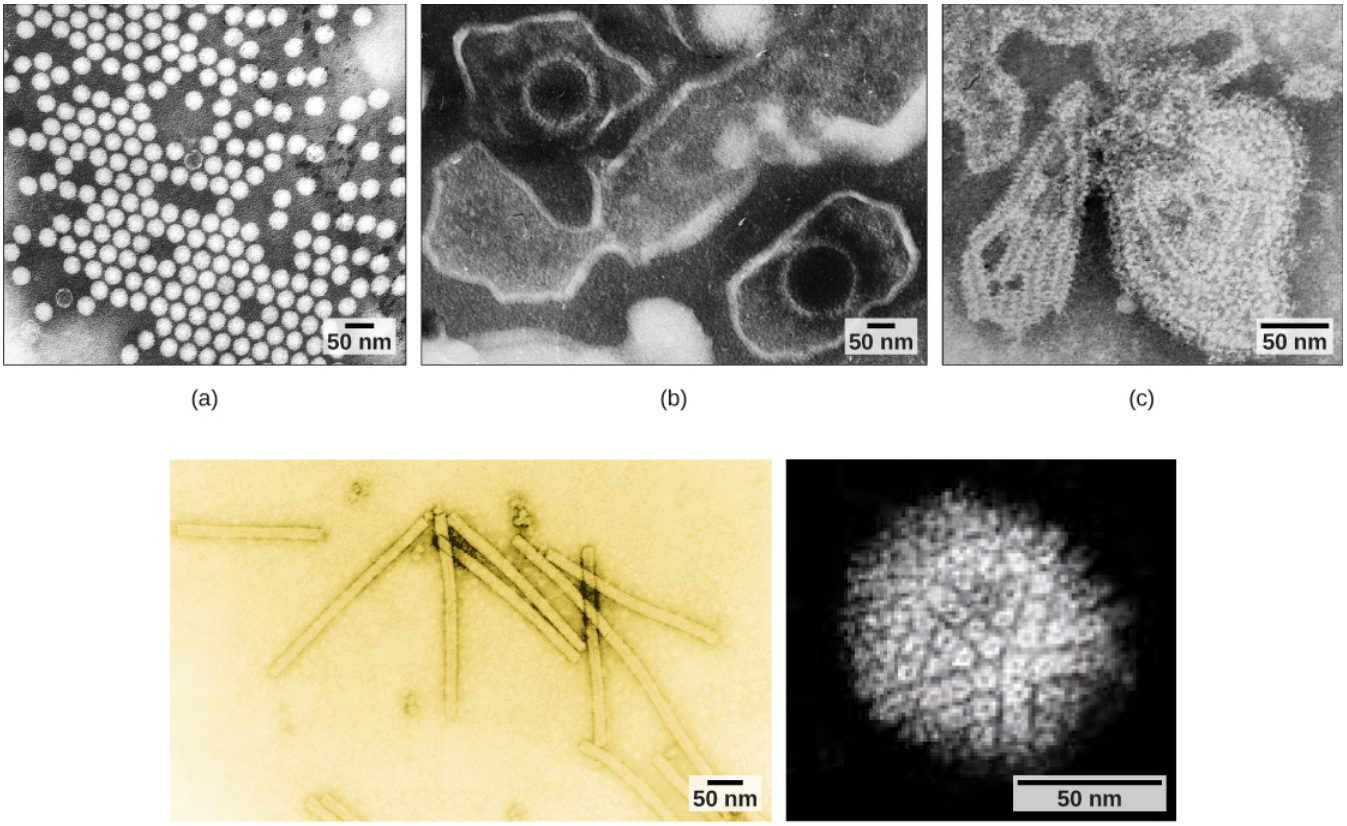


Figure 26.1.6: Transmission electron micrographs of various viruses show their structures. The capsid of the (a) polio virus is naked icosahedral; (b) the Epstein-Barr virus capsid is enveloped icosahedral; (c) the mumps virus capsid is an enveloped helix; (d) the tobacco mosaic virus capsid is naked helical; and (e) the herpesvirus capsid is complex. (credit a: modification of work by Dr. Fred Murphy, Sylvia Whitfield; credit b: modification of work by Liza Gross; credit c: modification of work by Dr. F. A. Murphy, CDC; credit d: modification of work by USDA ARS; credit e: modification of work by Linda Stannard, Department of Medical Microbiology, University of Cape Town, South Africa, NASA; scale-bar data from Matt Russell)

Baltimore Classification

The most commonly used system of virus classification was developed by Nobel Prize-winning biologist David Baltimore in the early 1970s. In addition to the differences in morphology and genetics mentioned above, the Baltimore classification scheme groups viruses according to how the mRNA is produced during the replicative cycle of the virus.

Group I viruses contain double-stranded DNA (dsDNA) as their genome. Their mRNA is produced by transcription in much the same way as with cellular DNA. Group II viruses have single-stranded DNA (ssDNA) as their genome. They convert their single-stranded genomes into a dsDNA intermediate before transcription to mRNA can occur. Group III viruses use dsRNA as their genome. The strands separate, and one of them is used as a template for the generation of mRNA using the RNA-dependent RNA polymerase encoded by the virus. Group IV viruses have ssRNA as their genome with a positive polarity. Positive polarity means that the genomic RNA can serve directly as mRNA. Intermediates of dsRNA, called replicative intermediates, are made in the process of copying the genomic RNA. Multiple, full-length RNA strands of negative polarity (complimentary to the positive-stranded genomic RNA) are formed from these intermediates, which may then serve as templates for the production of RNA with positive polarity, including both full-length genomic RNA and shorter viral mRNAs. Group V viruses contain ssRNA genomes with a negative polarity, meaning that their sequence is complementary to the mRNA. As with Group IV viruses, dsRNA intermediates are used to make copies of the genome and produce mRNA. In this case, the negative-stranded genome can be converted directly to mRNA. Additionally, full-length positive RNA strands are made to serve as templates for the production of the negative-stranded genome. Group VI viruses have diploid (two copies) ssRNA genomes that must be converted, using the enzyme reverse transcriptase, to dsDNA; the dsDNA is then transported to the nucleus of the host cell and inserted into the host genome. Then, mRNA can be produced by transcription of the viral DNA that was integrated into the host genome. Group VII viruses have partial dsDNA genomes and make ssRNA intermediates that act as mRNA, but are also converted back into dsDNA genomes by reverse

transcriptase, necessary for genome replication. The characteristics of each group in the Baltimore classification are summarized in the Table **26.1.3** with examples of each group.

Table **26.1.3**: Baltimore Classification

Group	Characteristics	Mode of mRNA Production	Example
I	Double-stranded DNA	mRNA is transcribed directly from the DNA template	Herpes simplex (herpesvirus)
II	Single-stranded DNA	DNA is converted to double-stranded form before RNA is transcribed	Canine parvovirus (parvovirus)
III	Double-stranded RNA	mRNA is transcribed from the RNA genome	Childhood gastroenteritis (rotavirus)
IV	Single stranded RNA (+)	Genome functions as mRNA	Common cold (pircornavirus)
V	Single stranded RNA (-)	mRNA is transcribed from the RNA genome	Rabies (rhabdovirus)
VI	Single stranded RNA viruses with reverse transcriptase	Reverse transcriptase makes DNA from the RNA genome; DNA is then incorporated in the host genome; mRNA is transcribed from the incorporated DNA	Human immunodeficiency virus (HIV)
VII	Double stranded DNA viruses with reverse transcriptase	The viral genome is double-stranded DNA, but viral DNA is replicated through an RNA intermediate; the RNA may serve directly as mRNA or as a template to make mRNA	Hepatitis B virus (hepadnavirus)

Summary

Viruses are tiny, acellular entities that can usually only be seen with an electron microscope. Their genomes contain either DNA or RNA—never both—and they replicate using the replication proteins of a host cell. Viruses are diverse, infecting archaea, bacteria, fungi, plants, and animals. Viruses consist of a nucleic acid core surrounded by a protein capsid with or without an outer lipid envelope. The capsid shape, presence of an envelope, and core composition dictate some elements of the classification of viruses. The most commonly used classification method, the Baltimore classification, categorizes viruses based on how they produce their mRNA.

Glossary

acellular
lacking cells

capsid
protein coating of the viral core

capsomere
protein subunit that makes up the capsid

envelope
lipid bilayer that envelopes some viruses

group I virus
virus with a dsDNA genome

group II virus
virus with a ssDNA genome

group III virus
virus with a dsRNA genome

group IV virus
virus with a ssRNA genome with positive polarity

group V virus
virus with a ssRNA genome with negative polarity

group VI virus
virus with a ssRNA genomes converted into dsDNA by reverse transcriptase

group VII virus
virus with a single-stranded mRNA converted into dsDNA for genome replication

matrix protein
envelope protein that stabilizes the envelope and often plays a role in the assembly of progeny virions

negative polarity
ssRNA viruses with genomes complimentary to their mRNA

positive polarity
ssRNA virus with a genome that contains the same base sequences and codons found in their mRNA

replicative intermediate
dsRNA intermediate made in the process of copying genomic RNA

reverse transcriptase
enzyme found in Baltimore groups VI and VII that converts single-stranded RNA into double-stranded DNA

viral receptor
glycoprotein used to attach a virus to host cells via molecules on the cell

virion
individual virus particle outside a host cell

virus core
contains the virus genome

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26.1.1: Virus Infections and Hosts

Skills to Develop

- List the steps of replication and explain what occurs at each step
- Describe the lytic and lysogenic cycles of virus replication
- Explain the transmission and diseases of animal and plant viruses
- Discuss the economic impact of animal and plant viruses

Viruses can be seen as obligate, intracellular parasites. A virus must attach to a living cell, be taken inside, manufacture its proteins and copy its genome, and find a way to escape the cell so that the virus can infect other cells. Viruses can infect only certain species of hosts and only certain cells within that host. Cells that a virus may use to replicate are called permissive. For most viruses, the molecular basis for this specificity is that a particular surface molecule known as the viral receptor must be found on the host cell surface for the virus to attach. Also, metabolic and host cell immune response differences seen in different cell types based on differential gene expression are a likely factor in which cells a virus may target for replication. The permissive cell must make the substances that the virus needs or the virus will not be able to replicate there.

Steps of Virus Infections

A virus must use cell processes to replicate. The viral replication cycle can produce dramatic biochemical and structural changes in the host cell, which may cause cell damage. These changes, called cytopathic (causing cell damage) effects, can change cell functions or even destroy the cell. Some infected cells, such as those infected by the common cold virus known as rhinovirus, die through lysis (bursting) or apoptosis (programmed cell death or “cell suicide”), releasing all progeny virions at once. The symptoms of viral diseases result from the immune response to the virus, which attempts to control and eliminate the virus from the body, and from cell damage caused by the virus. Many animal viruses, such as HIV (human immunodeficiency virus), leave the infected cells of the immune system by a process known as budding, where virions leave the cell individually. During the budding process, the cell does not undergo lysis and is not immediately killed. However, the damage to the cells that the virus infects may make it impossible for the cells to function normally, even though the cells remain alive for a period of time. Most productive viral infections follow similar steps in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release (Figure 26.1.1.1).

Attachment

A virus attaches to a specific receptor site on the host cell membrane through attachment proteins in the capsid or via glycoproteins embedded in the viral envelope. The specificity of this interaction determines the host—and the cells within the host—that can be infected by a particular virus. This can be illustrated by thinking of several keys and several locks, where each key will fit only one specific lock.

Entry

The nucleic acid of bacteriophages enters the host cell naked, leaving the capsid outside the cell. Plant and animal viruses can enter through endocytosis, in which the cell membrane surrounds and engulfs the entire virus. Some enveloped viruses enter the cell when the viral envelope fuses directly with the cell membrane. Once inside the cell, the viral capsid is degraded, and the viral nucleic acid is released, which then becomes available for replication and transcription.

Replication and Assembly

The replication mechanism depends on the viral genome. DNA viruses usually use host cell proteins and enzymes to make additional DNA that is transcribed to messenger RNA (mRNA), which is then used to direct protein synthesis. RNA viruses usually use the RNA core as a template for synthesis of viral genomic RNA and mRNA. The viral mRNA directs the host cell to synthesize viral enzymes and capsid proteins, and assemble new virions. Of course, there are exceptions to this pattern. If a host cell does not provide the enzymes necessary for viral replication, viral genes supply the information to direct synthesis of the missing proteins. Retroviruses, such as HIV, have an RNA genome that must be reverse transcribed into DNA, which then is incorporated into the host cell genome. They are within group VI of the Baltimore classification scheme. To convert RNA into DNA, retroviruses must

contain genes that encode the virus-specific enzyme reverse transcriptase that transcribes an RNA template to DNA. Reverse transcription never occurs in uninfected host cells—the needed enzyme reverse transcriptase is only derived from the expression of viral genes within the infected host cells. The fact that HIV produces some of its own enzymes not found in the host has allowed researchers to develop drugs that inhibit these enzymes. These drugs, including the reverse transcriptase inhibitor AZT, inhibit HIV replication by reducing the activity of the enzyme without affecting the host's metabolism. This approach has led to the development of a variety of drugs used to treat HIV and has been effective at reducing the number of infectious virions (copies of viral RNA) in the blood to non-detectable levels in many HIV-infected individuals.

Egress

The last stage of viral replication is the release of the new virions produced in the host organism, where they are able to infect adjacent cells and repeat the replication cycle. As you've learned, some viruses are released when the host cell dies, and other viruses can leave infected cells by budding through the membrane without directly killing the cell.

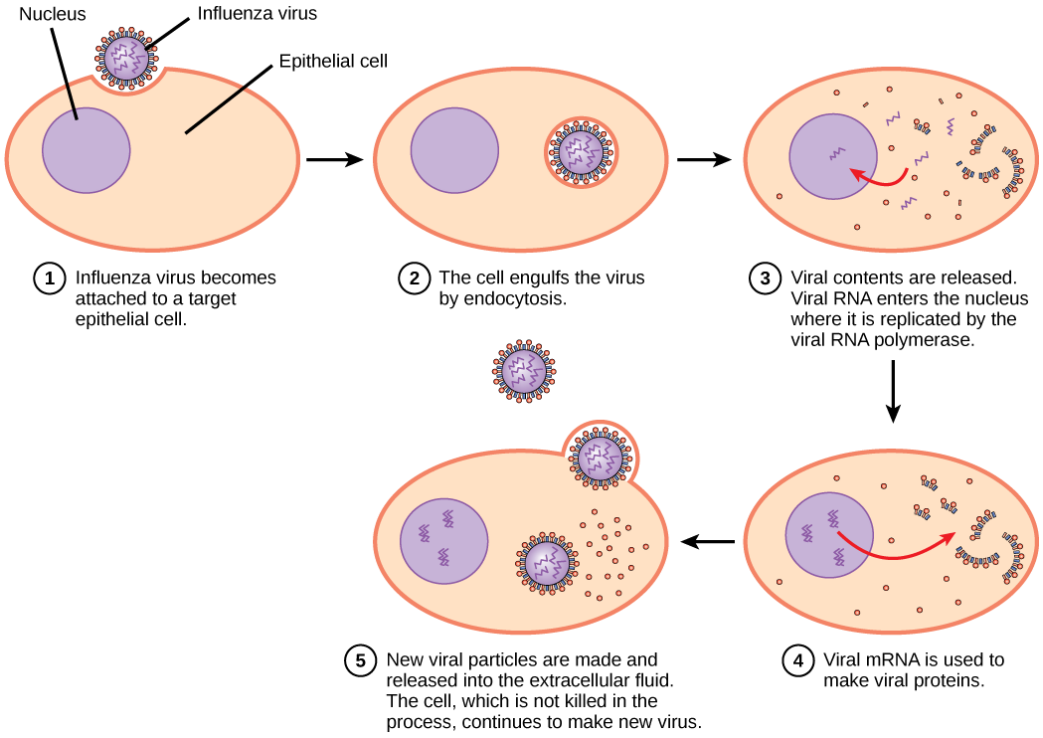


Figure **26.1.1.1**: In influenza virus infection, glycoproteins attach to a host epithelial cell. As a result, the virus is engulfed. RNA and proteins are made and assembled into new virions.

Exercise 26.1.1.1

Influenza virus is packaged in a viral envelope that fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

Answer

The host cell can continue to make new virus particles.

Link to Learning



Watch a video on viruses, identifying structures, modes of transmission, replication, and more.

Different Hosts and Their Viruses

As you've learned, viruses are often very specific as to which hosts and which cells within the host they will infect. This feature of a virus makes it specific to one or a few species of life on Earth. On the other hand, so many different types of viruses exist on Earth that nearly every living organism has its own set of viruses that tries to infect its cells. Even the smallest and simplest of cells, prokaryotic bacteria, may be attacked by specific types of viruses.

Bacteriophages

Bacteriophages are viruses that infect bacteria (Figure **26.1.1.2**). When infection of a cell by a bacteriophage results in the production of new virions, the infection is said to be productive. If the virions are released by bursting the cell, the virus replicates by means of a lytic cycle (Figure **26.1.1.3**).

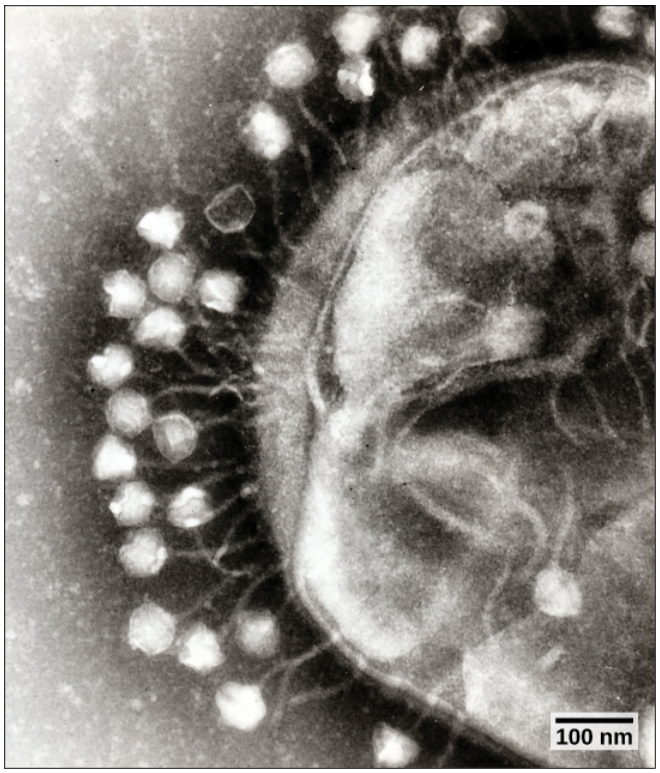


Figure **26.1.1.2**: This transmission electron micrograph shows bacteriophages attached to a bacterial cell. (credit: modification of work by Dr. Graham Beards; scale-bar data from Matt Russell)

An example of a lytic bacteriophage is T4, which infects *Escherichia coli* found in the human intestinal tract. Sometimes, however, a virus can remain within the cell without being released. For example, when a temperate bacteriophage infects a bacterial cell, it replicates by means of a lysogenic cycle (Figure **26.1.1.3**), and the viral genome is incorporated into the genome of the host cell. When the phage DNA is incorporated into the host cell genome, it is called a prophage. An example of a lysogenic bacteriophage is the λ (lambda) virus, which also infects the *E. coli* bacterium. Viruses that infect plant or animal cells may also undergo infections where they are not producing virions for long periods. An example is the animal herpesviruses, including herpes simplex viruses, the cause of oral and genital herpes in humans. In a process called latency, these viruses can exist in nervous tissue for long periods of time without producing new virions, only to leave latency periodically and cause lesions in the skin where the virus replicates. Even though there are similarities between lysogeny and latency, the term lysogenic cycle is usually reserved to describe bacteriophages. Latency will be described in more detail below.

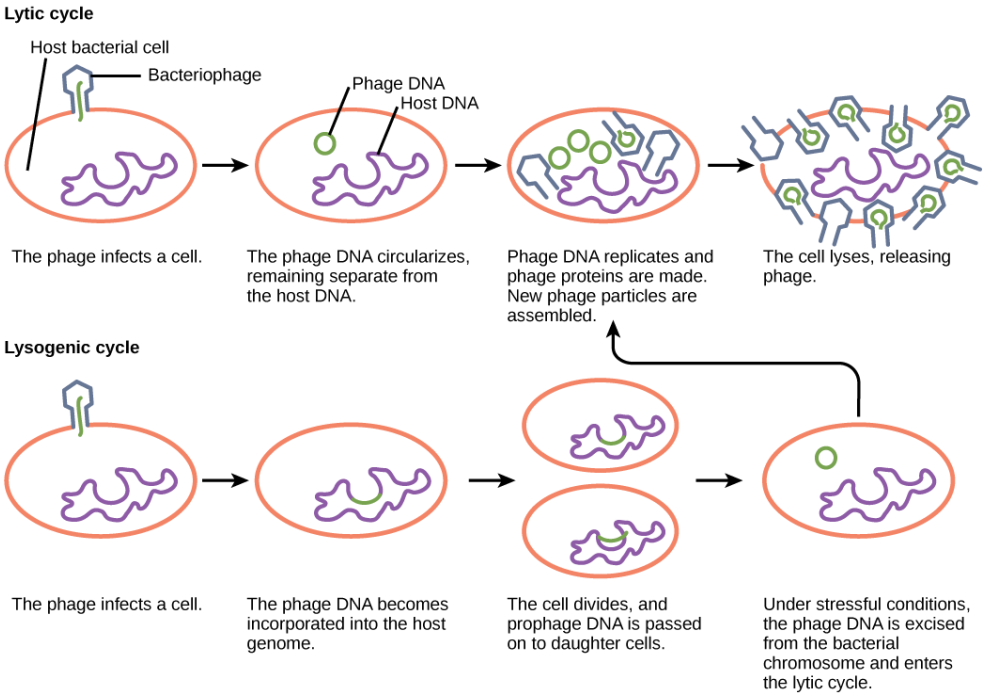


Figure **26.1.1.3**: A temperate bacteriophage has both lytic and lysogenic cycles. In the lytic cycle, the phage replicates and lyses the host cell. In the lysogenic cycle, phage DNA is incorporated into the host genome, where it is passed on to subsequent generations. Environmental stressors such as starvation or exposure to toxic chemicals may cause the prophage to excise and enter the lytic cycle.

Exercise 26.1.1.2

Which of the following statements is false?

A. In the lytic cycle, new phage are produced and released into the environment.
B. In the lysogenic cycle, phage DNA is incorporated into the host genome.
C. An environmental stressor can cause the phage to initiate the lysogenic cycle.
D. Cell lysis only occurs in the lytic cycle.

Answer

C

Animal Viruses

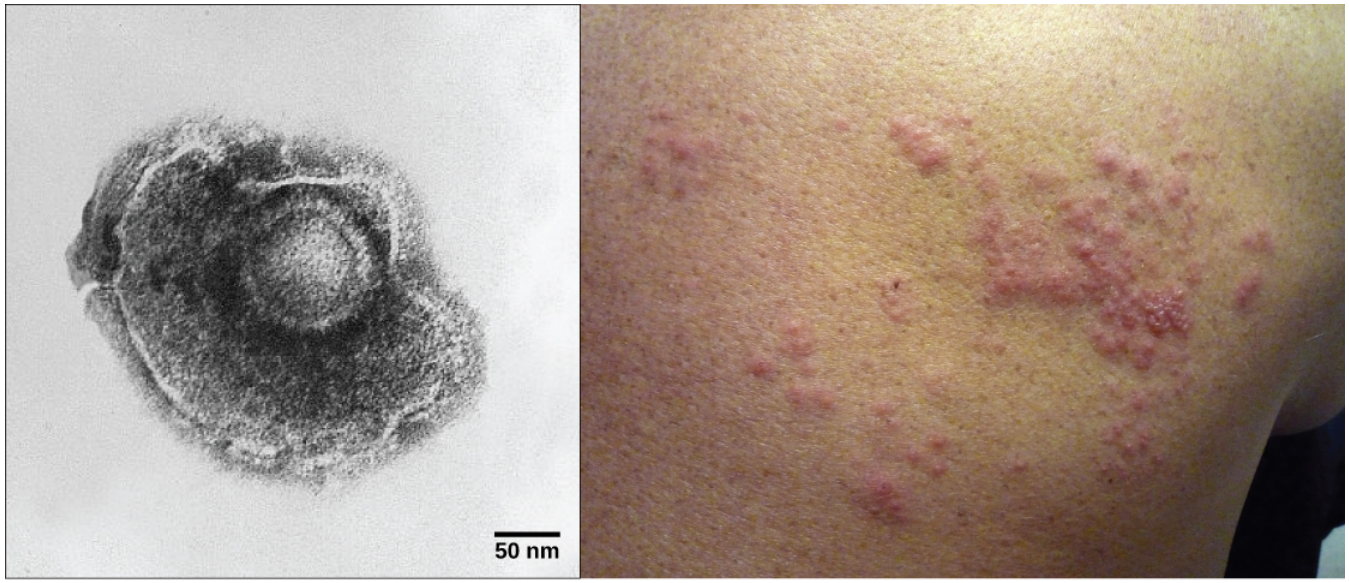
Animal viruses, unlike the viruses of plants and bacteria, do not have to penetrate a cell wall to gain access to the host cell. Non-enveloped or “naked” animal viruses may enter cells in two different ways. As a protein in the viral capsid binds to its receptor on the host cell, the virus may be taken inside the cell via a vesicle during the normal cell process of receptor-mediated endocytosis. An alternative method of cell penetration used by non-enveloped viruses is for capsid proteins to undergo shape changes after binding to the receptor, creating channels in the host cell membrane. The viral genome is then “injected” into the host cell through these channels in a manner analogous to that used by many bacteriophages. Enveloped viruses also have two ways of entering cells after binding to their receptors: receptor-mediated endocytosis, or fusion. Many enveloped viruses enter the cell by receptor-mediated endocytosis in a fashion similar to some non-enveloped viruses. On the other hand, fusion only occurs with enveloped virions. These viruses, which include HIV among others, use special fusion proteins in their envelopes to cause the envelope to fuse with the plasma membrane of the cell, thus releasing the genome and capsid of the virus into the cell cytoplasm.

After making their proteins and copying their genomes, animal viruses complete the assembly of new virions and exit the cell. As we have already discussed using the example of HIV, enveloped animal viruses may bud from the cell membrane as they assemble themselves, taking a piece of the cell’s plasma membrane in the process. On the other hand, non-enveloped viral progeny, such as rhinoviruses, accumulate in infected cells until there is a signal for lysis or apoptosis, and all virions are released together.

As you will learn in the next module, animal viruses are associated with a variety of human diseases. Some of them follow the classic pattern of acute disease, where symptoms get increasingly worse for a short period followed by the elimination of the virus from the body by the immune system and eventual recovery from the infection. Examples of acute viral diseases are the common cold and influenza. Other viruses cause long-term chronic infections, such as the virus causing hepatitis C, whereas others, like herpes simplex virus, only cause intermittent symptoms. Still other viruses, such as human herpesviruses 6 and 7, which in some cases can cause the minor childhood disease roseola, often successfully cause productive infections without causing any symptoms at all in the host, and thus we say these patients have an asymptomatic infection.

In hepatitis C infections, the virus grows and reproduces in liver cells, causing low levels of liver damage. The damage is so low that infected individuals are often unaware that they are infected, and many infections are detected only by routine blood work on patients with risk factors such as intravenous drug use. On the other hand, since many of the symptoms of viral diseases are caused by immune responses, a lack of symptoms is an indication of a weak immune response to the virus. This allows for the virus to escape elimination by the immune system and persist in individuals for years, all the while producing low levels of progeny virions in what is known as a chronic viral disease. Chronic infection of the liver by this virus leads to a much greater chance of developing liver cancer, sometimes as much as 30 years after the initial infection.

As already discussed, herpes simplex virus can remain in a state of latency in nervous tissue for months, even years. As the virus “hides” in the tissue and makes few if any viral proteins, there is nothing for the immune response to act against, and immunity to the virus slowly declines. Under certain conditions, including various types of physical and psychological stress, the latent herpes simplex virus may be reactivated and undergo a lytic replication cycle in the skin, causing the lesions associated with the disease. Once virions are produced in the skin and viral proteins are synthesized, the immune response is again stimulated and resolves the skin lesions in a few days by destroying viruses in the skin. As a result of this type of replicative cycle, appearances of cold sores and genital herpes outbreaks only occur intermittently, even though the viruses remain in the nervous tissue for life. Latent infections are common with other herpesviruses as well, including the varicella-zoster virus that causes chickenpox. After having a chickenpox infection in childhood, the varicella-zoster virus can remain latent for many years and reactivate in adults to cause the painful condition known as “shingles” (Figure **26.1.1.4**).



(a) (b)

Figure **26.1.1.4**: (a) Varicella-zoster, the virus that causes chickenpox, has an enveloped icosahedral capsid visible in this transmission electron micrograph. Its double-stranded DNA genome becomes incorporated in the host DNA and can reactivate after latency in the form of (b) shingles, often exhibiting a rash. (credit a: modification of work by Dr. Erskine Palmer, B. G. Martin, CDC; credit b: modification of work by "rosmary"/Flickr; scale-bar data from Matt Russell)

Some animal-infecting viruses, including the hepatitis C virus discussed above, are known as oncogenic viruses: They have the ability to cause cancer. These viruses interfere with the normal regulation of the host cell cycle either by either introducing genes that stimulate unregulated cell growth (oncogenes) or by interfering with the expression of genes that inhibit cell growth. Oncogenic viruses can be either DNA or RNA viruses. Cancers known to be associated with viral infections include cervical cancer caused by human papillomavirus (HPV) (Figure **26.1.1.5**), liver cancer caused by hepatitis B virus, T-cell leukemia, and several types of lymphoma.

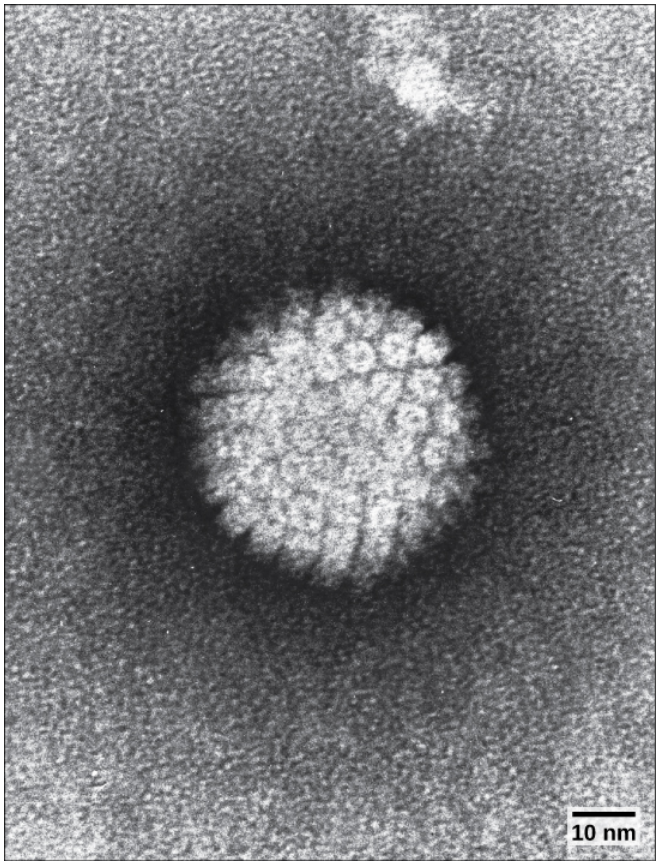
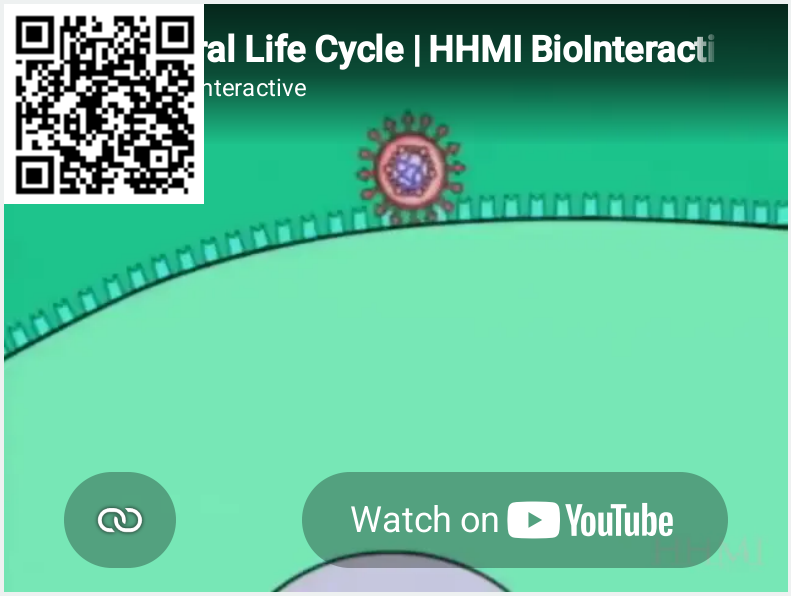


Figure **26.1.1.5**: HPV, or human papillomavirus, has a naked icosahedral capsid visible in this transmission electron micrograph and a double-stranded DNA genome that is incorporated into the host DNA. The virus, which is sexually transmitted, is oncogenic and can lead to cervical cancer. (credit: modification of work by NCI, NIH; scale-bar data from Matt Russell)

Link to Learning



Visit the interactive animations showing the various stages of the replicative cycles of animal viruses and click on the flash animation links.

Plant Viruses

Plant viruses, like other viruses, contain a core of either DNA or RNA. You have already learned about one of these, the tobacco mosaic virus. As plant viruses have a cell wall to protect their cells, these viruses do not use receptor-mediated endocytosis to enter host cells as is seen with animal viruses. For many plant viruses to be transferred from plant to plant, damage to some of the plants' cells must occur to allow the virus to enter a new host. This damage is often caused by weather, insects, animals, fire, or human activities like farming or landscaping. Additionally, plant offspring may inherit viral diseases from parent plants. Plant viruses can be transmitted by a variety of vectors, through contact with an infected plant's sap, by living organisms such as insects and nematodes, and through pollen. When plants viruses are transferred between different plants, this is known as horizontal transmission, and when they are inherited from a parent, this is called vertical transmission.

Symptoms of viral diseases vary according to the virus and its host (Table **26.1.1.1**). One common symptom is hyperplasia, the abnormal proliferation of cells that causes the appearance of plant tumors known as galls. Other viruses induce hypoplasia, or decreased cell growth, in the leaves of plants, causing thin, yellow areas to appear. Still other viruses affect the plant by directly killing plant cells, a process known as cell necrosis. Other symptoms of plant viruses include malformed leaves, black streaks on the stems of the plants, altered growth of stems, leaves, or fruits, and ring spots, which are circular or linear areas of discoloration found in a leaf.

Table **26.1.1.1**: Some Common Symptoms of Plant Viral Diseases

Symptom	Appears as
Hyperplasia	Galls (tumors)
Hypoplasia	Thinned, yellow splotches on leaves
Cell necrosis	Dead, blackened stems, leaves, or fruit
Abnormal growth patterns	Malformed stems, leaves, or fruit
Discoloration	Yellow, red, or black lines, or rings in stems, leaves, or fruit

Plant viruses can seriously disrupt crop growth and development, significantly affecting our food supply. They are responsible for poor crop quality and quantity globally, and can bring about huge economic losses annually. Others viruses may damage plants used in landscaping. Some viruses that infect agricultural food plants include the name of the plant they infect, such as tomato spotted wilt virus, bean common mosaic virus, and cucumber mosaic virus. In plants used for landscaping, two of the most common viruses are peony ring spot and rose mosaic virus. There are far too many plant viruses to discuss each in detail, but symptoms of bean common mosaic virus result in lowered bean production and stunted, unproductive plants. In the ornamental rose, the rose mosaic disease causes wavy yellow lines and colored splotches on the leaves of the plant.

Summary

Viral replication within a living cell always produces changes in the cell, sometimes resulting in cell death and sometimes slowly killing the infected cells. There are six basic stages in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release. A viral infection may be productive, resulting in new virions, or nonproductive, which means that the virus remains inside the cell without producing new virions. Bacteriophages are viruses that infect bacteria. They have two different modes of replication: the lytic cycle, where the virus replicates and bursts out of the bacteria, and the lysogenic cycle, which involves the incorporation of the viral genome into the bacterial host genome. Animal viruses cause a variety of infections, with some causing chronic symptoms (hepatitis C), some intermittent symptoms (latent viruses such a herpes simplex virus 1), and others that cause very few symptoms, if any (human herpesviruses 6 and 7). Oncogenic viruses in animals have the ability to cause cancer by interfering with the regulation of the host cell cycle. Viruses of plants are responsible for significant economic damage in both agriculture and plants used for ornamentation.

Glossary

acute disease

disease where the symptoms rise and fall within a short period of time

asymptomatic disease
disease where there are no symptoms and the individual is unaware of being infected unless lab tests are performed

AZT
anti-HIV drug that inhibits the viral enzyme reverse transcriptase

bacteriophage
virus that infects bacteria

budding
method of exit from the cell used in certain animal viruses, where virions leave the cell individually by capturing a piece of the host plasma membrane

cell necrosis
cell death

chronic infection
describes when the virus persists in the body for a long period of time

cytopathic
causing cell damage

fusion
method of entry by some enveloped viruses, where the viral envelope fuses with the plasma membrane of the host cell

gall
appearance of a plant tumor

horizontal transmission
transmission of a disease from parent to offspring

hyperplasia
abnormally high cell growth and division

hypoplasia
abnormally low cell growth and division

intermittent symptom
symptom that occurs periodically

latency
virus that remains in the body for a long period of time but only causes intermittent symptoms

lysis
bursting of a cell

lytic cycle
type of virus replication in which virions are released through lysis, or bursting, of the cell

lysogenic cycle
type of virus replication in which the viral genome is incorporated into the genome of the host cell

oncogenic virus

virus that has the ability to cause cancer

permissive

cell type that is able to support productive replication of a virus

productive

viral infection that leads to the production of new virions

prophage

phage DNA that is incorporated into the host cell genome

vertical transmission

transmission of disease between unrelated individuals

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26.2: Viral Diversity

Learning Objectives

- Describe how viruses are classified

To understand the features shared among different groups of viruses, a classification scheme is necessary. However, most viruses are not thought to have evolved from a common ancestor, so the methods that scientists use to classify living things are not very useful. Biologists have used several classification systems in the past, based on the morphology and genetics of the different viruses. However, these earlier classification methods grouped viruses based on which features of the virus they were using to classify them. The most commonly-used classification method today is called the Baltimore classification scheme which is based on how messenger RNA (mRNA) is generated in each particular type of virus. The surface structure of virions can be observed by both scanning and transmission electron microscopy, whereas the internal structures of the virus can only be observed in images from a transmission electron microscope.

Past Systems of Classification

Viruses are classified in several ways: by factors such as their core content, the structure of their capsids, and whether they have an outer envelope. Viruses may use either DNA or RNA as their genetic material. The virus core contains the genome or total genetic content of the virus. Viral genomes tend to be small, containing only those genes that encode proteins that the virus cannot obtain from the host cell. This genetic material may be single- or double-stranded. It may also be linear or circular. While most viruses contain a single nucleic acid, others have genomes that have several, which are called segments. The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures.

Virus Classification by Genome Structure and Core

Core Classifications	Examples
RNA	Rabies virus, retroviruses
DNA	Herpesviruses, smallpox virus
Single-stranded	Rabies virus, retroviruses
Double-stranded	Herpesviruses, smallpox virus
Linear	Rabies virus, retroviruses, herpesviruses, smallpox virus
Circular	Papillomaviruses, many bacteriophages
Non-segmented: genome consists of a single segment of genetic material	Parainfluenza viruses
Segmented: genome is divided into multiple segments	Influenza viruses

Figure **26.2.1**: Virus classification by genome structure and core: The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures.

Viruses can also be classified by the design of their capsids. Isometric viruses have shapes that are roughly spherical, such as poliovirus or herpesviruses. Enveloped viruses have membranes surrounding capsids. Animal viruses, such as HIV, are frequently enveloped. Head and tail viruses infect bacteria and have a head that is similar to icosahedral viruses and a tail shape like filamentous viruses. Capsids are classified as naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex. For example, the tobacco mosaic virus has a naked helical capsid. The adenovirus has an icosahedral capsid.

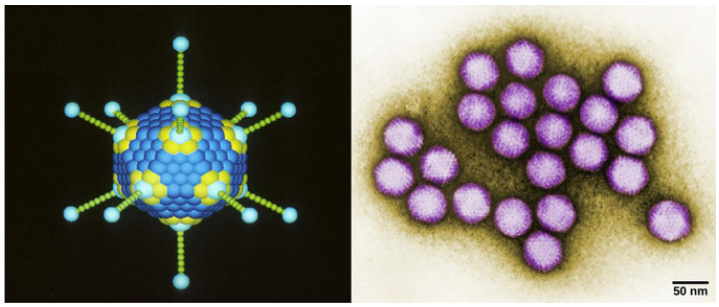


Figure 26.2.1: Adenovirus classification: Adenovirus (left) is depicted with a double-stranded DNA genome enclosed in an icosahedral capsid that is 90–100 nm across. The virus, shown clustered in the micrograph (right), is transmitted orally and causes a variety of illnesses in vertebrates, including human eye and respiratory infections.

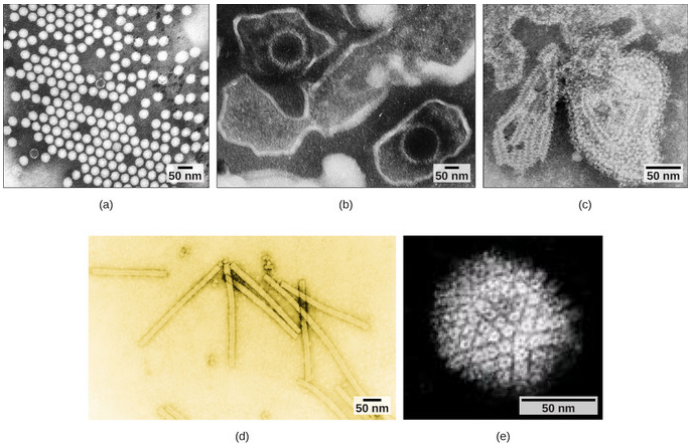


Figure 26.2.1: Transmission electron micrograph of viruses: Transmission electron micrographs of various viruses show their structures. The capsid of the (a) polio virus is naked icosahedral; (b) the Epstein-Barr virus capsid is enveloped icosahedral; (c) the mumps virus capsid is an enveloped helix; (d) the tobacco mosaic virus capsid is naked helical; and (e) the herpesvirus capsid is complex.

Virus Classification by Capsid Structure	
Capsid Classification	**Examples**
Naked icosahedral	Hepatitis A virus, polioviruses
Enveloped icosahedral	Epstein-Barr virus, herpes simplex virus, rubella virus, yellow fever virus, HIV-1
Enveloped helical	Influenza viruses, mumps virus, measles virus, rabies virus
Naked helical	Tobacco mosaic virus
Complex with many proteins; some have combinations of icosahedral and helical capsid structures	Herpesviruses, smallpox virus, hepatitis B virus, T4 bacteriophage

Figure 26.2.1: Virus classification by capsid structure: Viruses can also be classified by the design of their capsids which are classified as naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex.

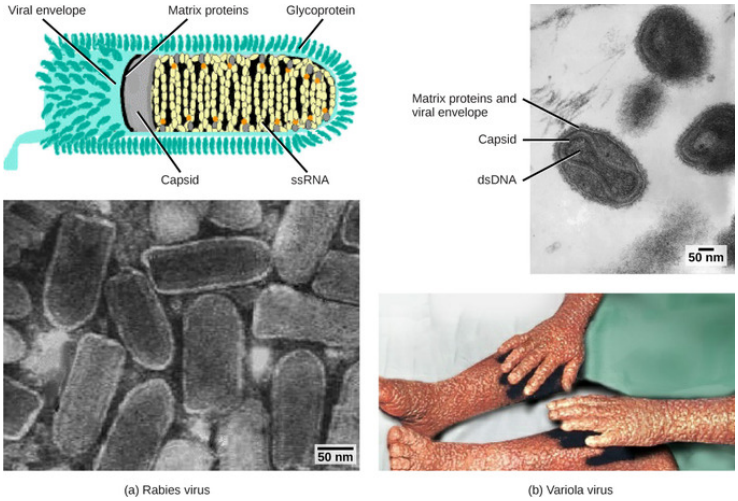


Figure 26.2.1: Example of viruses classified by caspid design: Viruses are classified based on their core genetic material and capsid design. (a) Rabies virus has a single-stranded RNA (ssRNA) core and an enveloped helical capsid, whereas (b) variola virus, the causative agent of smallpox, has a double-stranded DNA (dsDNA) core and a complex capsid.

Baltimore Classification

The most commonly-used system of virus classification was developed by Nobel Prize-winning biologist David Baltimore in the early 1970s. In addition to the differences in morphology and genetics mentioned above, the Baltimore classification scheme groups viruses according to how the mRNA is produced during the replicative cycle of the virus. Viruses can contain double-stranded DNA (dsDNA), single-stranded DNA (ssDNA), double-stranded RNA (dsRNA), single-stranded RNA with a positive polarity (ssRNA), ssRNA with a negative polarity, diploid (two copies) ssRNA, and partial dsDNA genomes. Positive polarity means that the genomic RNA can serve directly as mRNA and a negative polarity means that their sequence is complementary to the mRNA.

Baltimore Classification

Group	Characteristics	Mode of mRNA Production	Example
I	Double-stranded DNA	mRNA is transcribed directly from the DNA template	Herpes simplex (herpesvirus)
II	Single-stranded DNA	DNA is converted to double-stranded form before RNA is transcribed	Canine parvovirus (parvovirus)
III	Double-stranded RNA	mRNA is transcribed from the RNA genome	Childhood gastroenteritis (rotavirus)
IV	Single stranded RNA (+)	Genome functions as mRNA	Common cold (picornavirus)
V	Single stranded RNA (-)	mRNA is transcribed from the RNA genome	Rabies (rhabdovirus)
VI	Single stranded RNA viruses with reverse transcriptase	Reverse transcriptase makes DNA from the RNA genome; DNA is then incorporated in the host genome; mRNA is transcribed from the incorporated DNA	Human immunodeficiency virus (HIV)
VII	Double stranded DNA viruses with reverse transcriptase	The viral genome is double-stranded DNA, but viral DNA is replicated through an RNA intermediate; the RNA may serve directly as mRNA or as a template to make mRNA	Hepatitis B virus (hepadnavirus)

Figure **26.2.1**: Baltimore classification: The Baltimore classification scheme, the most commonly used, was developed by Nobel Prize-winning biologist David Baltimore in the early 1970s. The scheme groups viruses according to how the mRNA is produced during the replicative cycle of the virus, in addition to the differences in morphology and genetics.

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Key Points

- The type of genetic material, either DNA or RNA, and whether its structure is single- or double-stranded, linear or circular, and segmented or non-segmented are factors for classification.
- Virus capsids can be classified as naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex.
- Virus can either have an envelope or not.
- A more recent system, the Baltimore classification scheme, groups viruses into seven classes according to how the mRNA is produced during the replicative cycle of the virus.

Key Terms

- **Baltimore classification**: a classification scheme that groups viruses into seven classes according to how the mRNA is produced during the replicative cycle of the virus
- **messenger RNA**: Messenger RNA (mRNA) is a molecule of RNA that encodes a chemical “blueprint” for a protein product.

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26.3: Bacteriophage- Bacterial Viruses

Learning Objectives

- Describe the lytic and lysogenic cycles of bacteriophages

Different Hosts and Their Viruses

Viruses are often very specific as to which hosts and which cells within the host they will infect. This feature of a virus makes it specific to one or a few species of life on earth. So many different types of viruses exist that nearly every living organism has its own set of viruses that try to infect its cells. Even the smallest and simplest of cells, prokaryotic bacteria, may be attacked by specific types of viruses.

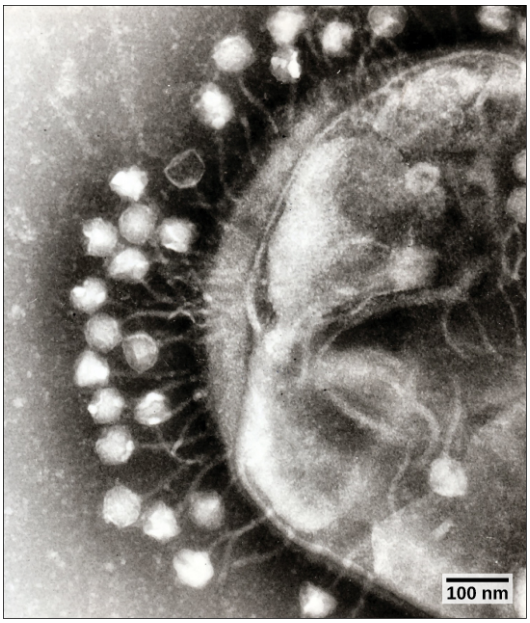


Figure **26.3.1**: Bacteriophage: This transmission electron micrograph shows bacteriophages attached to a bacterial cell.

Bacteriophages

Bacteriophages are viruses that infect bacteria. Bacteriophages may have a lytic cycle or a lysogenic cycle, and a few viruses are capable of carrying out both. When infection of a cell by a bacteriophage results in the production of new virions, the infection is said to be productive.

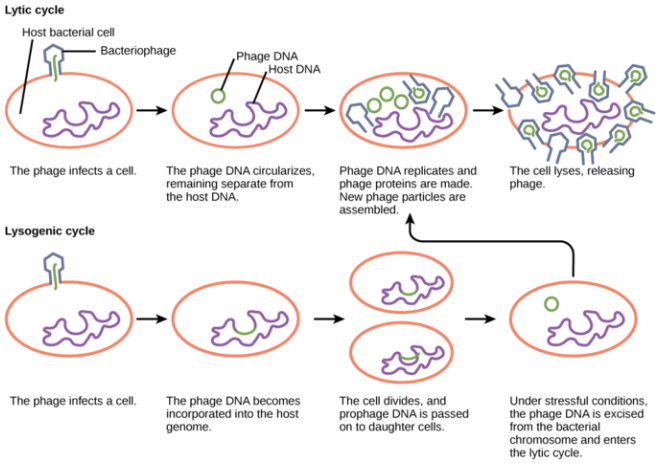


Figure **26.3.1**: Lytic versus lysogenic cycle: A temperate bacteriophage has both lytic and lysogenic cycles. In the lytic cycle, the phage replicates and lyses the host cell. In the lysogenic cycle, phage DNA is incorporated into the host genome, where it is passed on to subsequent generations. Environmental stressors such as starvation or exposure to toxic chemicals may cause the prophage to excise and enter the lytic cycle.

Lytic Cycle

With lytic phages, bacterial cells are broken open (lysed) and destroyed after immediate replication of the virion. As soon as the cell is destroyed, the phage progeny can find new hosts to infect. An example of a lytic bacteriophage is T4, which infects *E. coli* found in the human intestinal tract. Lytic phages are more suitable for phage therapy.

Some lytic phages undergo a phenomenon known as lysis inhibition, where completed phage progeny will not immediately lyse out of the cell if extracellular phage concentrations are high.

Lysogenic Cycle

In contrast, the lysogenic cycle does not result in immediate lysing of the host cell. Those phages able to undergo lysogeny are known as temperate phages. Their viral genome will integrate with host DNA and replicate along with it fairly harmlessly, or may even become established as a plasmid. The virus remains dormant until host conditions deteriorate, perhaps due to depletion of nutrients; then, the endogenous phages (known as prophages) become active. At this point they initiate the reproductive cycle, resulting in lysis of the host cell. As the lysogenic cycle allows the host cell to continue to survive and reproduce, the virus is reproduced in all of the cell's offspring. An example of a bacteriophage known to follow the lysogenic cycle and the lytic cycle is the phage lambda of E. coli.

Latency Period

Viruses that infect plant or animal cells may also undergo infections where they are not producing virions for long periods. An example is the animal herpes viruses, including herpes simplex viruses, which cause oral and genital herpes in humans. In a process called latency, these viruses can exist in nervous tissue for long periods of time without producing new virions, only to leave latency periodically and cause lesions in the skin where the virus replicates. Even though there are similarities between lysogeny and latency, the term lysogenic cycle is usually reserved to describe bacteriophages.

Key Points

- Viruses are species specific, but almost every species on Earth can be affected by some form of virus.
- The lytic cycle involves the reproduction of viruses using a host cell to manufacture more viruses; the viruses then burst out of the cell.
- The lysogenic cycle involves the incorporation of the viral genome into the host cell genome, infecting it from within.

Key Terms

- **latency**: The ability of a pathogenic virus to lie dormant within a cell.
- **bacteriophage**: A virus that specifically infects bacteria.

- **lytic cycle**: The normal process of viral reproduction involving penetration of the cell membrane, nucleic acid synthesis, and lysis of the host cell.
- **lysogenic cycle**: A form of viral reproduction involving the fusion of the nucleic acid of a bacteriophage with that of a host, followed by proliferation of the resulting prophage.

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26.4: Viral Diseases of Humans

Learning Objectives

- Describe various animal viruses and the diseases they cause

Animal Viruses

Animal viruses, unlike the viruses of plants and bacteria, do not have to penetrate a cell wall to gain access to the host cell. Non-enveloped or “naked” animal viruses may enter cells in two different ways. When a protein in the viral capsid binds to its receptor on the host cell, the virus may be taken inside the cell via a vesicle during the normal cell process of receptor-mediated endocytosis. An alternative method of cell penetration used by non-enveloped viruses is for capsid proteins to undergo shape changes after binding to the receptor, creating channels in the host cell membrane. The viral genome is then “injected” into the host cell through these channels in a manner analogous to that used by many bacteriophages. Enveloped viruses also have two ways of entering cells after binding to their receptors: receptor-mediated endocytosis and fusion. Many enveloped viruses enter the cell by receptor-mediated endocytosis in a fashion similar to some non-enveloped viruses. On the other hand, fusion only occurs with enveloped virions. These viruses, which include HIV among others, use special fusion proteins in their envelopes to cause the envelope to fuse with the plasma membrane of the cell, thus releasing the genome and capsid of the virus into the cell cytoplasm.

After making their proteins and copying their genomes, animal viruses complete the assembly of new virions and exit the cell. Using the example of HIV, enveloped animal viruses may bud from the cell membrane as they assemble themselves, taking a piece of the cell’s plasma membrane in the process. On the other hand, non-enveloped viral progeny, such as rhinoviruses, accumulate in infected cells until there is a signal for lysis or apoptosis, and all virions are released together.

Animal viruses are associated with a variety of human diseases. Some of them follow the classic pattern of acute disease, where symptoms worsen for a short period followed by the elimination of the virus from the body by the immune system with eventual recovery from the infection. Examples of acute viral diseases are the common cold and influenza. Other viruses cause long-term chronic infections, such as the virus causing hepatitis C, whereas others, like herpes simplex virus, cause only intermittent symptoms. Still other viruses, such as human herpes viruses 6 and 7, which in some cases can cause the minor childhood disease roseola, often successfully cause productive infections without causing any symptoms at all in the host; these patients have an asymptomatic infection.

In hepatitis C infections, the virus grows and reproduces in liver cells, causing low levels of liver damage. The damage is so low that infected individuals are often unaware that they are infected, with many infections only detected by routine blood work on patients with risk factors such as intravenous drug use. Since many of the symptoms of viral diseases are caused by immune responses, a lack of symptoms is an indication of a weak immune response to the virus. This allows the virus to escape elimination by the immune system and persist in individuals for years, while continuing to produce low levels of progeny virions in what is known as a chronic viral disease. Chronic infection of the liver by this virus leads to a much greater chance of developing liver cancer, sometimes as much as 30 years after the initial infection.

As mentioned, herpes simplex virus can remain in a state of latency in nervous tissue for months, even years. As the virus “hides” in the tissue and makes few if any viral proteins, there is nothing for the immune response to act against; immunity to the virus slowly declines. Under certain conditions, including various types of physical and psychological stress, the latent herpes simplex virus may be reactivated and undergo a lytic replication cycle in the skin, causing the lesions associated with the disease. Once virions are produced in the skin and viral proteins are synthesized, the immune response is again stimulated and resolves the skin lesions in a few days by destroying viruses in the skin. As a result of this type of replicative cycle, appearances of cold sores and genital herpes outbreaks only occur intermittently, even though the viruses remain in the nervous tissue for life. Latent infections are common with other herpes viruses as well, including the varicella-zoster virus that causes chickenpox. After having a chickenpox infection in childhood, the varicella-zoster virus can remain latent for many years and reactivate in adults to cause the painful condition known as “shingles”.

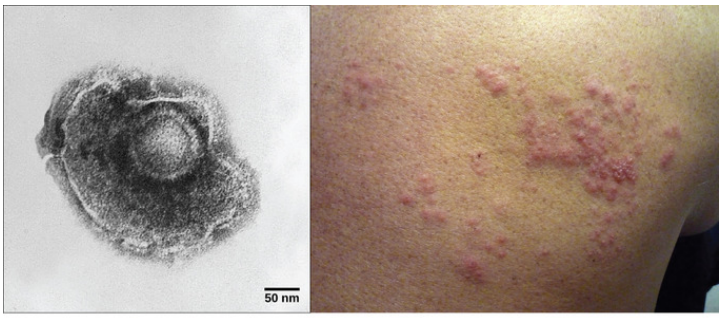


Figure **26.4.1**: Chicken pox virus: (a) Varicella-zoster, the virus that causes chickenpox, has an enveloped icosahedral capsid visible in this transmission electron micrograph. Its double-stranded DNA genome incorporates into the host DNA and reactivates after latency in the form of (b) shingles, often exhibiting a rash.

Key Points

- Animal viruses may enter a host cell by either receptor -mediated endocytosis or by changing shape and entering the cell through the cell membrane.
- Viruses cause diseases in humans and other animals; they often have to run their course before symptoms disappear.
- Examples of viral animal diseases include hepatitis C, chicken pox, and shingles.

Key Terms

- **receptor-mediated endocytosis**: a process by which cells internalize molecules (endocytosis) by the inward budding of plasma membrane vesicles containing proteins with receptor sites specific to the molecules being internalized

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26.5: Prions and Viroids- Infectious Subviral Particles

Learning Objectives

- Describe prions and viroids and their basic properties

Prions

Prions, so-called because they are proteinaceous, are infectious particles, smaller than viruses, that contain no nucleic acids (neither DNA nor RNA). Historically, the idea of an infectious agent that did not use nucleic acids was considered impossible, but pioneering work by Nobel Prize-winning biologist Stanley Prusiner has convinced the majority of biologists that such agents do indeed exist.

Fatal neurodegenerative diseases, such as kuru in humans and bovine spongiform encephalopathy (BSE) in cattle (commonly known as “mad cow disease”), were shown to be transmitted by prions. The disease was spread by the consumption of meat, nervous tissue, or internal organs between members of the same species. Kuru, native to humans in Papua New Guinea, was spread from human to human via ritualistic cannibalism. BSE, originally detected in the United Kingdom, spread between cattle by the practice of including cattle nervous tissue in feed for other cattle. Individuals with kuru and BSE show symptoms of loss of motor control and unusual behaviors, such as uncontrolled bursts of laughter with kuru, followed by death. Kuru was controlled by inducing the population to abandon its ritualistic cannibalism.

On the other hand, BSE was initially thought to affect only cattle. Cattle that died of BSE had developed lesions or “holes” in the brain, causing the brain tissue to resemble a sponge. Later on in the outbreak, however, it was shown that a similar encephalopathy in humans known as variant Creutzfeldt-Jakob disease (CJD) could be acquired from eating beef from animals with BSE, sparking bans by various countries on the importation of British beef and causing considerable economic damage to the British beef industry. BSE still exists in various areas. Although a rare disease, individuals that acquire CJD are difficult to treat. The disease spreads from human to human by blood, so many countries have banned blood donation from regions associated with BSE.

The cause of spongiform encephalopathies, such as kuru and BSE, is an infectious structural variant of a normal cellular protein called PrP (prion protein). It is this variant that constitutes the prion particle. PrP exists in two forms: PrP^{C}, the normal form of the protein, and PrP^{Sc}, the infectious form. Once introduced into the body, the PrP^{Sc} contained within the prion binds to PrP^{C} and converts it to PrP^{Sc}. This leads to an exponential increase of the PrP^{Sc} protein, which aggregates. PrP^{Sc} is folded abnormally; the resulting conformation (shape) is directly responsible for the lesions seen in the brains of infected cattle. Thus, although not without some detractors among scientists, the prion appears to be an entirely new form of infectious agent; the first one found whose transmission is not reliant upon genes made of DNA or RNA.

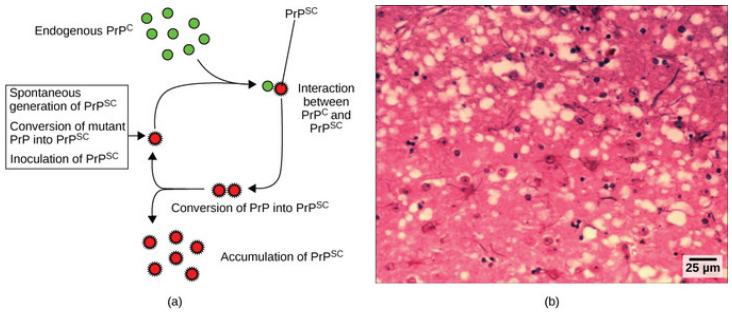


Figure **26.5.1**: Example of the formation of a prion: (a) Endogenous normal prion protein (PrPc) is converted into the disease-causing form (PrPsc) when it encounters this variant form of the protein. PrPsc may arise spontaneously in brain tissue, especially if a mutant form of the protein is present, or it may occur via the spread of misfolded prions consumed in food into brain tissue. (b) This prion-infected brain tissue, visualized using light microscopy, shows the vacuoles that give it a spongy texture, typical of transmissible spongiform encephalopathies.

Viroids

Viroids are plant pathogens: small, single-stranded, circular RNA particles that are much simpler than a virus. They do not have a capsid or outer envelope, but, as with viruses, can reproduce only within a host cell. Viroids do not, however, manufacture any

proteins. They produce only a single, specific RNA molecule. Human diseases caused by viroids have yet to be identified.

Viroid-infected plants are responsible for crop failures and the loss of millions of dollars in agricultural revenue each year. Some of the plants they infect include potatoes, cucumbers, tomatoes, chrysanthemums, avocados, and coconut palms.



Figure **26.5.1**: Potatoes infected by a viroid: These potatoes have been infected by the potato spindle tuber viroid (PSTV). It is typically spread when infected knives are used to cut healthy potatoes, which are then planted.

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Key Points

- The prion appears to be the first infectious agent found whose transmission is not reliant upon genes made of DNA or RNA.
- An infectious structural variant of a normal cellular protein called PrP (prion protein) is known to cause spongiform encephalopathies.
- Prions have been implicated in fatal neurodegenerative diseases, such as kuru in humans and bovine spongiform encephalopathy (BSE) in cattle.
- Loss of motor control and unusual behaviors are common symptoms of individuals with kuru and BSE; symptoms are usually followed by death.
- Viroids do not have a capsid or outer envelope and can reproduce only within a host cell.
- Viroids are not known to cause any human diseases, but they are responsible for crop failures and the loss of millions of dollars in agricultural revenue each year.

Key Terms

- **prion**: a self-propagating misfolded conformer of a protein that is responsible for a number of diseases that affect the brain and other neural tissue
- **proteinaceous**: of, pertaining to, or consisting of protein
- **viroid**: plant pathogens that consist of just a short section of RNA, but without the protein coat typical of viruses

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CHAPTER OVERVIEW

27: Prokaryotes

27.1: Prokaryotic Diversity
27.2: Prokaryotic Cell Structure
27.3: Prokaryotic Genetics
27.4: The Metabolic Diversity of Prokaryotes
27.5: Microbial Ecology
27.6: Bacterial Diseases of Humans

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27.1: Prokaryotic Diversity

Learning Objectives

- Discuss the origins of prokaryotic organisms in terms of the geologic timeline

Evolution of Prokaryotes

In the recent past, scientists grouped living things into five kingdoms (animals, plants, fungi, protists, and prokaryotes) based on several criteria such as: the absence or presence of a nucleus and other membrane-bound organelles, the absence or presence of cell walls, multicellularity, etc. In the late 20th century, the pioneering work of Carl Woese and others compared sequences of small-subunit ribosomal RNA (SSU rRNA) which resulted in a more fundamental way to group organisms on earth. Based on differences in the structure of cell membranes and in rRNA, Woese and his colleagues proposed that all life on earth evolved along three lineages, called domains. The domain Bacteria comprises all organisms in the kingdom Bacteria, the domain Archaea comprises the rest of the prokaryotes, and the domain Eukarya comprises all eukaryotes, including organisms in the kingdoms Animalia, Plantae, Fungi, and Protista.

The current model of the evolution of the first, living organisms is that these were some form of prokaryotes, which may have evolved out of protobionts. In general, the eukaryotes are thought to have evolved later in the history of life. However, some authors have questioned this conclusion, arguing that the current set of prokaryotic species may have evolved from more complex eukaryotic ancestors through a process of simplification. Others have argued that the three domains of life arose simultaneously, from a set of varied cells that formed a single gene pool.

Two of the three domains, Bacteria and Archaea, are prokaryotic. Based on fossil evidence, prokaryotes were the first inhabitants on Earth, appearing 3.5 to 3.8 billion years ago during the Precambrian Period. These organisms are abundant and ubiquitous; that is, they are present everywhere. In addition to inhabiting moderate environments, they are found in extreme conditions: from boiling springs to permanently frozen environments in Antarctica; from salty environments like the Dead Sea to environments under tremendous pressure, such as the depths of the ocean; and from areas without oxygen, such as a waste management plant, to radioactively-contaminated regions, such as Chernobyl. Prokaryotes reside in the human digestive system and on the skin, are responsible for certain illnesses, and serve an important role in the preparation of many foods.



Figure **27.1.1**: Prokaryotes in extreme environments: Certain prokaryotes can live in extreme environments such as the Morning Glory pool, a hot spring in Yellowstone National Park. The spring's vivid blue color is from the prokaryotes that thrive in its very hot waters.

Key Points

- All living things can be classified into three main groups called domains; these include the Archaea, the Bacteria, and the Eukarya.
- Prokaryotes arose during the Precambrian Period 3.5 to 3.8 billion years ago.
- Prokaryotic organisms can live in every type of environment on Earth, from very hot, to very cold, to super haline, to very acidic.
- The domains Bacteria and Archaea are the ones containing prokaryotic organisms.

- The Archaea are prokaryotes that inhabit extreme environments, such as inside of volcanoes, while Bacteria are more common organisms, such as *E. coli*.

Key Terms

- **prokaryote**: an organism whose cell (or cells) are characterized by the absence of a nucleus or any other membrane-bound organelles
- **domain**: in the three-domain system, the highest rank in the classification of organisms, above kingdom: Bacteria, Archaea, and Eukarya
- **archaea**: a taxonomic domain of single-celled organisms lacking nuclei, formerly called archaebacteria, but now known to differ fundamentally from bacteria

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27.2: Prokaryotic Cell Structure

Skills to Develop

- Describe the basic structure of a typical prokaryote
- Describe important differences in structure between Archaea and Bacteria

There are many differences between prokaryotic and eukaryotic cells. However, all cells have four common structures: the plasma membrane, which functions as a barrier for the cell and separates the cell from its environment; the cytoplasm, a jelly-like substance inside the cell; nucleic acids, the genetic material of the cell; and ribosomes, where protein synthesis takes place. Prokaryotes come in various shapes, but many fall into three categories: cocci (spherical), bacilli (rod-shaped), and spirilli (spiral-shaped) (Figure 27.2.1).

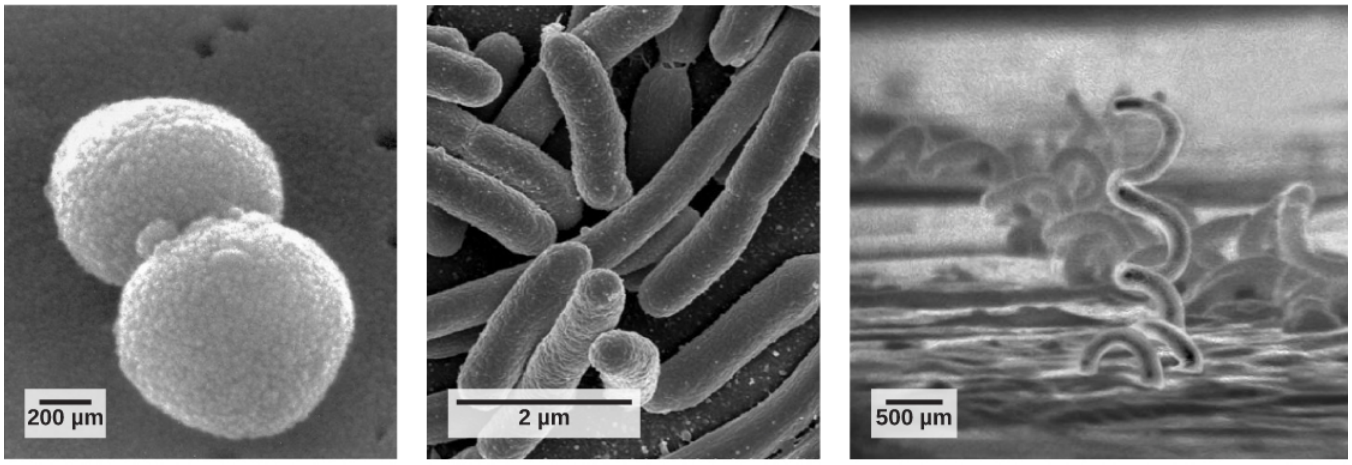


Figure 27.2.1: Prokaryotes fall into three basic categories based on their shape, visualized here using scanning electron microscopy: (a) cocci, or spherical (a pair is shown); (b) bacilli, or rod-shaped; and (c) spirilli, or spiral-shaped. (credit a: modification of work by Janice Haney Carr, Dr. Richard Facklam, CDC; credit c: modification of work by Dr. David Cox; scale-bar data from Matt Russell)

The Prokaryotic Cell

Recall that prokaryotes (Figure 27.2.2) are unicellular organisms that lack organelles or other internal membrane-bound structures. Therefore, they do not have a nucleus but instead generally have a single chromosome—a piece of circular, double-stranded DNA located in an area of the cell called the nucleoid. Most prokaryotes have a cell wall outside the plasma membrane.

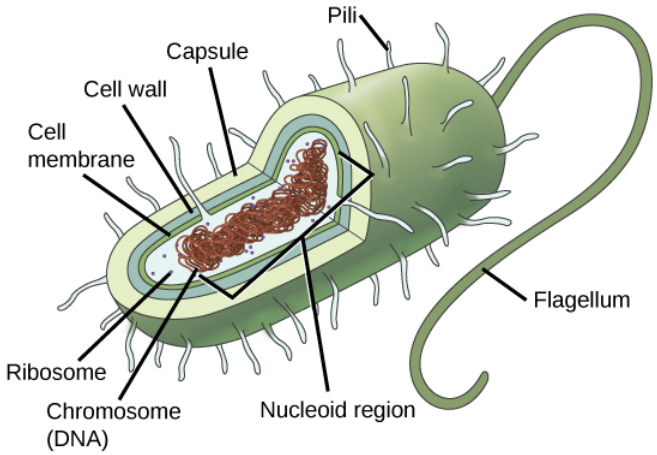


Figure 27.2.2: The features of a typical prokaryotic cell are shown.

Recall that prokaryotes are divided into two different domains, Bacteria and Archaea, which together with Eukarya, comprise the three domains of life (Figure **27.2.3**).

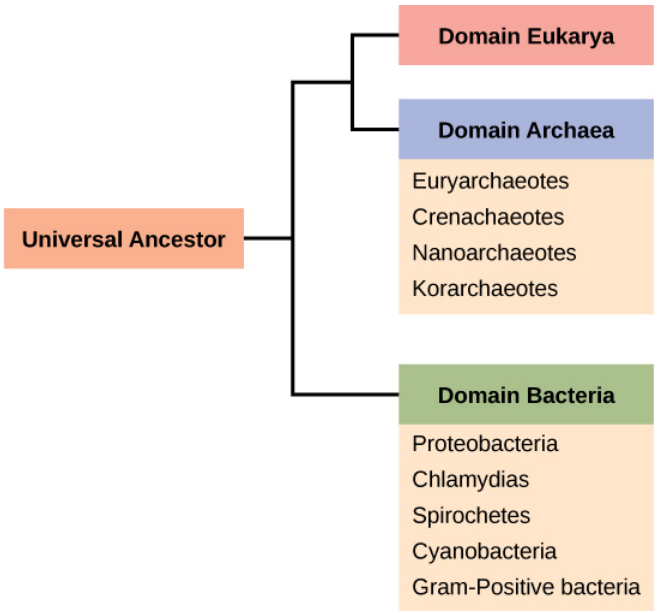


Figure **27.2.3**: Bacteria and Archaea are both prokaryotes but differ enough to be placed in separate domains. An ancestor of modern Archaea is believed to have given rise to Eukarya, the third domain of life. Archaeal and bacterial phyla are shown; the evolutionary relationship between these phyla is still open to debate.

The composition of the cell wall differs significantly between the domains Bacteria and Archaea. The composition of their cell walls also differs from the eukaryotic cell walls found in plants (cellulose) or fungi and insects (chitin). The cell wall functions as a protective layer, and it is responsible for the organism's shape. Some bacteria have an outer capsule outside the cell wall. Other structures are present in some prokaryotic species, but not in others (Table **27.2.1**). For example, the capsule found in some species enables the organism to attach to surfaces, protects it from dehydration and attack by phagocytic cells, and makes pathogens more resistant to our immune responses. Some species also have flagella (singular, flagellum) used for locomotion, and pili (singular, pilus) used for attachment to surfaces. Plasmids, which consist of extra-chromosomal DNA, are also present in many species of bacteria and archaea.

Characteristics of phyla of Bacteria are described in Figure **27.2.4** and Figure **27.2.5**; Archaea are described in Figure **27.2.6**.

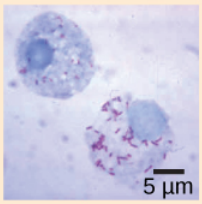
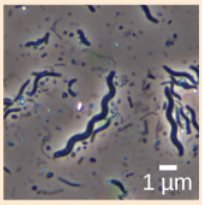
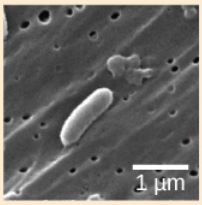
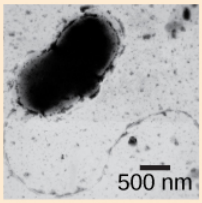
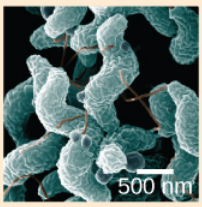
Bacteria of Phylum Proteobacteria		
Class	**Representative organisms**	**Representative micrograph**
Alpha Proteobacteria Some species are photoautotrophic but some are symbionts of plants and animals and others are pathogens. Eukaryotic mitochondria are thought be derived from bacteria in this group.	*Rhizobium* Nitrogen-fixing endosymbiont associated with the roots of legumes *Rickettsia* Obligate intracellular parasite that causes typhus and Rocky Mountain Spotted Fever (but not rickets, which is caused by Vitamin C deficiency)	 *Rickettsia rickettsia,* stained red, grow inside a host cell.
Beta Proteobacteria This group of bacteria is diverse. Some species play an important role in the nitrogen cycle.	*Nitrosomas* Species from this group oxidize ammonia into nitrite. *Spirillum minus* Causes rat-bite fever	 *Spirillum minus*
Gamma Proteobacteria Many are beneficial symbionts that populate the human gut, but others are familiar human pathogens. Some species from this subgroup oxidize sulfur compounds.	*Escherichia coli* Normally beneficial microbe of the human gut, but some strains cause disease *Salmonella* Certain strains cause food poisoning or typhoid fever *Yersinia pestis* Causative agent of Bubonic plague *Psuedomonas aeruginosa* Causes lung infections *Vibrio cholera* Causative agent of cholera *Chromatium* Sulfur-producing bacteria that oxidize sulfur, producing H_2S	 *Vibrio cholera*
Delta Proteobacteria Some species generate a spore-forming fruiting body in adverse conditions. Others reduce sulfate and sulfur.	*Myxobacteria* Generate spore-forming fruiting bodies in adverse conditions *Desulfovibrio vulgaris* Aneorobic, sulfate-reducing bacterium	 *Desulfovibrio vulgaris*
Epsilon Proteobacteria Many species inhabit the digestive tract of animals as symbionts or pathogens. Bacteria from this group have been found in deep-sea hydrothermal vents and cold seep habitats.	*Campylobacter* Causes blood poisoning and intestinal inflammation *Heliobacter pylori* Causes stomach ulcers	 *Campylobacter*

Figure **27.2.4**: Phylum Proteobacteria is one of up to 52 bacteria phyla. Proteobacteria is further subdivided into five classes, Alpha through Epsilon. (credit "Rickettsia rickettsia": modification of work by CDC; credit "Spirillum minus": modification of work by Wolframm Adlassnig; credit "Vibrio cholera": modification of work by Janice Haney Carr, CDC; credit "Desulfovibrio vulgaris": modification of work by Graham Bradley; credit "Campylobacter": modification of work by De Wood, Pooley, USDA, ARS, EMU; scale-bar data from Matt Russell)

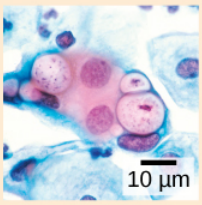
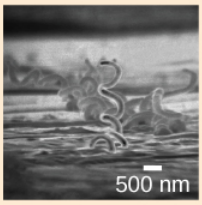
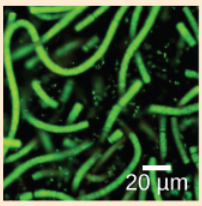
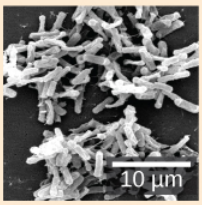
Bacteria: Chlamydia, Spirochaetae, Cyanobacteria, and Gram-positive		
Phylum	**Representative organisms**	**Representative micrograph**
Chlamydias All members of this group are obligate intracellular parasites of animal cells. Cells walls lack peptidoglycan.	*Chlamydia trachomatis* Common sexually transmitted disease that can lead to blindness	 In this pap smear, *Chlamydia trachomatis* appear as pink inclusions inside cells.
Spirochetes Most members of this species, which has spiral-shaped cells, are free-living aneaerobes, but some are pathogenic. Flagella run lengthwise in the periplasmic space between the inner and outer membrane.	*Treponema pallidum* Causative agent of syphilis *Borrelia burgdorferi* Causative agent of Lyme disease	 *Treponema pallidum*
Cyanobacteria Also known as blue-green algae, these bacteria obtain their energy through photosynthesis. They are ubiquitous, found in terrestrial, marine, and freshwater environments. Eukaryotic chloroplasts are thought be derived from bacteria in this group.	*Prochlorococcus* Believed to be the most abundant photosynthetic organism on earth; responsible for generating half the world's oxygen	 *Phormidium*
Gram-positive Bacteria Soil-dwelling members of this subgroup decompose organic matter. Some species cause disease. They have a thick cell wall and lack an outer membrane.	*Bacillus anthracis* Causes anthrax *Clostridium botulinum* Causes Botulism *Clostridium difficile* Causes diarrhea during antibiotic therapy *Streptomyces* Many antibiotics, including streptomycin, are derived from these bacteria. *Mycoplasmas* These tiny bacteria, the smallest known, lack a cell wall. Some are free-living, and some are pathogenic.	 *Clostridium difficile*

Figure **27.2.5**: Chlamydia, Spirochetes, Cyanobacteria, and Gram-positive bacteria are described in this table. Note that bacterial shape is not phylum-dependent; bacteria within a phylum may be cocci, rod-shaped, or spiral. (credit "Chlamydia trachomatis": modification of work by Dr. Lance Liotta Laboratory, NCI; credit "Treponema pallidum": modification of work by Dr. David Cox, CDC; credit "Phormidium": modification of work by USGS; credit "Clostridium difficile": modification of work by Lois S. Wiggs, CDC; scale-bar data from Matt Russell)

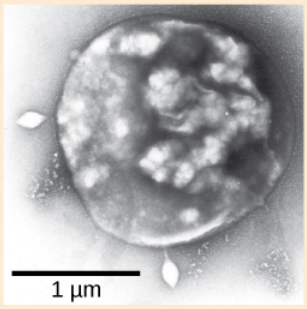
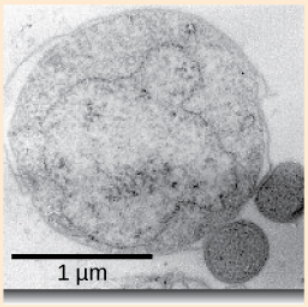
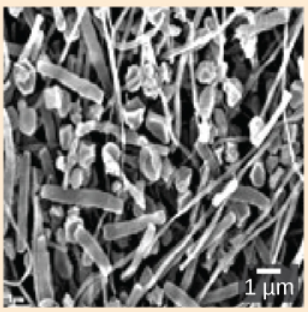
Archaea		
Phylum	**Representative organisms**	**Representative micrograph**
Euryarchaeota This phylum includes methanogens, which produce methane as a metabolic waste product, and halobacteria, which live in an extreme saline environment.	*Methanogens* Methane production causes flatulence in humans and other animals. *Halobacteria* Large blooms of this salt-loving archaea appear reddish due to the presence of bacterirhodopsin in the membrane. Bacteriorhodopsin is related to the retinal pigment rhodopsin.	 *Halobacterium* strain NRC-1
Crenarchaeota Members of the ubiquitous phylum play an important role in the fixation of carbon. Many members of this group are sulfur-dependent extremophiles. Some are thermophilic or hyperthermophilic.	*Sulfolobus* Members of this genus grow in volcanic springs at temperatures between 75° and 80°C and at a pH between 2 and 3.	 *Sulfolobus* being infected by bacteriophage
Nanoarchaeota This group currently contains only one species, *Nanoarchaeum equitans*.	*Nanoarchaeum equitans* This species was isolated from the bottom of the Atlantic Ocean and from a hydrothermal vent at Yellowstone National Park. It is an obligate symbiont with *Ignicoccus*, another species of archaea.	 *Nanoarchaeum equitans* (small dark spheres) are in contact with their larger host, *Ignicoccus*.
Korarchaeota Members of this phylum, considered to be one of the most primitive forms of life, have only been found in the Obsidian Pool, a hot spring at Yellowstone National Park.	No members of this species have been cultivated.	 This image shows a variety of korarchaeota species from the Obsidian Pool at Yellowstone National Park.

Figure **27.2.6**: Archaea are separated into four phyla: the Korarchaeota, Euryarchaeota, Crenarchaeota, and Nanoarchaeota. (credit "Halobacterium": modification of work by NASA; credit "Nanoarchaeotum equitans": modification of work by Karl O. Stetter; credit "korarchaeota": modification of work by Office of Science of the U.S. Dept. of Energy; scale-bar data from Matt Russell)

The Plasma Membrane

The plasma membrane is a thin lipid bilayer (6 to 8 nanometers) that completely surrounds the cell and separates the inside from the outside. Its selectively permeable nature keeps ions, proteins, and other molecules within the cell and prevents them from diffusing into the extracellular environment, while other molecules may move through the membrane. Recall that the general structure of a cell membrane is a phospholipid bilayer composed of two layers of lipid molecules. In archaeal cell membranes, isoprene (phytanyl) chains linked to glycerol replace the fatty acids linked to glycerol in bacterial membranes. Some archaeal membranes are lipid monolayers instead of bilayers (Figure **27.2.7**).

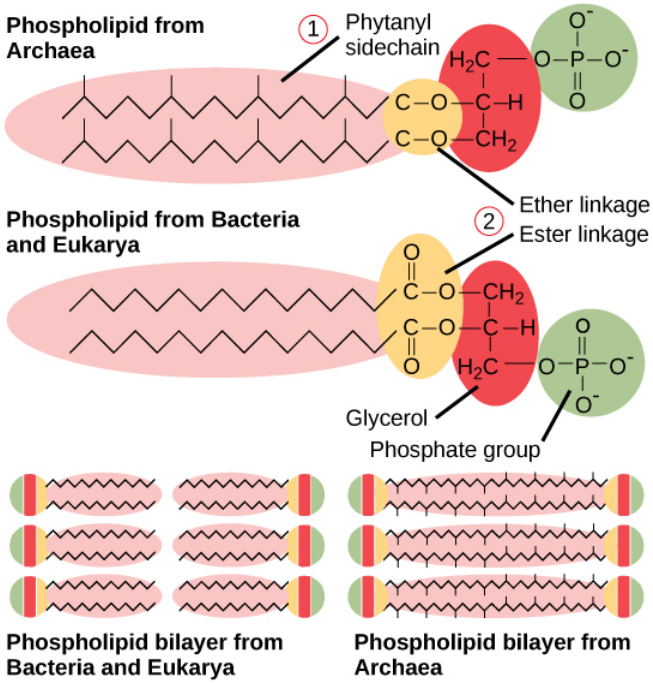


Figure **27.2.7**: Archaeal phospholipids differ from those found in Bacteria and Eukarya in two ways. First, they have branched phytanyl sidechains instead of linear ones. Second, an ether bond instead of an ester bond connects the lipid to the glycerol.

The Cell Wall

The cytoplasm of prokaryotic cells has a high concentration of dissolved solutes. Therefore, the osmotic pressure within the cell is relatively high. The cell wall is a protective layer that surrounds some cells and gives them shape and rigidity. It is located outside the cell membrane and prevents osmotic lysis (bursting due to increasing volume). The chemical composition of the cell walls varies between archaea and bacteria, and also varies between bacterial species.

Bacterial cell walls contain peptidoglycan, composed of polysaccharide chains that are cross-linked by unusual peptides containing both L- and D-amino acids including D-glutamic acid and D-alanine. Proteins normally have only L-amino acids; as a consequence, many of our antibiotics work by mimicking D-amino acids and therefore have specific effects on bacterial cell wall development. There are more than 100 different forms of peptidoglycan. S-layer (surface layer) proteins are also present on the outside of cell walls of both archaea and bacteria.

Bacteria are divided into two major groups: Gram positive and Gram negative, based on their reaction to Gram staining. Note that all Gram-positive bacteria belong to one phylum; bacteria in the other phyla (Proteobacteria, Chlamydias, Spirochetes, Cyanobacteria, and others) are Gram-negative. The Gram staining method is named after its inventor, Danish scientist Hans Christian Gram (1853–1938). The different bacterial responses to the staining procedure are ultimately due to cell wall structure. Gram-positive organisms typically lack the outer membrane found in Gram-negative organisms (Figure **27.2.8**). Up to 90 percent of the cell wall in Gram-positive bacteria is composed of peptidoglycan, and most of the rest is composed of acidic substances called teichoic acids. Teichoic acids may be covalently linked to lipids in the plasma membrane to form lipoteichoic acids. Lipoteichoic acids anchor the cell wall to the cell membrane. Gram-negative bacteria have a relatively thin cell wall composed of a few layers of peptidoglycan (only 10 percent of the total cell wall), surrounded by an outer envelope containing lipopolysaccharides (LPS) and

lipoproteins. This outer envelope is sometimes referred to as a second lipid bilayer. The chemistry of this outer envelope is very different, however, from that of the typical lipid bilayer that forms plasma membranes.

Art Connection

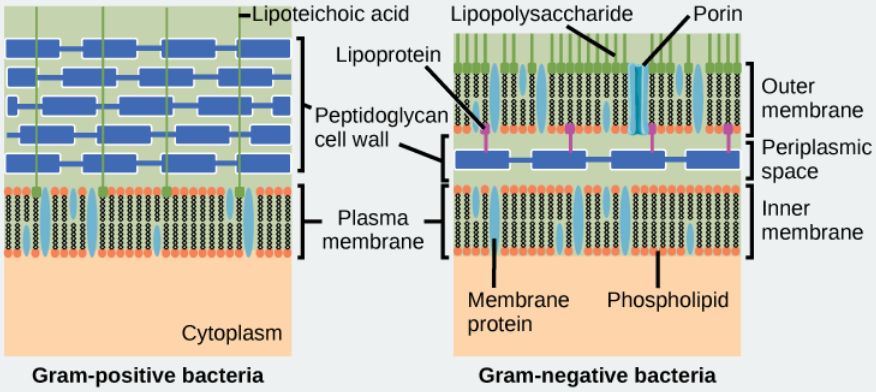


Figure **27.2.8**: Bacteria are divided into two major groups: Gram positive and Gram negative. Both groups have a cell wall composed of peptidoglycan: in Gram-positive bacteria, the wall is thick, whereas in Gram-negative bacteria, the wall is thin. In Gram-negative bacteria, the cell wall is surrounded by an outer membrane that contains lipopolysaccharides and lipoproteins. Porins are proteins in this cell membrane that allow substances to pass through the outer membrane of Gram-negative bacteria. In Gram-positive bacteria, lipoteichoic acid anchors the cell wall to the cell membrane. (credit: modification of work by "Franciscosp2"/Wikimedia Commons)

Which of the following statements is true?

A. Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.
B. Porins allow entry of substances into both Gram-positive and Gram-negative bacteria.
C. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
D. Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.

Archaean cell walls do not have peptidoglycan. There are four different types of Archaean cell walls. One type is composed of pseudopeptidoglycan, which is similar to peptidoglycan in morphology but contains different sugars in the polysaccharide chain. The other three types of cell walls are composed of polysaccharides, glycoproteins, or pure protein.

Table 27.2.1: Structural Differences and Similarities between Bacteria and Archaea

Structural Characteristic	Bacteria	Archaea
Cell type	Prokaryotic	Prokaryotic
Cell morphology	Variable	Variable
Cell wall	Contains peptidoglycan	Does not contain peptidoglycan
Cell membrane type	Lipid bilayer	Lipid bilayer or lipid monolayer
Plasma membrane lipids	Fatty acids	Phytanyl groups

Reproduction

Reproduction in prokaryotes is asexual and usually takes place by binary fission. Recall that the DNA of a prokaryote exists as a single, circular chromosome. Prokaryotes do not undergo mitosis. Rather the chromosome is replicated and the two resulting copies separate from one another, due to the growth of the cell. The prokaryote, now enlarged, is pinched inward at its equator and the two resulting cells, which are clones, separate. Binary fission does not provide an opportunity for genetic recombination or genetic diversity, but prokaryotes can share genes by three other mechanisms.

In transformation, the prokaryote takes in DNA found in its environment that is shed by other prokaryotes. If a nonpathogenic bacterium takes up DNA for a toxin gene from a pathogen and incorporates the new DNA into its own chromosome, it too may

become pathogenic. In transduction, bacteriophages, the viruses that infect bacteria, sometimes also move short pieces of chromosomal DNA from one bacterium to another. Transduction results in a recombinant organism. Archaea are not affected by bacteriophages but instead have their own viruses that translocate genetic material from one individual to another. In conjugation, DNA is transferred from one prokaryote to another by means of a pilus, which brings the organisms into contact with one another. The DNA transferred can be in the form of a plasmid or as a hybrid, containing both plasmid and chromosomal DNA. These three processes of DNA exchange are shown in Figure **27.2.9**.

Reproduction can be very rapid: a few minutes for some species. This short generation time coupled with mechanisms of genetic recombination and high rates of mutation result in the rapid evolution of prokaryotes, allowing them to respond to environmental changes (such as the introduction of an antibiotic) very quickly.

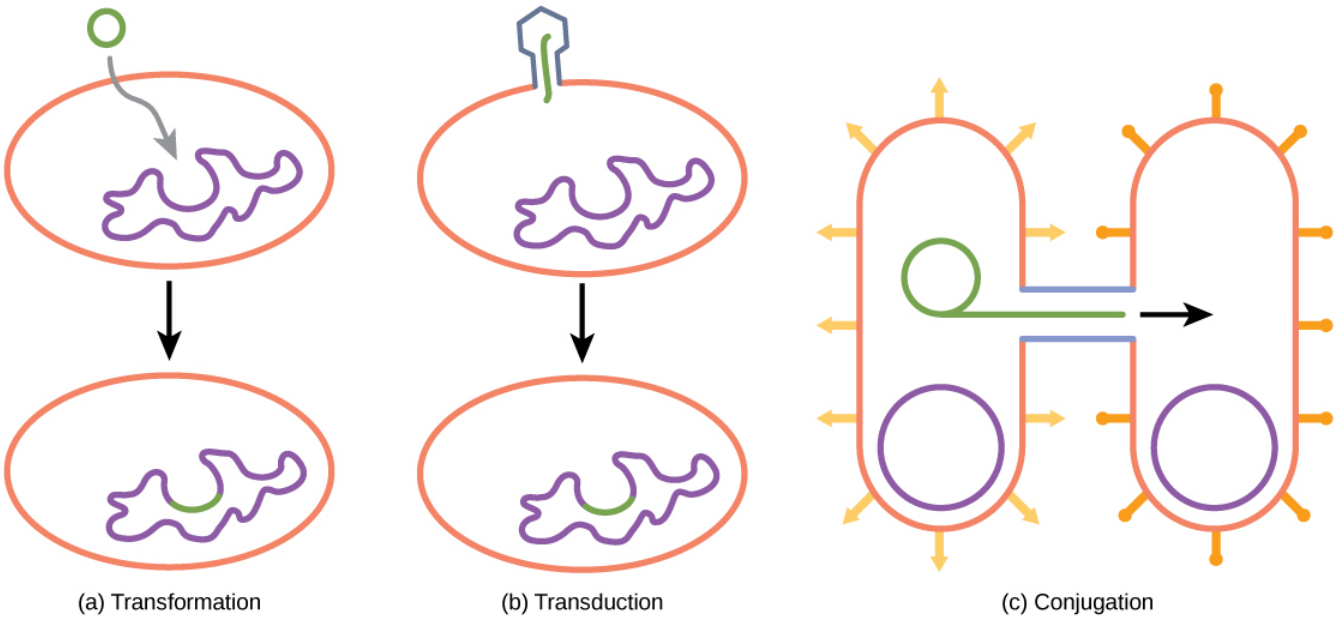


Figure **27.2.9**: Besides binary fission, there are three other mechanisms by which prokaryotes can exchange DNA. In (a) transformation, the cell takes up prokaryotic DNA directly from the environment. The DNA may remain separate as plasmid DNA or be incorporated into the host genome. In (b) transduction, a bacteriophage injects DNA into the cell that contains a small fragment of DNA from a different prokaryote. In (c) conjugation, DNA is transferred from one cell to another via a mating bridge that connects the two cells after the sex pilus draws the two bacteria close enough to form the bridge.

Evolution Connection: The Evolution of Prokaryotes

How do scientists answer questions about the evolution of prokaryotes? Unlike with animals, artifacts in the fossil record of prokaryotes offer very little information. Fossils of ancient prokaryotes look like tiny bubbles in rock. Some scientists turn to genetics and to the principle of the molecular clock, which holds that the more recently two species have diverged, the more similar their genes (and thus proteins) will be. Conversely, species that diverged long ago will have more genes that are dissimilar.

Scientists at the NASA Astrobiology Institute and at the European Molecular Biology Laboratory collaborated to analyze the molecular evolution of 32 specific proteins common to 72 species of prokaryotes.[1] The model they derived from their data indicates that three important groups of bacteria—Actinobacteria, *Deinococcus*, and Cyanobacteria (which the authors call *Terrabacteria*)—were the first to colonize land. (Recall that *Deinococcus* is a genus of prokaryote—a bacterium—that is highly resistant to ionizing radiation.) Cyanobacteria are photosynthesizers, while Actinobacteria are a group of very common bacteria that include species important in decomposition of organic wastes.

The timelines of divergence suggest that bacteria (members of the domain Bacteria) diverged from common ancestral species between 2.5 and 3.2 billion years ago, whereas archaea diverged earlier: between 3.1 and 4.1 billion years ago. Eukarya later diverged off the Archaean line. The work further suggests that stromatolites that formed prior to the advent of cyanobacteria (about 2.6 billion years ago) photosynthesized in an anoxic environment and that because of the modifications of the

Terrabacteria for land (resistance to drying and the possession of compounds that protect the organism from excess light), photosynthesis using oxygen may be closely linked to adaptations to survive on land.

Summary

Prokaryotes (domains Archaea and Bacteria) are single-celled organisms lacking a nucleus. They have a single piece of circular DNA in the nucleoid area of the cell. Most prokaryotes have a cell wall that lies outside the boundary of the plasma membrane. Some prokaryotes may have additional structures such as a capsule, flagella, and pili. Bacteria and Archaea differ in the lipid composition of their cell membranes and the characteristics of the cell wall. In archaeal membranes, phytanyl units, rather than fatty acids, are linked to glycerol. Some archaeal membranes are lipid monolayers instead of bilayers.

The cell wall is located outside the cell membrane and prevents osmotic lysis. The chemical composition of cell walls varies between species. Bacterial cell walls contain peptidoglycan. Archaean cell walls do not have peptidoglycan, but they may have pseudopeptidoglycan, polysaccharides, glycoproteins, or protein-based cell walls. Bacteria can be divided into two major groups: Gram positive and Gram negative, based on the Gram stain reaction. Gram-positive organisms have a thick cell wall, together with teichoic acids. Gram-negative organisms have a thin cell wall and an outer envelope containing lipopolysaccharides and lipoproteins.

Art Connections

Figure 27.2.8: Which of the following statements is true?

A. Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.
B. Porins allow entry of substances into both Gram-positive and Gram-negative bacteria.
C. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
D. Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.

Answer

A

Footnotes

1. 1 Battistuzzi, FU, Feijao, A, and Hedges, SB. A genomic timescale of prokaryote evolution: Insights into the origin of methanogenesis, phototrophy, and the colonization of land. *BioMed Central: Evolutionary Biology* 4 (2004): 44, doi:10.1186/1471-2148-4-44.

Glossary

capsule
external structure that enables a prokaryote to attach to surfaces and protects it from dehydration

conjugation
process by which prokaryotes move DNA from one individual to another using a pilus

Gram negative
bacterium whose cell wall contains little peptidoglycan but has an outer membrane

Gram positive
bacterium that contains mainly peptidoglycan in its cell walls

peptidoglycan
material composed of polysaccharide chains cross-linked to unusual peptides

pilus

surface appendage of some prokaryotes used for attachment to surfaces including other prokaryotes

pseudopeptidoglycan
component of archaea cell walls that is similar to peptidoglycan in morphology but contains different sugars

S-layer
surface-layer protein present on the outside of cell walls of archaea and bacteria

teichoic acid
polymer associated with the cell wall of Gram-positive bacteria

transduction
process by which a bacteriophage moves DNA from one prokaryote to another

transformation
process by which a prokaryote takes in DNA found in its environment that is shed by other prokaryotes

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27.3: Prokaryotic Genetics

Skills to Develop

- Describe the basic structure of a typical prokaryote
- Describe important differences in structure between Archaea and Bacteria

There are many differences between prokaryotic and eukaryotic cells. However, all cells have four common structures: the plasma membrane, which functions as a barrier for the cell and separates the cell from its environment; the cytoplasm, a jelly-like substance inside the cell; nucleic acids, the genetic material of the cell; and ribosomes, where protein synthesis takes place. Prokaryotes come in various shapes, but many fall into three categories: cocci (spherical), bacilli (rod-shaped), and spirilli (spiral-shaped) (Figure **27.3.1**).

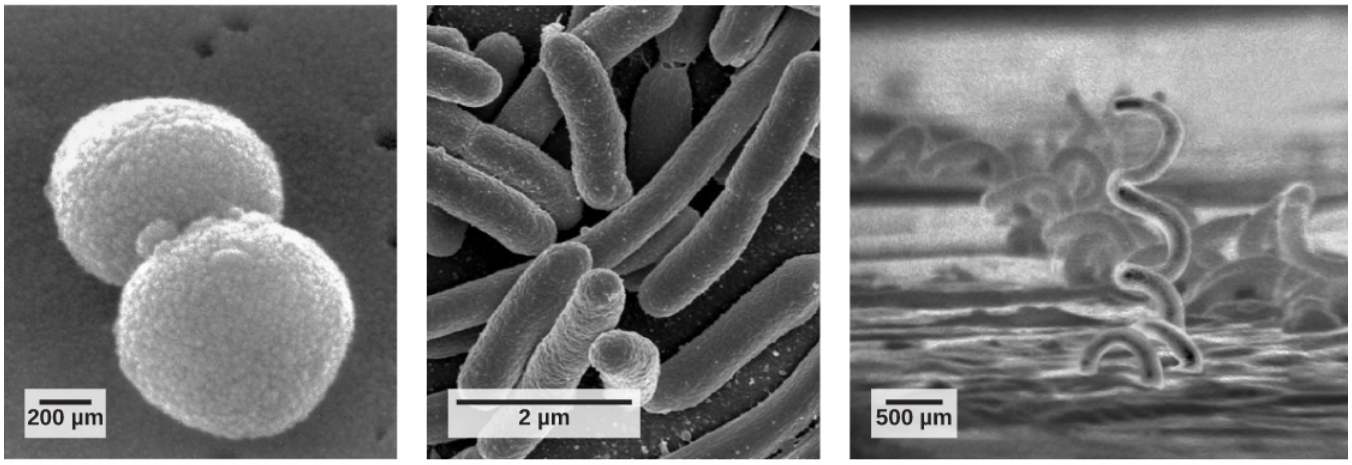


Figure **27.3.1**: Prokaryotes fall into three basic categories based on their shape, visualized here using scanning electron microscopy: (a) cocci, or spherical (a pair is shown); (b) bacilli, or rod-shaped; and (c) spirilli, or spiral-shaped. (credit a: modification of work by Janice Haney Carr, Dr. Richard Facklam, CDC; credit c: modification of work by Dr. David Cox; scale-bar data from Matt Russell)

The Prokaryotic Cell

Recall that prokaryotes (Figure **27.3.2**) are unicellular organisms that lack organelles or other internal membrane-bound structures. Therefore, they do not have a nucleus but instead generally have a single chromosome—a piece of circular, double-stranded DNA located in an area of the cell called the nucleoid. Most prokaryotes have a cell wall outside the plasma membrane.

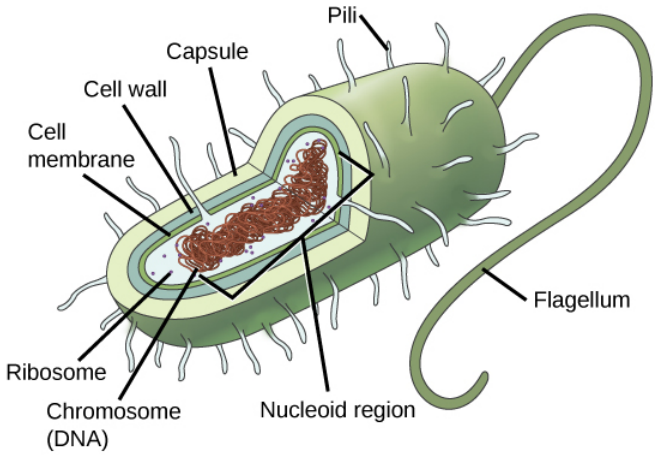


Figure **27.3.2**: The features of a typical prokaryotic cell are shown.

Recall that prokaryotes are divided into two different domains, Bacteria and Archaea, which together with Eukarya, comprise the three domains of life (Figure **27.3.3**).

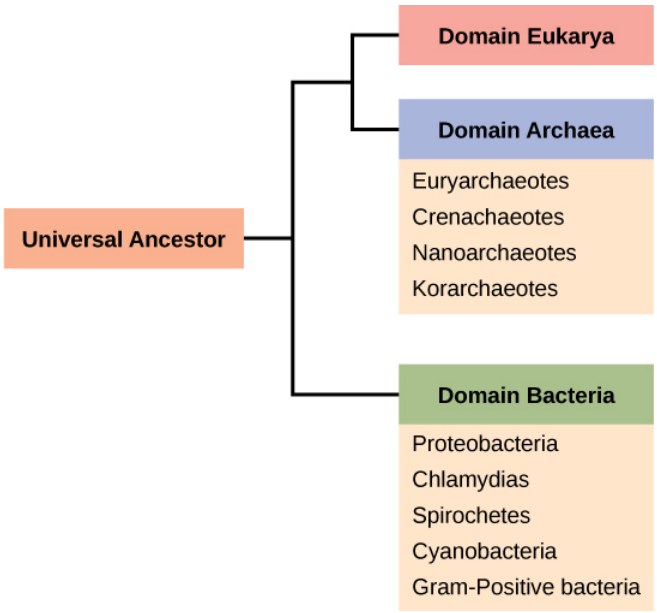


Figure **27.3.3**: Bacteria and Archaea are both prokaryotes but differ enough to be placed in separate domains. An ancestor of modern Archaea is believed to have given rise to Eukarya, the third domain of life. Archaeal and bacterial phyla are shown; the evolutionary relationship between these phyla is still open to debate.

The composition of the cell wall differs significantly between the domains Bacteria and Archaea. The composition of their cell walls also differs from the eukaryotic cell walls found in plants (cellulose) or fungi and insects (chitin). The cell wall functions as a protective layer, and it is responsible for the organism's shape. Some bacteria have an outer capsule outside the cell wall. Other structures are present in some prokaryotic species, but not in others (Table **27.3.1**). For example, the capsule found in some species enables the organism to attach to surfaces, protects it from dehydration and attack by phagocytic cells, and makes pathogens more resistant to our immune responses. Some species also have flagella (singular, flagellum) used for locomotion, and pili (singular, pilus) used for attachment to surfaces. Plasmids, which consist of extra-chromosomal DNA, are also present in many species of bacteria and archaea.

Characteristics of phyla of Bacteria are described in Figure **27.3.4** and Figure **27.3.5**; Archaea are described in Figure **27.3.6**.

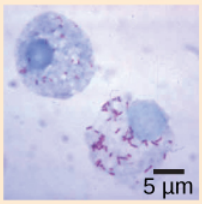
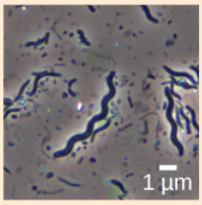
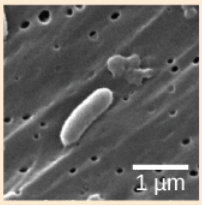
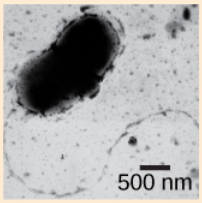
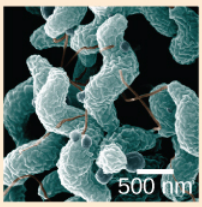
Bacteria of Phylum Proteobacteria		
Class	**Representative organisms**	**Representative micrograph**
Alpha Proteobacteria Some species are photoautotrophic but some are symbionts of plants and animals and others are pathogens. Eukaryotic mitochondria are thought be derived from bacteria in this group.	*Rhizobium* Nitrogen-fixing endosymbiont associated with the roots of legumes *Rickettsia* Obligate intracellular parasite that causes typhus and Rocky Mountain Spotted Fever (but not rickets, which is caused by Vitamin C deficiency)	 *Rickettsia rickettsia,* stained red, grow inside a host cell.
Beta Proteobacteria This group of bacteria is diverse. Some species play an important role in the nitrogen cycle.	*Nitrosomas* Species from this group oxidize ammonia into nitrite. *Spirillum minus* Causes rat-bite fever	 *Spirillum minus*
Gamma Proteobacteria Many are beneficial symbionts that populate the human gut, but others are familiar human pathogens. Some species from this subgroup oxidize sulfur compounds.	*Escherichia coli* Normally beneficial microbe of the human gut, but some strains cause disease *Salmonella* Certain strains cause food poisoning or typhoid fever *Yersinia pestis* Causative agent of Bubonic plague *Psuedomonas aeruginosa* Causes lung infections *Vibrio cholera* Causative agent of cholera *Chromatium* Sulfur-producing bacteria that oxidize sulfur, producing H_2S	 *Vibrio cholera*
Delta Proteobacteria Some species generate a spore-forming fruiting body in adverse conditions. Others reduce sulfate and sulfur.	*Myxobacteria* Generate spore-forming fruiting bodies in adverse conditions *Desulfovibrio vulgaris* Aneorobic, sulfate-reducing bacterium	 *Desulfovibrio vulgaris*
Epsilon Proteobacteria Many species inhabit the digestive tract of animals as symbionts or pathogens. Bacteria from this group have been found in deep-sea hydrothermal vents and cold seep habitats.	*Campylobacter* Causes blood poisoning and intestinal inflammation *Heliobacter pylori* Causes stomach ulcers	 *Campylobacter*

Figure **27.3.4**: Phylum Proteobacteria is one of up to 52 bacteria phyla. Proteobacteria is further subdivided into five classes, Alpha through Epsilon. (credit "Rickettsia rickettsia": modification of work by CDC; credit "Spirillum minus": modification of work by Wolframm Adlassnig; credit "Vibrio cholera": modification of work by Janice Haney Carr, CDC; credit "Desulfovibrio vulgaris": modification of work by Graham Bradley; credit "Campylobacter": modification of work by De Wood, Pooley, USDA, ARS, EMU; scale-bar data from Matt Russell)

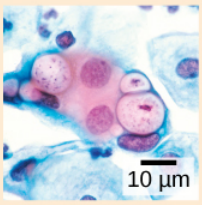
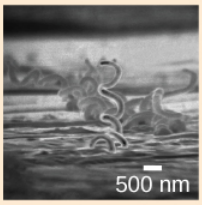
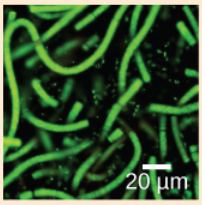
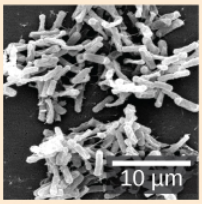
Bacteria: Chlamydia, Spirochaetae, Cyanobacteria, and Gram-positive		
Phylum	**Representative organisms**	**Representative micrograph**
Chlamydias All members of this group are obligate intracellular parasites of animal cells. Cells walls lack peptidoglycan.	*Chlamydia trachomatis* Common sexually transmitted disease that can lead to blindness	 In this pap smear, *Chlamydia trachomatis* appear as pink inclusions inside cells.
Spirochetes Most members of this species, which has spiral-shaped cells, are free-living aneaerobes, but some are pathogenic. Flagella run lengthwise in the periplasmic space between the inner and outer membrane.	*Treponema pallidum* Causative agent of syphilis *Borrelia burgdorferi* Causative agent of Lyme disease	 *Treponema pallidum*
Cyanobacteria Also known as blue-green algae, these bacteria obtain their energy through photosynthesis. They are ubiquitous, found in terrestrial, marine, and freshwater environments. Eukaryotic chloroplasts are thought be derived from bacteria in this group.	*Prochlorococcus* Believed to be the most abundant photosynthetic organism on earth; responsible for generating half the world's oxygen	 *Phormidium*
Gram-positive Bacteria Soil-dwelling members of this subgroup decompose organic matter. Some species cause disease. They have a thick cell wall and lack an outer membrane.	*Bacillus anthracis* Causes anthrax *Clostridium botulinum* Causes Botulism *Clostridium difficile* Causes diarrhea during antibiotic therapy *Streptomyces* Many antibiotics, including streptomyocin, are derived from these bacteria. *Mycoplasmas* These tiny bacteria, the smallest known, lack a cell wall. Some are free-living, and some are pathogenic.	 *Clostridium difficile*

Figure **27.3.5**: Chlamydia, Spirochetes, Cyanobacteria, and Gram-positive bacteria are described in this table. Note that bacterial shape is not phylum-dependent; bacteria within a phylum may be cocci, rod-shaped, or spiral. (credit "Chlamydia trachomatis": modification of work by Dr. Lance Liotta Laboratory, NCI; credit "Treponema pallidum": modification of work by Dr. David Cox, CDC; credit "Phormidium": modification of work by USGS; credit "Clostridium difficile": modification of work by Lois S. Wiggs, CDC; scale-bar data from Matt Russell)

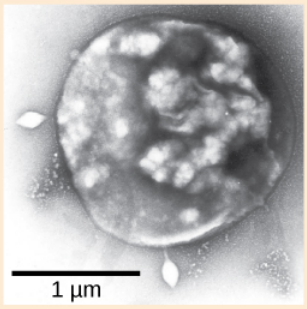
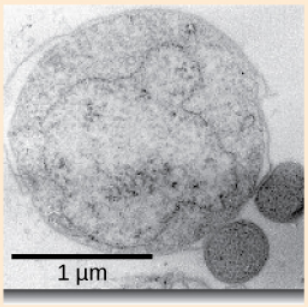
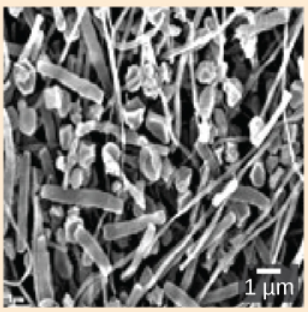
Archaea		
Phylum	**Representative organisms**	**Representative micrograph**
Euryarchaeota This phylum includes methanogens, which produce methane as a metabolic waste product, and halobacteria, which live in an extreme saline environment.	*Methanogens* Methane production causes flatulence in humans and other animals. *Halobacteria* Large blooms of this salt-loving archaea appear reddish due to the presence of bacterirhodopsin in the membrane. Bacteriorhodopsin is related to the retinal pigment rhodopsin.	 *Halobacterium* strain NRC-1
Crenarchaeota Members of the ubiquitous phylum play an important role in the fixation of carbon. Many members of this group are sulfur-dependent extremophiles. Some are thermophilic or hyperthermophilic.	*Sulfolobus* Members of this genus grow in volcanic springs at temperatures between 75° and 80°C and at a pH between 2 and 3.	 *Sulfolobus* being infected by bacteriophage
Nanoarchaeota This group currently contains only one species, *Nanoarchaeum equitans*.	*Nanoarchaeum equitans* This species was isolated from the bottom of the Atlantic Ocean and from a hydrothermal vent at Yellowstone National Park. It is an obligate symbiont with *Ignicoccus*, another species of archaea.	 *Nanoarchaeum equitans* (small dark spheres) are in contact with their larger host, *Ignicoccus*.
Korarchaeota Members of this phylum, considered to be one of the most primitive forms of life, have only been found in the Obsidian Pool, a hot spring at Yellowstone National Park.	No members of this species have been cultivated.	 This image shows a variety of korarchaeota species from the Obsidian Pool at Yellowstone National Park.

Figure **27.3.6**: Archaea are separated into four phyla: the Korarchaeota, Euryarchaeota, Crenarchaeota, and Nanoarchaeota. (credit "Halobacterium": modification of work by NASA; credit "Nanoarchaeotum equitans": modification of work by Karl O. Stetter; credit "korarchaeota": modification of work by Office of Science of the U.S. Dept. of Energy; scale-bar data from Matt Russell)

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The Plasma Membrane

The plasma membrane is a thin lipid bilayer (6 to 8 nanometers) that completely surrounds the cell and separates the inside from the outside. Its selectively permeable nature keeps ions, proteins, and other molecules within the cell and prevents them from diffusing into the extracellular environment, while other molecules may move through the membrane. Recall that the general structure of a cell membrane is a phospholipid bilayer composed of two layers of lipid molecules. In archaeal cell membranes, isoprene (phytanyl) chains linked to glycerol replace the fatty acids linked to glycerol in bacterial membranes. Some archaeal membranes are lipid monolayers instead of bilayers (Figure **27.3.7**).

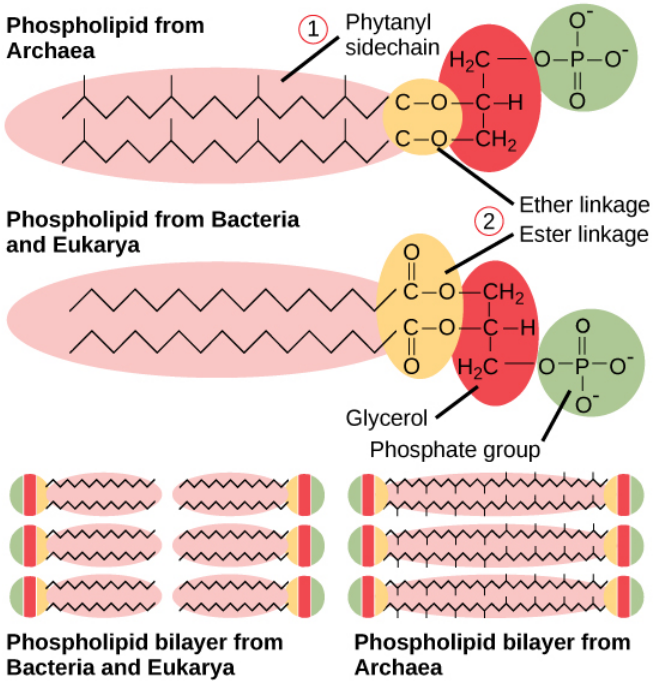


Figure **27.3.7**: Archaeal phospholipids differ from those found in Bacteria and Eukarya in two ways. First, they have branched phytanyl sidechains instead of linear ones. Second, an ether bond instead of an ester bond connects the lipid to the glycerol.

The Cell Wall

The cytoplasm of prokaryotic cells has a high concentration of dissolved solutes. Therefore, the osmotic pressure within the cell is relatively high. The cell wall is a protective layer that surrounds some cells and gives them shape and rigidity. It is located outside the cell membrane and prevents osmotic lysis (bursting due to increasing volume). The chemical composition of the cell walls varies between archaea and bacteria, and also varies between bacterial species.

Bacterial cell walls contain peptidoglycan, composed of polysaccharide chains that are cross-linked by unusual peptides containing both L- and D-amino acids including D-glutamic acid and D-alanine. Proteins normally have only L-amino acids; as a consequence, many of our antibiotics work by mimicking D-amino acids and therefore have specific effects on bacterial cell wall development. There are more than 100 different forms of peptidoglycan. S-layer (surface layer) proteins are also present on the outside of cell walls of both archaea and bacteria.

Bacteria are divided into two major groups: Gram positive and Gram negative, based on their reaction to Gram staining. Note that all Gram-positive bacteria belong to one phylum; bacteria in the other phyla (Proteobacteria, Chlamydias, Spirochetes, Cyanobacteria, and others) are Gram-negative. The Gram staining method is named after its inventor, Danish scientist Hans Christian Gram (1853–1938). The different bacterial responses to the staining procedure are ultimately due to cell wall structure. Gram-positive organisms typically lack the outer membrane found in Gram-negative organisms (Figure **27.3.8**). Up to 90 percent of the cell wall in Gram-positive bacteria is composed of peptidoglycan, and most of the rest is composed of acidic substances called teichoic acids. Teichoic acids may be covalently linked to lipids in the plasma membrane to form lipoteichoic acids. Lipoteichoic acids anchor the cell wall to the cell membrane. Gram-negative bacteria have a relatively thin cell wall composed of a few layers of peptidoglycan (only 10 percent of the total cell wall), surrounded by an outer envelope containing lipopolysaccharides (LPS) and

lipoproteins. This outer envelope is sometimes referred to as a second lipid bilayer. The chemistry of this outer envelope is very different, however, from that of the typical lipid bilayer that forms plasma membranes.

Art Connection

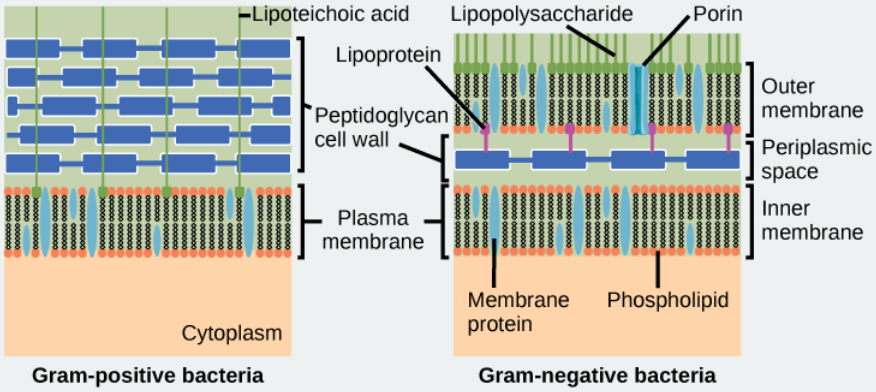


Figure **27.3.8**: Bacteria are divided into two major groups: Gram positive and Gram negative. Both groups have a cell wall composed of peptidoglycan: in Gram-positive bacteria, the wall is thick, whereas in Gram-negative bacteria, the wall is thin. In Gram-negative bacteria, the cell wall is surrounded by an outer membrane that contains lipopolysaccharides and lipoproteins. Porins are proteins in this cell membrane that allow substances to pass through the outer membrane of Gram-negative bacteria. In Gram-positive bacteria, lipoteichoic acid anchors the cell wall to the cell membrane. (credit: modification of work by "Franciscosp2"/Wikimedia Commons)

Which of the following statements is true?

A. Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.
B. Porins allow entry of substances into both Gram-positive and Gram-negative bacteria.
C. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
D. Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.

Archaean cell walls do not have peptidoglycan. There are four different types of Archaean cell walls. One type is composed of pseudopeptidoglycan, which is similar to peptidoglycan in morphology but contains different sugars in the polysaccharide chain. The other three types of cell walls are composed of polysaccharides, glycoproteins, or pure protein.

Table 27.3.1: Structural Differences and Similarities between Bacteria and Archaea

Structural Characteristic	Bacteria	Archaea
Cell type	Prokaryotic	Prokaryotic
Cell morphology	Variable	Variable
Cell wall	Contains peptidoglycan	Does not contain peptidoglycan
Cell membrane type	Lipid bilayer	Lipid bilayer or lipid monolayer
Plasma membrane lipids	Fatty acids	Phytanyl groups

Reproduction

Reproduction in prokaryotes is asexual and usually takes place by binary fission. Recall that the DNA of a prokaryote exists as a single, circular chromosome. Prokaryotes do not undergo mitosis. Rather the chromosome is replicated and the two resulting copies separate from one another, due to the growth of the cell. The prokaryote, now enlarged, is pinched inward at its equator and the two resulting cells, which are clones, separate. Binary fission does not provide an opportunity for genetic recombination or genetic diversity, but prokaryotes can share genes by three other mechanisms.

In transformation, the prokaryote takes in DNA found in its environment that is shed by other prokaryotes. If a nonpathogenic bacterium takes up DNA for a toxin gene from a pathogen and incorporates the new DNA into its own chromosome, it too may

become pathogenic. In transduction, bacteriophages, the viruses that infect bacteria, sometimes also move short pieces of chromosomal DNA from one bacterium to another. Transduction results in a recombinant organism. Archaea are not affected by bacteriophages but instead have their own viruses that translocate genetic material from one individual to another. In conjugation, DNA is transferred from one prokaryote to another by means of a pilus, which brings the organisms into contact with one another. The DNA transferred can be in the form of a plasmid or as a hybrid, containing both plasmid and chromosomal DNA. These three processes of DNA exchange are shown in Figure **27.3.9**.

Reproduction can be very rapid: a few minutes for some species. This short generation time coupled with mechanisms of genetic recombination and high rates of mutation result in the rapid evolution of prokaryotes, allowing them to respond to environmental changes (such as the introduction of an antibiotic) very quickly.

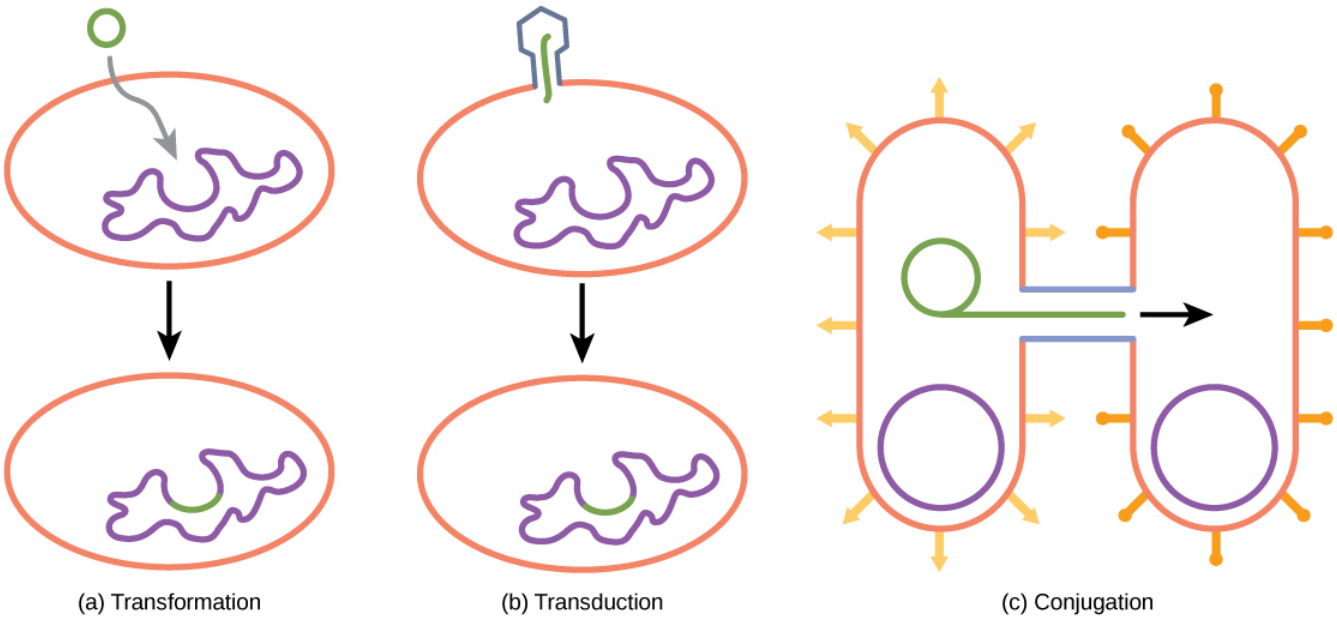


Figure **27.3.9**: Besides binary fission, there are three other mechanisms by which prokaryotes can exchange DNA. In (a) transformation, the cell takes up prokaryotic DNA directly from the environment. The DNA may remain separate as plasmid DNA or be incorporated into the host genome. In (b) transduction, a bacteriophage injects DNA into the cell that contains a small fragment of DNA from a different prokaryote. In (c) conjugation, DNA is transferred from one cell to another via a mating bridge that connects the two cells after the sex pilus draws the two bacteria close enough to form the bridge.

Evolution Connection: The Evolution of Prokaryotes

How do scientists answer questions about the evolution of prokaryotes? Unlike with animals, artifacts in the fossil record of prokaryotes offer very little information. Fossils of ancient prokaryotes look like tiny bubbles in rock. Some scientists turn to genetics and to the principle of the molecular clock, which holds that the more recently two species have diverged, the more similar their genes (and thus proteins) will be. Conversely, species that diverged long ago will have more genes that are dissimilar.

Scientists at the NASA Astrobiology Institute and at the European Molecular Biology Laboratory collaborated to analyze the molecular evolution of 32 specific proteins common to 72 species of prokaryotes.[1] The model they derived from their data indicates that three important groups of bacteria—Actinobacteria, *Deinococcus*, and Cyanobacteria (which the authors call *Terrabacteria*)—were the first to colonize land. (Recall that *Deinococcus* is a genus of prokaryote—a bacterium—that is highly resistant to ionizing radiation.) Cyanobacteria are photosynthesizers, while Actinobacteria are a group of very common bacteria that include species important in decomposition of organic wastes.

The timelines of divergence suggest that bacteria (members of the domain Bacteria) diverged from common ancestral species between 2.5 and 3.2 billion years ago, whereas archaea diverged earlier: between 3.1 and 4.1 billion years ago. Eukarya later diverged off the Archaean line. The work further suggests that stromatolites that formed prior to the advent of cyanobacteria (about 2.6 billion years ago) photosynthesized in an anoxic environment and that because of the modifications of the

Terrabacteria for land (resistance to drying and the possession of compounds that protect the organism from excess light), photosynthesis using oxygen may be closely linked to adaptations to survive on land.

Summary

Prokaryotes (domains Archaea and Bacteria) are single-celled organisms lacking a nucleus. They have a single piece of circular DNA in the nucleoid area of the cell. Most prokaryotes have a cell wall that lies outside the boundary of the plasma membrane. Some prokaryotes may have additional structures such as a capsule, flagella, and pili. Bacteria and Archaea differ in the lipid composition of their cell membranes and the characteristics of the cell wall. In archaeal membranes, phytanyl units, rather than fatty acids, are linked to glycerol. Some archaeal membranes are lipid monolayers instead of bilayers.

The cell wall is located outside the cell membrane and prevents osmotic lysis. The chemical composition of cell walls varies between species. Bacterial cell walls contain peptidoglycan. Archaean cell walls do not have peptidoglycan, but they may have pseudopeptidoglycan, polysaccharides, glycoproteins, or protein-based cell walls. Bacteria can be divided into two major groups: Gram positive and Gram negative, based on the Gram stain reaction. Gram-positive organisms have a thick cell wall, together with teichoic acids. Gram-negative organisms have a thin cell wall and an outer envelope containing lipopolysaccharides and lipoproteins.

Art Connections

Figure **27.3.8**: Which of the following statements is true?

A. Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.
B. Porins allow entry of substances into both Gram-positive and Gram-negative bacteria.
C. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
D. Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.

Answer

A

Footnotes

1. 1 Battistuzzi, FU, Feijao, A, and Hedges, SB. A genomic timescale of prokaryote evolution: Insights into the origin of methanogenesis, phototrophy, and the colonization of land. *BioMed Central: Evolutionary Biology* 4 (2004): 44, doi:10.1186/1471-2148-4-44.

Glossary

capsule
external structure that enables a prokaryote to attach to surfaces and protects it from dehydration

conjugation
process by which prokaryotes move DNA from one individual to another using a pilus

Gram negative
bacterium whose cell wall contains little peptidoglycan but has an outer membrane

Gram positive
bacterium that contains mainly peptidoglycan in its cell walls

peptidoglycan
material composed of polysaccharide chains cross-linked to unusual peptides

pilus

surface appendage of some prokaryotes used for attachment to surfaces including other prokaryotes

pseudopeptidoglycan
component of archaea cell walls that is similar to peptidoglycan in morphology but contains different sugars

S-layer
surface-layer protein present on the outside of cell walls of archaea and bacteria

teichoic acid
polymer associated with the cell wall of Gram-positive bacteria

transduction
process by which a bacteriophage moves DNA from one prokaryote to another

transformation
process by which a prokaryote takes in DNA found in its environment that is shed by other prokaryotes

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27.4: The Metabolic Diversity of Prokaryotes

Skills to Develop

- Identify the macronutrients needed by prokaryotes, and explain their importance
- Describe the ways in which prokaryotes get energy and carbon for life processes
- Describe the roles of prokaryotes in the carbon and nitrogen cycles

Prokaryotes are metabolically diverse organisms. There are many different environments on Earth with various energy and carbon sources, and variable conditions. Prokaryotes have been able to live in every environment by using whatever energy and carbon sources are available. Prokaryotes fill many niches on Earth, including being involved in nutrient cycles such as nitrogen and carbon cycles, decomposing dead organisms, and thriving inside living organisms, including humans. The very broad range of environments that prokaryotes occupy is possible because they have diverse metabolic processes.

Needs of Prokaryotes

The diverse environments and ecosystems on Earth have a wide range of conditions in terms of temperature, available nutrients, acidity, salinity, and energy sources. Prokaryotes are very well equipped to make their living out of a vast array of nutrients and conditions. To live, prokaryotes need a source of energy, a source of carbon, and some additional nutrients.

Macronutrients

Cells are essentially a well-organized assemblage of macromolecules and water. Recall that macromolecules are produced by the polymerization of smaller units called monomers. For cells to build all of the molecules required to sustain life, they need certain substances, collectively called nutrients. When prokaryotes grow in nature, they obtain their nutrients from the environment. Nutrients that are required in large amounts are called macronutrients, whereas those required in smaller or trace amounts are called micronutrients. Just a handful of elements are considered macronutrients—carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur. (A mnemonic for remembering these elements is the acronym *CHONPS*.)

Why are these macronutrients needed in large amounts? They are the components of organic compounds in cells, including water. Carbon is the major element in all macromolecules: carbohydrates, proteins, nucleic acids, lipids, and many other compounds. Carbon accounts for about 50 percent of the composition of the cell. Nitrogen represents 12 percent of the total dry weight of a typical cell and is a component of proteins, nucleic acids, and other cell constituents. Most of the nitrogen available in nature is either atmospheric nitrogen (N_2) or another inorganic form. Diatomic (N_2) nitrogen, however, can be converted into an organic form only by certain organisms, called nitrogen-fixing organisms. Both hydrogen and oxygen are part of many organic compounds and of water. Phosphorus is required by all organisms for the synthesis of nucleotides and phospholipids. Sulfur is part of the structure of some amino acids such as cysteine and methionine, and is also present in several vitamins and coenzymes. Other important macronutrients are potassium (K), magnesium (Mg), calcium (Ca), and sodium (Na). Although these elements are required in smaller amounts, they are very important for the structure and function of the prokaryotic cell.

Micronutrients

In addition to these macronutrients, prokaryotes require various metallic elements in small amounts. These are referred to as micronutrients or trace elements. For example, iron is necessary for the function of the cytochromes involved in electron-transport reactions. Some prokaryotes require other elements—such as boron (B), chromium (Cr), and manganese (Mn)—primarily as enzyme cofactors.

The Ways in Which Prokaryotes Obtain Energy

Prokaryotes can use different sources of energy to assemble macromolecules from smaller molecules. Phototrophs (or phototrophic organisms) obtain their energy from sunlight. Chemotrophs (or chemosynthetic organisms) obtain their energy from chemical compounds. Chemotrophs that can use organic compounds as energy sources are called chemoorganotrophs. Those that can also use inorganic compounds as energy sources are called chemolitotrophs.

The Ways in Which Prokaryotes Obtain Carbon

Prokaryotes not only can use different sources of energy but also different sources of carbon compounds. Recall that organisms that are able to fix inorganic carbon are called autotrophs. Autotrophic prokaryotes synthesize organic molecules from carbon dioxide. In contrast, heterotrophic prokaryotes obtain carbon from organic compounds. To make the picture more complex, the terms that describe how prokaryotes obtain energy and carbon can be combined. Thus, photoautotrophs use energy from sunlight, and carbon from carbon dioxide and water, whereas chemoheterotrophs obtain energy and carbon from an organic chemical source. Chemolitoautotrophs obtain their energy from inorganic compounds, and they build their complex molecules from carbon dioxide. Table **27.4.1** summarizes carbon and energy sources in prokaryotes.

Table 27.4.1: Carbon and Energy Sources in Prokaryotes

Energy Sources			Carbon Sources	
Light	Chemicals		Carbon dioxide	Organic compounds
Phototrophs	Chemotrophs		Autotrophs	Heterotrophs
	Organic chemicals	Inorganic chemicals		
	Chemo-organotrophs	Chemolithotrophs		

Role of Prokaryotes in Ecosystems

Prokaryotes are ubiquitous: There is no niche or ecosystem in which they are not present. Prokaryotes play many roles in the environments they occupy. The roles they play in the carbon and nitrogen cycles are vital to life on Earth.

Prokaryotes and the Carbon Cycle

Carbon is one of the most important macronutrients, and prokaryotes play an important role in the carbon cycle (Figure **27.4.1**). Carbon is cycled through Earth's major reservoirs: land, the atmosphere, aquatic environments, sediments and rocks, and biomass. The movement of carbon is via carbon dioxide, which is removed from the atmosphere by land plants and marine prokaryotes, and is returned to the atmosphere via the respiration of chemoorganotrophic organisms, including prokaryotes, fungi, and animals. Although the largest carbon reservoir in terrestrial ecosystems is in rocks and sediments, that carbon is not readily available.

A large amount of available carbon is found in land plants. Plants, which are producers, use carbon dioxide from the air to synthesize carbon compounds. Related to this, one very significant source of carbon compounds is humus, which is a mixture of organic materials from dead plants and prokaryotes that have resisted decomposition. Consumers such as animals use organic compounds generated by producers and release carbon dioxide to the atmosphere. Then, bacteria and fungi, collectively called decomposers, carry out the breakdown (decomposition) of plants and animals and their organic compounds. The most important contributor of carbon dioxide to the atmosphere is microbial decomposition of dead material (dead animals, plants, and humus) that undergo respiration.

In aqueous environments and their anoxic sediments, there is another carbon cycle taking place. In this case, the cycle is based on one-carbon compounds. In anoxic sediments, prokaryotes, mostly archaea, produce methane (CH_4). This methane moves into the zone above the sediment, which is richer in oxygen and supports bacteria called methane oxidizers that oxidize methane to carbon dioxide, which then returns to the atmosphere.

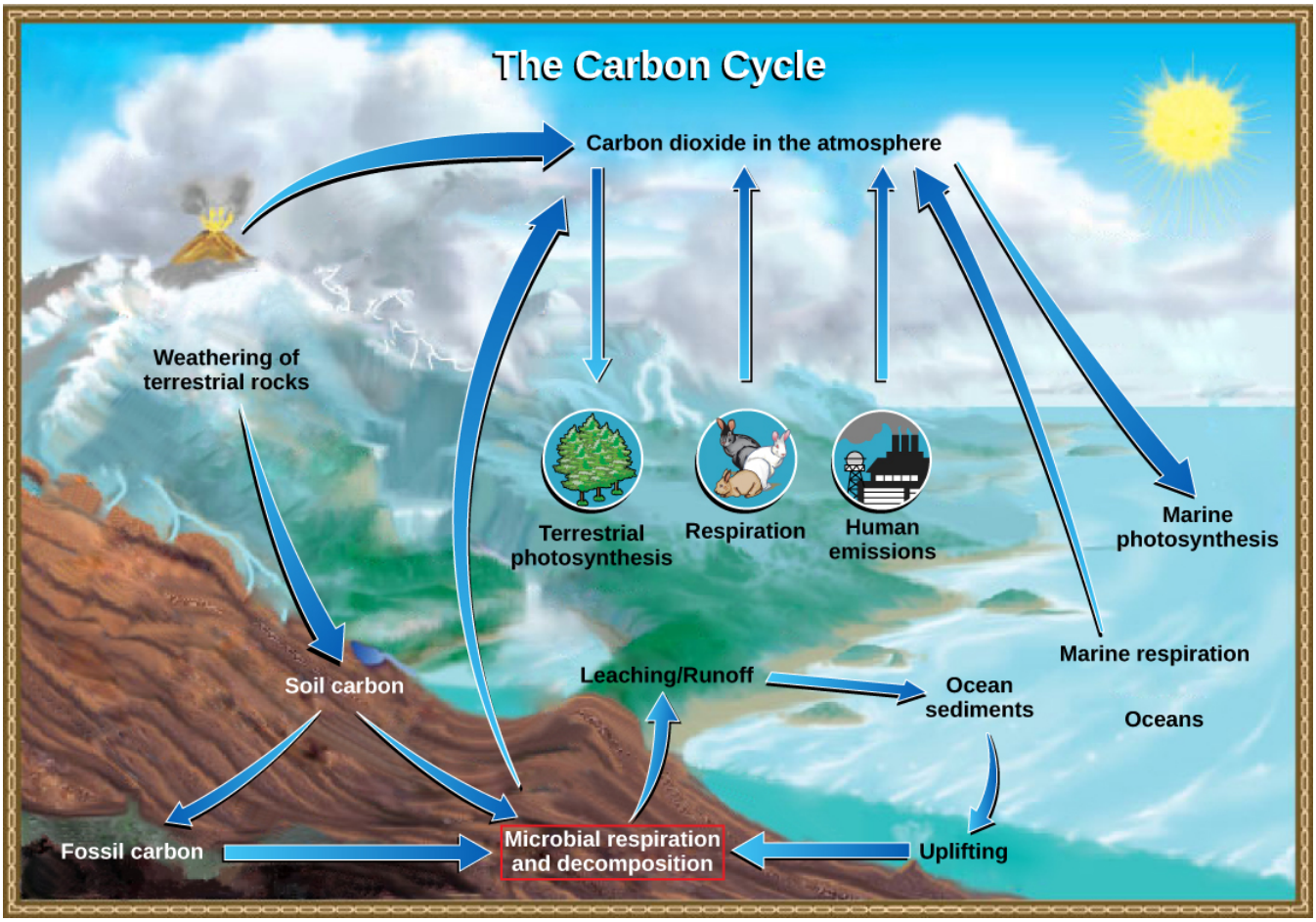


Figure **27.4.1**: Prokaryotes play a significant role in continuously moving carbon through the biosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Prokaryotes and the Nitrogen Cycle

Nitrogen is a very important element for life because it is part of proteins and nucleic acids. It is a macronutrient, and in nature, it is recycled from organic compounds to ammonia, ammonium ions, nitrate, nitrite, and nitrogen gas by myriad processes, many of which are carried out only by prokaryotes. As illustrated in Figure **27.4.2**, prokaryotes are key to the nitrogen cycle. The largest pool of nitrogen available in the terrestrial ecosystem is gaseous nitrogen from the air, but this nitrogen is not usable by plants, which are primary producers. Gaseous nitrogen is transformed, or "fixed" into more readily available forms such as ammonia through the process of nitrogen fixation. Ammonia can be used by plants or converted to other forms.

Another source of ammonia is ammonification, the process by which ammonia is released during the decomposition of nitrogen-containing organic compounds. Ammonia released to the atmosphere, however, represents only 15 percent of the total nitrogen released; the rest is as N_2 and N_2O. Ammonia is catabolized anaerobically by some prokaryotes, yielding N_2 as the final product. Nitrification is the conversion of ammonium to nitrite and nitrate. Nitrification in soils is carried out by bacteria belonging to the genera *Nitrosomas*, *Nitrobacter*, and *Nitrospira*. The bacteria performs the reverse process, the reduction of nitrate from the soils to gaseous compounds such as N_2O, NO, and N_2, a process called denitrification.

Art Connection

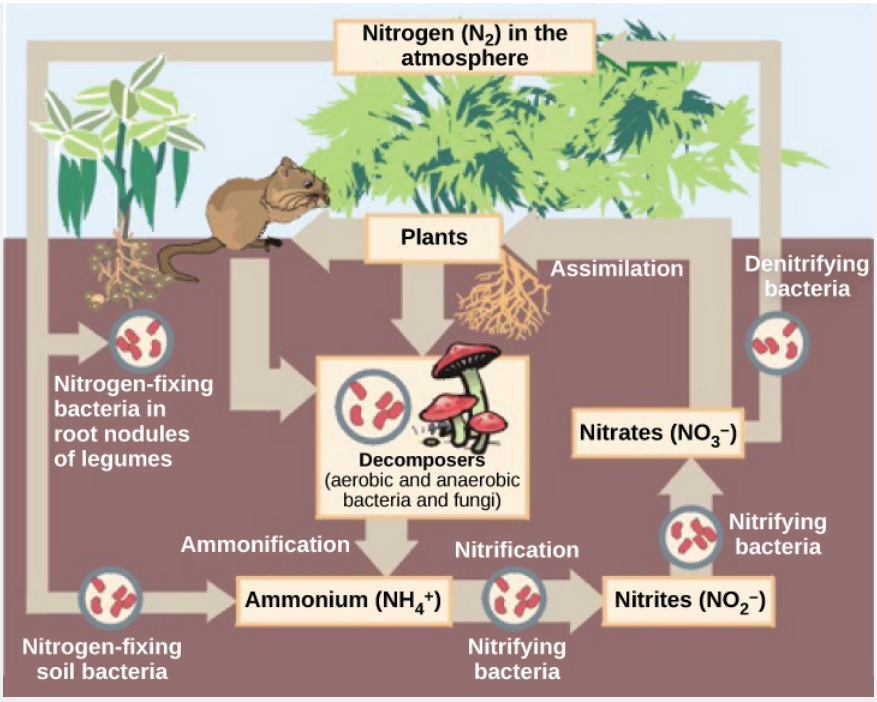


Figure **27.4.2**: Prokaryotes play a key role in the nitrogen cycle. (credit: Environmental Protection Agency)

Which of the following statements about the nitrogen cycle is false?

A. Nitrogen fixing bacteria exist on the root nodules of legumes and in the soil.
B. Denitrifying bacteria convert nitrates (NO_3^-) into nitrogen gas (N_2).
C. Ammonification is the process by which ammonium ion (NH_4^+) is released from decomposing organic compounds.
D. Nitrification is the process by which nitrites (NO_2^-) are converted to ammonium ion (NH_4^+).

Summary

Prokaryotes are the most metabolically diverse organisms; they flourish in many different environments with various carbon energy and carbon sources, variable temperature, pH, pressure, and water availability. Nutrients required in large amounts are called macronutrients, whereas those required in trace amounts are called micronutrients or trace elements. Macronutrients include C, H, O, N, P, S, K, Mg, Ca, and Na. In addition to these macronutrients, prokaryotes require various metallic elements for growth and enzyme function. Prokaryotes use different sources of energy to assemble macromolecules from smaller molecules. Phototrophs obtain their energy from sunlight, whereas chemotrophs obtain energy from chemical compounds.

Prokaryotes play roles in the carbon and nitrogen cycles. Carbon is returned to the atmosphere by the respiration of animals and other chemoorganotrophic organisms. Consumers use organic compounds generated by producers and release carbon dioxide into the atmosphere. The most important contributor of carbon dioxide to the atmosphere is microbial decomposition of dead material. Nitrogen is recycled in nature from organic compounds to ammonia, ammonium ions, nitrite, nitrate, and nitrogen gas. Gaseous nitrogen is transformed into ammonia through nitrogen fixation. Ammonia is anaerobically catabolized by some prokaryotes, yielding N_2 as the final product. Nitrification is the conversion of ammonium into nitrite. Nitrification in soils is carried out by bacteria. Denitrification is also performed by bacteria and transforms nitrate from soils into gaseous nitrogen compounds, such as N_2O, NO, and N_2.

Art Connections

Figure **27.4.2**: Which of the following statements about the nitrogen cycle is false?

A. Nitrogen fixing bacteria exist on the root nodules of legumes and in the soil.
B. Denitrifying bacteria convert nitrates (NO_3^-) into nitrogen gas (N_2).
C. Ammonification is the process by which ammonium ion (NH_4^+) is released from decomposing organic compounds.

D. Nitrification is the process by which nitrites (NO_2^-) are converted to ammonium ion (NH_4^+).

Answer

D

Glossary

ammonification
process by which ammonia is released during the decomposition of nitrogen-containing organic compounds

chemotroph
organism that obtains energy from chemical compounds

decomposer
organism that carries out the decomposition of dead organisms

denitrification
transformation of nitrate from soil to gaseous nitrogen compounds such as N_2O, NO and N_2

nitrification
conversion of ammonium into nitrite and nitrate in soils

nitrogen fixation
process by which gaseous nitrogen is transformed, or “fixed” into more readily available forms such as ammonia

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27.5: Microbial Ecology

Learning Objectives

- Give examples of the beneficial roles played by prokaryotes in different ecosystems

Role of Prokaryotes in Ecosystems

Prokaryotes are ubiquitous: There is no niche or ecosystem in which they are not present. Prokaryotes play many roles in the environments they occupy, but the roles they play in the carbon and nitrogen cycles are vital to life on earth.

Prokaryotes and the Carbon Cycle

Carbon is one of the most important macronutrients. Prokaryotes play an important role in the carbon cycle. Carbon is cycled through earth's major reservoirs: land, the atmosphere, aquatic environments, sediments and rocks, and biomass. The movement of carbon is via carbon dioxide, which is removed from the atmosphere by land plants and marine prokaryotes and is returned to the atmosphere via the respiration of chemoorganotrophic organisms, including prokaryotes, fungi, and animals. Although the largest carbon reservoir in terrestrial ecosystems is in rocks and sediments, that carbon is not readily available.

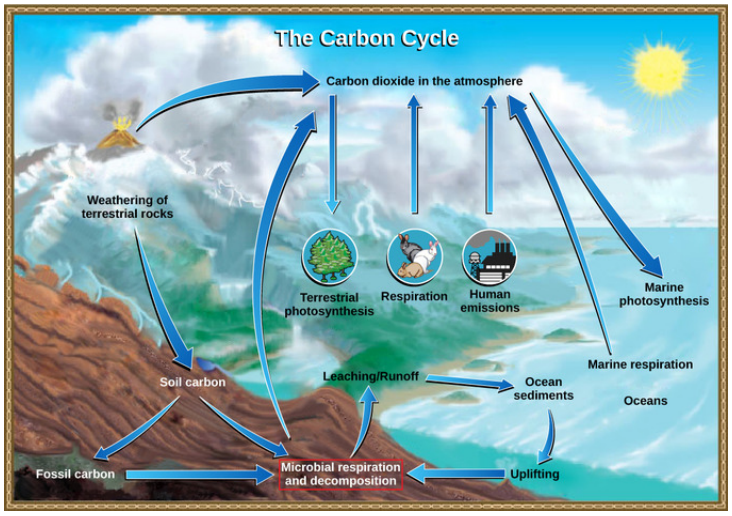


Figure 27.5.1: Carbon cycle: Prokaryotes play a significant role in continuously moving carbon through the biosphere.

A large amount of available carbon is found in land plants, which are producers that use carbon dioxide from the air to synthesize carbon compounds. Related to this, one very significant source of carbon compounds is humus, which is a mixture of organic materials from dead plants and prokaryotes that have resisted decomposition. Consumers such as animals use organic compounds generated by producers, releasing carbon dioxide to the atmosphere. Then, bacteria and fungi, collectively called decomposers, carry out the breakdown (decomposition) of plants and animals and their organic compounds. The most important contributor of carbon dioxide to the atmosphere is microbial decomposition of dead material (dead animals, plants, and humus).

In aqueous environments and their anoxic sediments, there is another carbon cycle taking place. In this case, the cycle is based on one-carbon compounds. In anoxic sediments, prokaryotes, mostly archaea, produce methane (CH_4). This methane moves into the zone above the sediment, which is richer in oxygen and supports bacteria called methane oxidizers that oxidize methane to carbon dioxide, which then returns to the atmosphere.

Prokaryotes and the Nitrogen Cycle

Nitrogen is a very important element for life because it is part of proteins and nucleic acids. As a macronutrient in nature, it is recycled from organic compounds to ammonia, ammonium ions, nitrate, nitrite, and nitrogen gas by myriad processes, many of which are carried out solely by prokaryotes; they are key to the nitrogen cycle. The largest pool of nitrogen available in the terrestrial ecosystem is gaseous nitrogen from the air, but this nitrogen is not usable by plants, which are primary producers. Gaseous nitrogen is transformed, or "fixed," into more-readily available forms such as ammonia through the process of nitrogen

fixation by natural means, especially by microorganisms (prokayotes) in the soil. Ammonia can then be used by plants or converted to other forms.

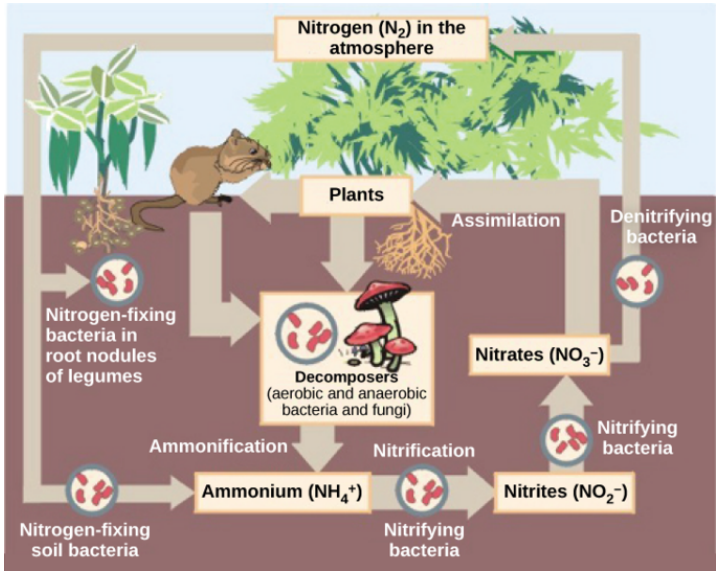


Figure **27.5.1**: Nitrogen cycle: Prokaryotes play a key role in the nitrogen cycle.

Another source of ammonia is ammonification, the process by which ammonia is released during the decomposition of nitrogen-containing organic compounds. Ammonia released to the atmosphere, however, represents only 15 percent of the total nitrogen released; the rest is as N_2 and N_2O. Ammonia is catabolized anaerobically by some prokaryotes, yielding N_2 as the final product. Nitrification is the conversion of ammonium to nitrite and nitrate. Nitrification in soils is carried out by bacteria belonging to the genera *Nitrosomas*, *Nitrobacter*, and *Nitrospira*. The bacteria perform the reverse process, the reduction of nitrate from the soils to gaseous compounds such as N_2O, NO, and N_2, a process called denitrification.

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Key Points

- Carbon and nitrogen are both macronutrients that are necessary for life on earth; prokaryotes play vital roles in their cycles.
- The carbon cycle is maintained by prokaryotes that remove carbon dioxide and return it to the atmosphere.
- Prokaryotes play a major role in the nitrogen cycle by fixing atomspheric nitrogen into ammonia that plants can use and by converting ammonia into other forms of nitrogen sources.

Key Terms

- **carbon cycle**: the physical cycle of carbon through the earth's biosphere, geosphere, hydrosphere, and atmosphere that includes such processes as photosynthesis, decomposition, respiration and carbonification
- **nitrogen cycle**: the natural circulation of nitrogen, in which atmospheric nitrogen is converted to nitrogen oxides and deposited in the soil, where it is used by organisms or decomposed back to elemental nitrogen
- **nitrogen fixation**: the conversion of atmospheric nitrogen into ammonia and organic derivatives, by natural means, especially by microorganisms in the soil, into a form that can be assimilated by plants

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27.6: Bacterial Diseases of Humans

Skills to Develop

- Identify bacterial diseases that caused historically important plagues and epidemics
- Describe the link between biofilms and foodborne diseases
- Explain how overuse of antibiotic may be creating “super bugs”
- Explain the importance of MRSA with respect to the problems of antibiotic resistance

Devastating pathogen-borne diseases and plagues, both viral and bacterial in nature, have affected humans since the beginning of human history. The true cause of these diseases was not understood at the time, and some people thought that diseases were a spiritual punishment. Over time, people came to realize that staying apart from afflicted persons, and disposing of the corpses and personal belongings of victims of illness, reduced their own chances of getting sick.

Epidemiologists study how diseases affect a population. An epidemic is a disease that occurs in an unusually high number of individuals in a population at the same time. A pandemic is a widespread, usually worldwide, epidemic. An endemic disease is a disease that is constantly present, usually at low incidence, in a population.

Long History of Bacterial Disease

There are records about infectious diseases as far back as 3000 B.C. A number of significant pandemics caused by bacteria have been documented over several hundred years. Some of the most memorable pandemics led to the decline of cities and nations.

In the 21st century, infectious diseases remain among the leading causes of death worldwide, despite advances made in medical research and treatments in recent decades. A disease spreads when the pathogen that causes it is passed from one person to another. For a pathogen to cause disease, it must be able to reproduce in the host’s body and damage the host in some way.

The Plague of Athens

In 430 B.C., the Plague of Athens killed one-quarter of the Athenian troops that were fighting in the great Peloponnesian War and weakened Athens’ dominance and power. The plague impacted people living in overcrowded Athens as well as troops aboard ships that had to return to Athens. The source of the plague may have been identified recently when researchers from the University of Athens were able to use DNA from teeth recovered from a mass grave. The scientists identified nucleotide sequences from a pathogenic bacterium, *Salmonella enterica* serovar Typhi (Figure **27.6.1**), which causes typhoid fever.[1] This disease is commonly seen in overcrowded areas and has caused epidemics throughout recorded history.

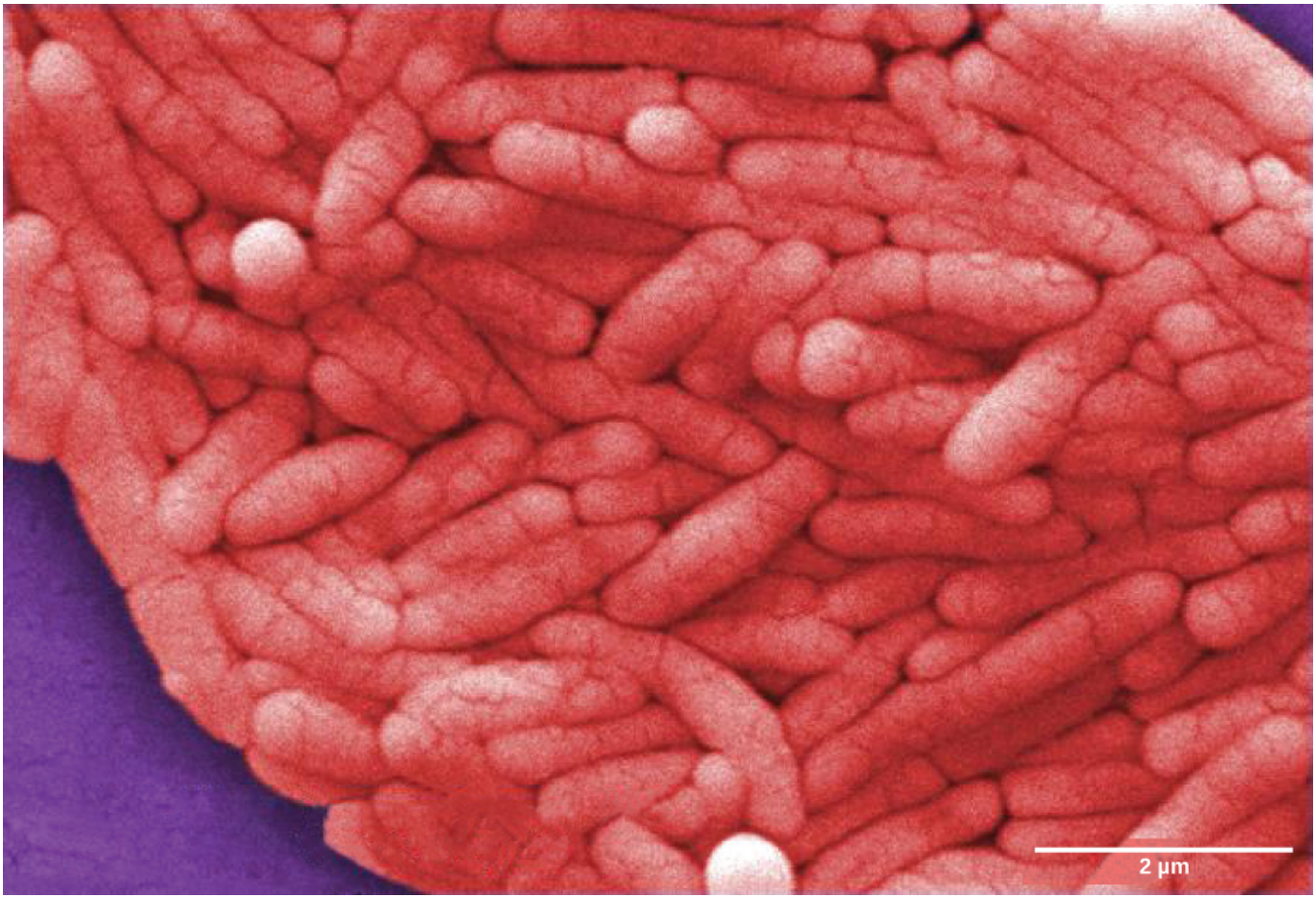
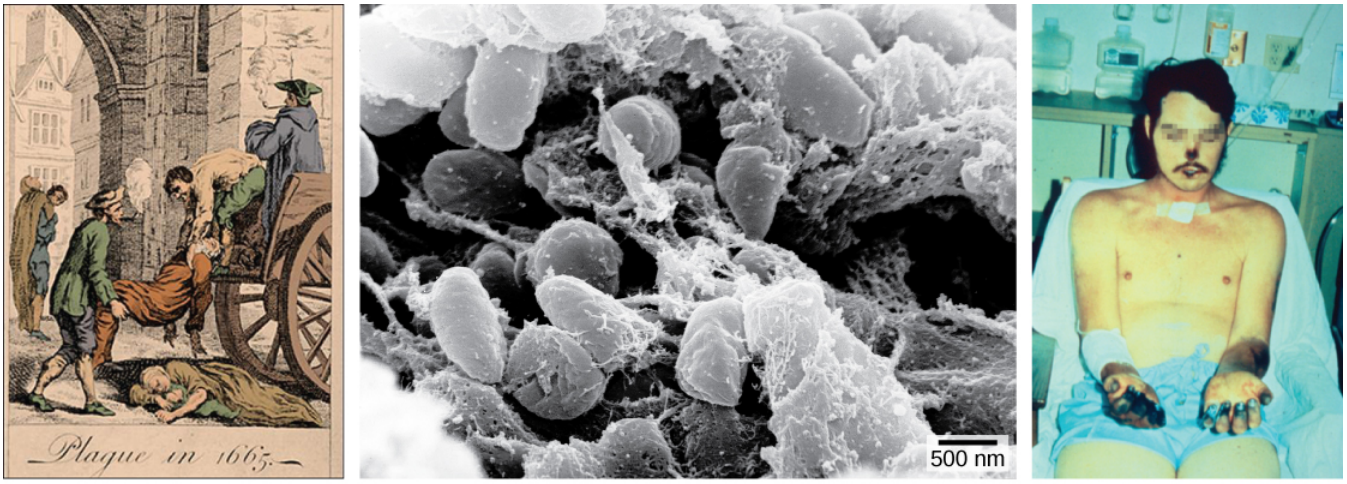


Figure **27.6.1**: *Salmonella enterica* serovar Typhi, the causative agent of Typhoid fever, is a Gram-negative, rod-shaped gamma protobacterium. Typhoid fever, which is spread through feces, causes intestinal hemorrhage, high fever, delirium and dehydration. Today, between 16 and 33 million cases of this re-emerging disease occur annually, resulting in over 200,000 deaths. Carriers of the disease can be asymptomatic. In a famous case in the early 1900s, a cook named Mary Mallon unknowingly spread the disease to over fifty people, three of whom died. Other *Salmonella* serotypes cause food poisoning. (credit: modification of work by NCI, CDC)

Bubonic Plagues

From 541 to 750, an outbreak of what was likely a bubonic plague (the Plague of Justinian), eliminated one-quarter to one-half of the human population in the eastern Mediterranean region. The population in Europe dropped by 50 percent during this outbreak. Bubonic plague would strike Europe more than once.

One of the most devastating pandemics was the Black Death (1346 to 1361) that is believed to have been another outbreak of bubonic plague caused by the bacterium *Yersinia pestis*. It is thought to have originated initially in China and spread along the Silk Road, a network of land and sea trade routes, to the Mediterranean region and Europe, carried by rat fleas living on black rats that were always present on ships. The Black Death reduced the world's population from an estimated 450 million to about 350 to 375 million. Bubonic plague struck London hard again in the mid-1600s (Figure **27.6.2**). In modern times, approximately 1,000 to 3,000 cases of plague arise globally each year. Although contracting bubonic plague before antibiotics meant almost certain death, the bacterium responds to several types of modern antibiotics, and mortality rates from plague are now very low.



(a) (b) (c)

Figure **27.6.2**: The (a) Great Plague of London killed an estimated 200,000 people, or about twenty percent of the city's population. The causative agent, the (b) bacterium *Yersinia pestis*, is a Gram-negative, rod-shaped bacterium from the class Gamma Proteobacteria. The disease is transmitted through the bite of an infected flea, which is infected by a rodent. Symptoms include swollen lymph nodes, fever, seizure, vomiting of blood, and (c) gangrene. (credit b: Rocky Mountain Laboratories, NIAID, NIH; scale-bar data from Matt Russell; credit c: Textbook of Military Medicine, Washington, D.C., U.S. Dept. of the Army, Office of the Surgeon General, Borden Institute)

Link to Learning



Watch a video on the modern understanding of the Black Death—bubonic plague in Europe during the 14th century.

Migration of Diseases to New Populations

Over the centuries, Europeans tended to develop genetic immunity to endemic infectious diseases, but when European conquerors reached the western hemisphere, they brought with them disease-causing bacteria and viruses, which triggered epidemics that completely devastated populations of Native Americans, who had no natural resistance to many European diseases. It has been estimated that up to 90 percent of Native Americans died from infectious diseases after the arrival of Europeans, making conquest of the New World a foregone conclusion.

Emerging and Re-emerging Diseases

The distribution of a particular disease is dynamic. Therefore, changes in the environment, the pathogen, or the host population can dramatically impact the spread of a disease. According to the World Health Organization (WHO) an emerging disease (Figure **27.6.3**) is one that has appeared in a population for the first time, or that may have existed previously but is rapidly increasing in incidence or geographic range. This definition also includes re-emerging diseases that were previously under control. Approximately 75 percent of recently emerging infectious diseases affecting humans are zoonotic diseases, zoonoses, diseases that

primarily infect animals and are transmitted to humans; some are of viral origin and some are of bacterial origin. Brucellosis is an example of a prokaryotic zoonosis that is re-emerging in some regions, and necrotizing fasciitis (commonly known as flesh-eating bacteria) has been increasing in virulence for the last 80 years for unknown reasons.

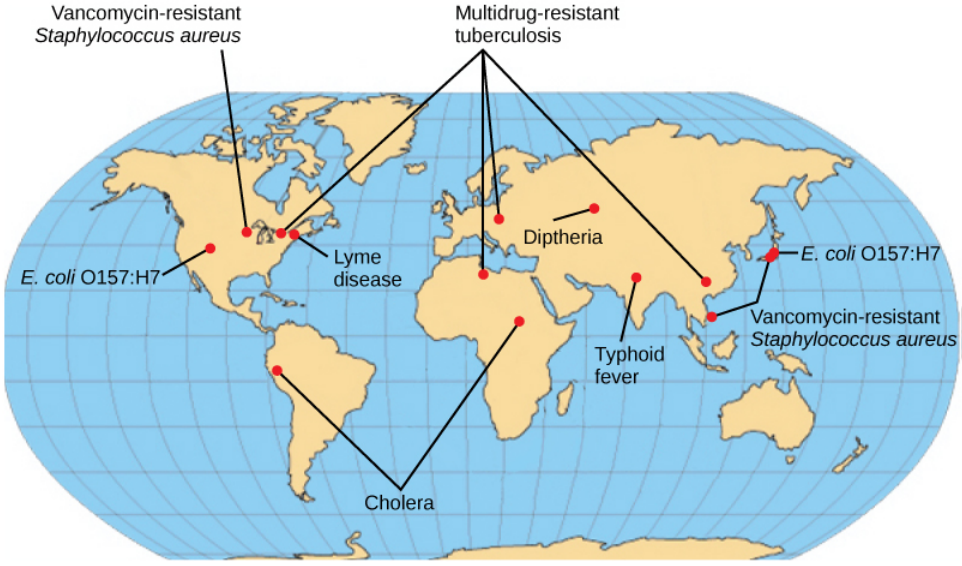
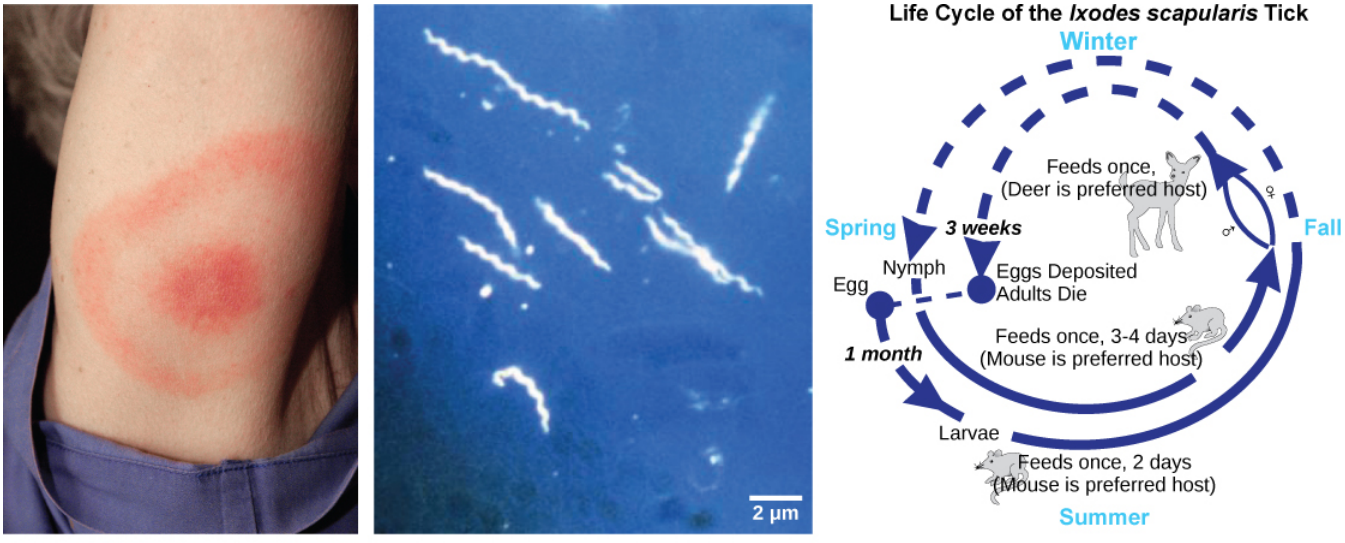


Figure **27.6.3**: The map shows regions where bacterial diseases are emerging or reemerging. (credit: modification of work by NIH)

Some of the present emerging diseases are not actually new, but are diseases that were catastrophic in the past (Figure **27.6.4**). They devastated populations and became dormant for a while, just to come back, sometimes more virulent than before, as was the case with bubonic plague. Other diseases, like tuberculosis, were never eradicated but were under control in some regions of the world until coming back, mostly in urban centers with high concentrations of immunocompromised people. The WHO has identified certain diseases whose worldwide re-emergence should be monitored. Among these are two viral diseases (dengue fever and yellow fever), and three bacterial diseases (diphtheria, cholera, and bubonic plague). The war against infectious diseases has no foreseeable end.



(a) (b) (c)

Figure **27.6.4**: Lyme disease often, but not always, results in (a) a characteristic bullseye rash. The disease is caused by a (b) Gram-negative spirochete bacterium of the genus *Borrelia*. The bacteria (c) infect ticks, which in turns infect mice. Deer are the preferred secondary host, but the ticks also may feed on humans. Untreated, the disease causes chronic disorders in the nervous system, eyes, joints, and heart. The disease is named after Lyme, Connecticut, where an outbreak occurred in 1995 and has subsequently spread. The disease is not new, however. Genetic evidence suggests that Ötzi the Iceman, a 5,300-year-old mummy found in the Alps, was infected with *Borrelia*. (credit a: James Gathany, CDC; credit b: CDC; scale-bar data from Matt Russell)

Biofilms and Disease

Recall that biofilms are microbial communities that are very difficult to destroy. They are responsible for diseases such as infections in patients with cystic fibrosis, Legionnaires' disease, and otitis media. They produce dental plaque and colonize catheters, prostheses, transcutaneous and orthopedic devices, contact lenses, and internal devices such as pacemakers. They also form in open wounds and burned tissue. In healthcare environments, biofilms grow on hemodialysis machines, mechanical ventilators, shunts, and other medical equipment. In fact, 65 percent of all infections acquired in the hospital (nosocomial infections) are attributed to biofilms. Biofilms are also related to diseases contracted from food because they colonize the surfaces of vegetable leaves and meat, as well as food-processing equipment that isn't adequately cleaned.

Biofilm infections develop gradually; sometimes, they do not cause symptoms immediately. They are rarely resolved by host defense mechanisms. Once an infection by a biofilm is established, it is very difficult to eradicate, because biofilms tend to be resistant to most of the methods used to control microbial growth, including antibiotics. Biofilms respond poorly or only temporarily to antibiotics; it has been said that they can resist up to 1,000 times the antibiotic concentrations used to kill the same bacteria when they are free-living or planktonic. An antibiotic dose that large would harm the patient; therefore, scientists are working on new ways to get rid of biofilms.

Antibiotics: Are We Facing a Crisis?

The word *antibiotic* comes from the Greek *anti* meaning "against" and *bios* meaning "life." An antibiotic is a chemical, produced either by microbes or synthetically, that is hostile to the growth of other organisms. Today's news and media often address concerns about an antibiotic crisis. Are the antibiotics that easily treated bacterial infections in the past becoming obsolete? Are there new "superbugs"—bacteria that have evolved to become more resistant to our arsenal of antibiotics? Is this the beginning of the end of antibiotics? All these questions challenge the healthcare community.

One of the main causes of resistant bacteria is the abuse of antibiotics. The imprudent and excessive use of antibiotics has resulted in the natural selection of resistant forms of bacteria. The antibiotic kills most of the infecting bacteria, and therefore only the resistant forms remain. These resistant forms reproduce, resulting in an increase in the proportion of resistant forms over non-resistant ones. Another major misuse of antibiotics is in patients with colds or the flu, for which antibiotics are useless. Another problem is the excessive use of antibiotics in livestock. The routine use of antibiotics in animal feed promotes bacterial resistance as well. In the United States, 70 percent of the antibiotics produced are fed to animals. These antibiotics are given to livestock in low doses, which maximize the probability of resistance developing, and these resistant bacteria are readily transferred to humans.

Link to Learning

Watch a recent news report on the problem of routine antibiotic administration to livestock and antibiotic-resistant bacteria.

One of the Superbugs: MRSA

The imprudent use of antibiotics has paved the way for bacteria to expand populations of resistant forms. For example, *Staphylococcus aureus*, often called "staph," is a common bacterium that can live in the human body and is usually easily treated with antibiotics. A very dangerous strain, however, methicillin-resistant *Staphylococcus aureus* (MRSA) has made the news over the past few years (Figure **27.6.5**). This strain is resistant to many commonly used antibiotics, including methicillin, amoxicillin, penicillin, and oxacillin. MRSA can cause infections of the skin, but it can also infect the bloodstream, lungs, urinary tract, or sites of injury. While MRSA infections are common among people in healthcare facilities, they have also appeared in healthy people who haven't been hospitalized but who live or work in tight populations (like military personnel and prisoners). Researchers have expressed concern about the way this latter source of MRSA targets a much younger population than those residing in care facilities. *The Journal of the American Medical Association* reported that, among MRSA-afflicted persons in healthcare facilities, the average age is 68, whereas people with "community-associated MRSA" (CA-MRSA) have an average age of 23.[2]

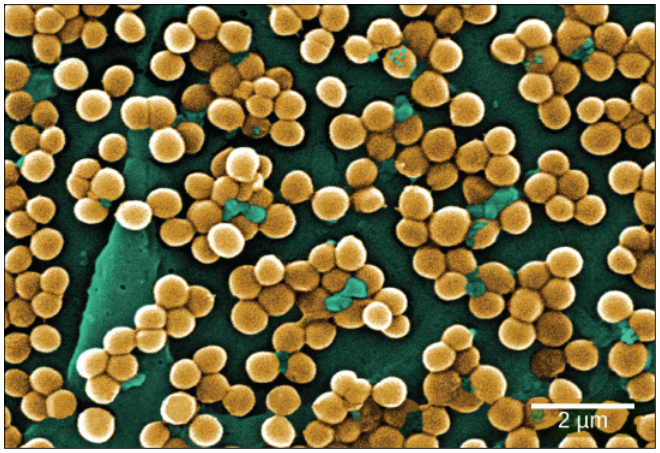


Figure **27.6.5**: This scanning electron micrograph shows methicillin-resistant *Staphylococcus aureus* bacteria, commonly known as MRSA. *S. aureus* is not always pathogenic, but can cause diseases such as food poisoning and skin and respiratory infections. (credit: modification of work by Janice Haney Carr; scale-bar data from Matt Russell)

In summary, the medical community is facing an antibiotic crisis. Some scientists believe that after years of being protected from bacterial infections by antibiotics, we may be returning to a time in which a simple bacterial infection could again devastate the human population. Researchers are developing new antibiotics, but it takes many years to of research and clinical trials, plus financial investments in the millions of dollars, to generate an effective and approved drug.

Foodborne Diseases

Prokaryotes are everywhere: They readily colonize the surface of any type of material, and food is not an exception. Most of the time, prokaryotes colonize food and food-processing equipment in the form of a biofilm. Outbreaks of bacterial infection related to food consumption are common. A foodborne disease (colloquially called “food poisoning”) is an illness resulting from the consumption the pathogenic bacteria, viruses, or other parasites that contaminate food. Although the United States has one of the safest food supplies in the world, the U.S. Centers for Disease Control and Prevention (CDC) has reported that “76 million people get sick, more than 300,000 are hospitalized, and 5,000 Americans die each year from foodborne illness.”

The characteristics of foodborne illnesses have changed over time. In the past, it was relatively common to hear about sporadic cases of botulism, the potentially fatal disease produced by a toxin from the anaerobic bacterium *Clostridium botulinum*. Some of the most common sources for this bacterium were non-acidic canned foods, homemade pickles, and processed meat and sausages. The can, jar, or package created a suitable anaerobic environment where *Clostridium* could grow. Proper sterilization and canning procedures have reduced the incidence of this disease.

While people may tend to think of foodborne illnesses as associated with animal-based foods, most cases are now linked to produce. There have been serious, produce-related outbreaks associated with raw spinach in the United States and with vegetable sprouts in Germany, and these types of outbreaks have become more common. The raw spinach outbreak in 2006 was produced by the bacterium *E. coli* serotype O157:H7. A serotype is a strain of bacteria that carries a set of similar antigens on its cell surface, and there are often many different serotypes of a bacterial species. Most *E. coli* are not particularly dangerous to humans, but serotype O157:H7 can cause bloody diarrhea and is potentially fatal.

All types of food can potentially be contaminated with bacteria. Recent outbreaks of *Salmonella* reported by the CDC occurred in foods as diverse as peanut butter, alfalfa sprouts, and eggs. A deadly outbreak in Germany in 2010 was caused by *E. coli* contamination of vegetable sprouts (Figure **27.6.6**). The strain that caused the outbreak was found to be a new serotype not previously involved in other outbreaks, which indicates that *E. coli* is continuously evolving.

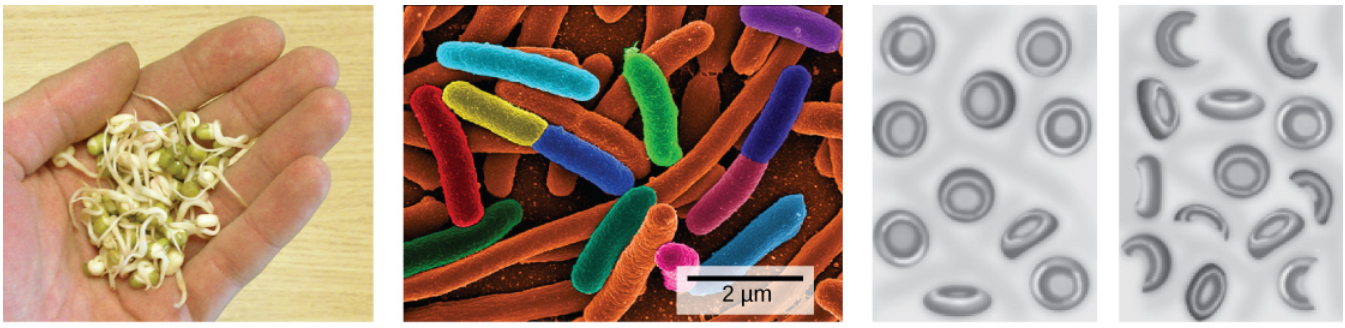


Figure **27.6.6**: (a) Vegetable sprouts grown at an organic farm were the cause of an (b) *E. coli* outbreak that killed 32 people and sickened 3,800 in Germany in 2011. The strain responsible, *E. coli* O104:H4, produces Shiga toxin, a substance that inhibits protein synthesis in the host cell. The toxin (c) destroys red blood cells resulting in bloody diarrhea. Deformed red blood cells clog the capillaries of the kidney, which can lead to kidney failure, as happened to 845 patients in the 2011 outbreak. Kidney failure is usually reversible, but some patients experience kidney problems years later. (credit c: NIDDK, NIH)

Career Connection: Epidemiologist

Epidemiology is the study of the occurrence, distribution, and determinants of health and disease in a population. It is, therefore, part of public health. An epidemiologist studies the frequency and distribution of diseases within human populations and environments.

Epidemiologists collect data about a particular disease and track its spread to identify the original mode of transmission. They sometimes work in close collaboration with historians to try to understand the way a disease evolved geographically and over time, tracking the natural history of pathogens. They gather information from clinical records, patient interviews, surveillance, and any other available means. That information is used to develop strategies, such as vaccinations (Figure **27.6.7**), and design public health policies to reduce the incidence of a disease or to prevent its spread. Epidemiologists also conduct rapid investigations in case of an outbreak to recommend immediate measures to control it.



Figure **27.6.7**: Vaccinations can slow the spread of communicable diseases. (credit: modification of work by Daniel Paquet)

An epidemiologist has a bachelor's degree, plus a master's degree in public health (MPH). Many epidemiologists are also physicians (and have an M.D.), or they have a Ph.D. in an associated field, such as biology or microbiology.

Summary

Devastating diseases and plagues have been among us since early times. There are records about microbial diseases as far back as 3000 B.C. Infectious diseases remain among the leading causes of death worldwide. Emerging diseases are those rapidly increasing in incidence or geographic range. They can be new or re-emerging diseases (previously under control). Many emerging diseases affecting humans, such as brucellosis, are zoonoses. The WHO has identified a group of diseases whose re-emergence should be monitored: Those caused by bacteria include bubonic plague, diphtheria, and cholera.

Biofilms are considered responsible for diseases such as bacterial infections in patients with cystic fibrosis, Legionnaires' disease, and otitis media. They produce dental plaque; colonize catheters, prostheses, transcutaneous, and orthopedic devices; and infect contact lenses, open wounds, and burned tissue. Biofilms also produce foodborne diseases because they colonize the surfaces of food and food-processing equipment. Biofilms are resistant to most of the methods used to control microbial growth. The excessive use of antibiotics has resulted in a major global problem, since resistant forms of bacteria have been selected over time. A very dangerous strain, methicillin-resistant *Staphylococcus aureus* (MRSA), has wreaked havoc recently. Foodborne diseases result from the consumption of contaminated food, pathogenic bacteria, viruses, or parasites that contaminate food.

Footnotes

1. 1 Papagrigorakis MJ, Synodinos PN, and Yapijakis C. Ancient typhoid epidemic reveals possible ancestral strain of *Salmonella enterica* serovar Typhi. *Infect Genet Evol* 7 (2007): 126–7, Epub 2006 Jun.
2. 2 Naimi, TS, LeDell, KH, Como-Sabetti, K, et al. Comparison of community- and health care-associated methicillin-resistant *Staphylococcus aureus* infection. *JAMA* 290 (2003): 2976–84, doi: 10.1001/jama.290.22.2976.

Glossary

antibiotic
biological substance that, in low concentration, is antagonistic to the growth of prokaryotes

Black Death
devastating pandemic that is believed to have been an outbreak of bubonic plague caused by the bacterium *Yersinia pestis*

botulism
disease produce by the toxin of the anaerobic bacterium *Clostridium botulinum*

CA-MRSA
MRSA acquired in the community rather than in a hospital setting

emerging disease
disease making an initial appearance in a population or that is increasing in incidence or geographic range

endemic disease
disease that is constantly present, usually at low incidence, in a population

epidemic
disease that occurs in an unusually high number of individuals in a population at the same time

foodborne disease
any illness resulting from the consumption of contaminated food, or of the pathogenic bacteria, viruses, or other parasites that contaminate food

MRSA
(methicillin-resistant *Staphylococcus aureus*) very dangerous *Staphylococcus aureus* strain resistant to multiple antibiotics

pandemic
widespread, usually worldwide, epidemic disease

serotype
strain of bacteria that carries a set of similar antigens on its cell surface, often many in a bacterial species

zoonosis
disease that primarily infects animals that is transmitted to humans

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CHAPTER OVERVIEW

28: Protists

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28.3: Characteristics of Excavata
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28.1: Eukaryotic Origins and Endosymbiosis

Skills to Develop

- List the unifying characteristics of eukaryotes
- Describe what scientists know about the origins of eukaryotes based on the last common ancestor
- Explain endosymbiotic theory

Living things fall into three large groups: Archaea, Bacteria, and Eukarya. The first two have prokaryotic cells, and the third contains all eukaryotes. A relatively sparse fossil record is available to help discern what the first members of each of these lineages looked like, so it is possible that all the events that led to the last common ancestor of extant eukaryotes will remain unknown. However, comparative biology of extant organisms and the limited fossil record provide some insight into the history of Eukarya.

The earliest fossils found appear to be Bacteria, most likely cyanobacteria. They are about 3.5 billion years old and are recognizable because of their relatively complex structure and, for prokaryotes, relatively large cells. Most other prokaryotes have small cells, 1 or 2 µm in size, and would be difficult to pick out as fossils. Most living eukaryotes have cells measuring 10 µm or greater. Structures this size, which might be fossils, appear in the geological record about 2.1 billion years ago.

Characteristics of Eukaryotes

Data from these fossils have led comparative biologists to the conclusion that living eukaryotes are all descendants of a single common ancestor. Mapping the characteristics found in all major groups of eukaryotes reveals that the following characteristics must have been present in the last common ancestor, because these characteristics are present in at least some of the members of each major lineage.

1. Cells with nuclei surrounded by a nuclear envelope with nuclear pores. This is the single characteristic that is both necessary and sufficient to define an organism as a eukaryote. All extant eukaryotes have cells with nuclei.
2. Mitochondria. Some extant eukaryotes have very reduced remnants of mitochondria in their cells, whereas other members of their lineages have “typical” mitochondria.
3. A cytoskeleton containing the structural and motility components called actin microfilaments and microtubules. All extant eukaryotes have these cytoskeletal elements.
4. Flagella and cilia, organelles associated with cell motility. Some extant eukaryotes lack flagella and/or cilia, but they are descended from ancestors that possessed them.
5. Chromosomes, each consisting of a linear DNA molecule coiled around basic (alkaline) proteins called histones. The few eukaryotes with chromosomes lacking histones clearly evolved from ancestors that had them.
6. Mitosis, a process of nuclear division wherein replicated chromosomes are divided and separated using elements of the cytoskeleton. Mitosis is universally present in eukaryotes.
7. Sex, a process of genetic recombination unique to eukaryotes in which diploid nuclei at one stage of the life cycle undergo meiosis to yield haploid nuclei and subsequent karyogamy, a stage where two haploid nuclei fuse together to create a diploid zygote nucleus.
8. Members of all major lineages have cell walls, and it might be reasonable to conclude that the last common ancestor could make cell walls during some stage of its life cycle. However, not enough is known about eukaryotes’ cell walls and their development to know how much homology exists among them. If the last common ancestor could make cell walls, it is clear that this ability must have been lost in many groups.

Endosymbiosis and the Evolution of Eukaryotes

In order to understand eukaryotic organisms fully, it is necessary to understand that all extant eukaryotes are descendants of a chimeric organism that was a composite of a host cell and the cell(s) of an alpha-proteobacterium that “took up residence” inside it. This major theme in the origin of eukaryotes is known as endosymbiosis, one cell engulfing another such that the engulfed cell survives and both cells benefit. Over many generations, a symbiotic relationship can result in two organisms that depend on each other so completely that neither could survive on its own. Endosymbiotic events likely contributed to the origin of the last common

ancestor of today's eukaryotes and to later diversification in certain lineages of eukaryotes (Figure 28.1.4). Before explaining this further, it is necessary to consider metabolism in prokaryotes.

Prokaryotic Metabolism

Many important metabolic processes arose in prokaryotes, and some of these, such as nitrogen fixation, are never found in eukaryotes. The process of aerobic respiration is found in all major lineages of eukaryotes, and it is localized in the mitochondria. Aerobic respiration is also found in many lineages of prokaryotes, but it is not present in all of them, and many forms of evidence suggest that such anaerobic prokaryotes never carried out aerobic respiration nor did their ancestors.

While today's atmosphere is about one-fifth molecular oxygen (O_2), geological evidence shows that it originally lacked O_2. Without oxygen, aerobic respiration would not be expected, and living things would have relied on fermentation instead. At some point before, about 3.5 billion years ago, some prokaryotes began using energy from sunlight to power anabolic processes that reduce carbon dioxide to form organic compounds. That is, they evolved the ability to photosynthesize. Hydrogen, derived from various sources, was captured using light-powered reactions to reduce fixed carbon dioxide in the Calvin cycle. The group of Gram-negative bacteria that gave rise to cyanobacteria used water as the hydrogen source and released O_2 as a waste product.

Eventually, the amount of photosynthetic oxygen built up in some environments to levels that posed a risk to living organisms, since it can damage many organic compounds. Various metabolic processes evolved that protected organisms from oxygen, one of which, aerobic respiration, also generated high levels of ATP. It became widely present among prokaryotes, including in a group we now call alpha-proteobacteria. Organisms that did not acquire aerobic respiration had to remain in oxygen-free environments. Originally, oxygen-rich environments were likely localized around places where cyanobacteria were active, but by about 2 billion years ago, geological evidence shows that oxygen was building up to higher concentrations in the atmosphere. Oxygen levels similar to today's levels only arose within the last 700 million years.

Recall that the first fossils that we believe to be eukaryotes date to about 2 billion years old, so they appeared as oxygen levels were increasing. Also, recall that all extant eukaryotes descended from an ancestor with mitochondria. These organelles were first observed by light microscopists in the late 1800s, where they appeared to be somewhat worm-shaped structures that seemed to be moving around in the cell. Some early observers suggested that they might be bacteria living inside host cells, but these hypotheses remained unknown or rejected in most scientific communities.

Endosymbiotic Theory

As cell biology developed in the twentieth century, it became clear that mitochondria were the organelles responsible for producing ATP using aerobic respiration. In the 1960s, American biologist Lynn Margulis developed endosymbiotic theory, which states that eukaryotes may have been a product of one cell engulfing another, one living within another, and evolving over time until the separate cells were no longer recognizable as such. In 1967, Margulis introduced new work on the theory and substantiated her findings through microbiological evidence. Although Margulis' work initially was met with resistance, this once-revolutionary hypothesis is now widely (but not completely) accepted, with work progressing on uncovering the steps involved in this evolutionary process and the key players involved. Much still remains to be discovered about the origins of the cells that now make up the cells in all living eukaryotes.

Broadly, it has become clear that many of our nuclear genes and the molecular machinery responsible for replication and expression appear closely related to those in Archaea. On the other hand, the metabolic organelles and genes responsible for many energy-harvesting processes had their origins in bacteria. Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of discovery in biology. For instance, it is not known whether the endosymbiotic event that led to mitochondria occurred before or after the host cell had a nucleus. Such organisms would be among the extinct precursors of the last common ancestor of eukaryotes.

Mitochondria

One of the major features distinguishing prokaryotes from eukaryotes is the presence of mitochondria. Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption. Each mitochondrion measures 1 to 10 or greater micrometers in length and exists in the cell as an organelle that can be ovoid to worm-shaped to intricately branched (Figure 28.1.1). Mitochondria arise from the division of existing mitochondria; they may fuse

together; and they may be moved around inside the cell by interactions with the cytoskeleton. However, mitochondria cannot survive outside the cell. As the atmosphere was oxygenated by photosynthesis, and as successful aerobic prokaryotes evolved, evidence suggests that an ancestral cell with some membrane compartmentalization engulfed a free-living aerobic prokaryote, specifically an alpha-proteobacterium, thereby giving the host cell the ability to use oxygen to release energy stored in nutrients. Alpha-proteobacteria are a large group of bacteria that includes species symbiotic with plants, disease organisms that can infect humans via ticks, and many free-living species that use light for energy. Several lines of evidence support that mitochondria are derived from this endosymbiotic event. Most mitochondria are shaped like alpha-proteobacteria and are surrounded by two membranes, which would result when one membrane-bound organism was engulfed into a vacuole by another membrane-bound organism. The mitochondrial inner membrane is extensive and involves substantial infoldings called cristae that resemble the textured, outer surface of alpha-proteobacteria. The matrix and inner membrane are rich with the enzymes necessary for aerobic respiration.

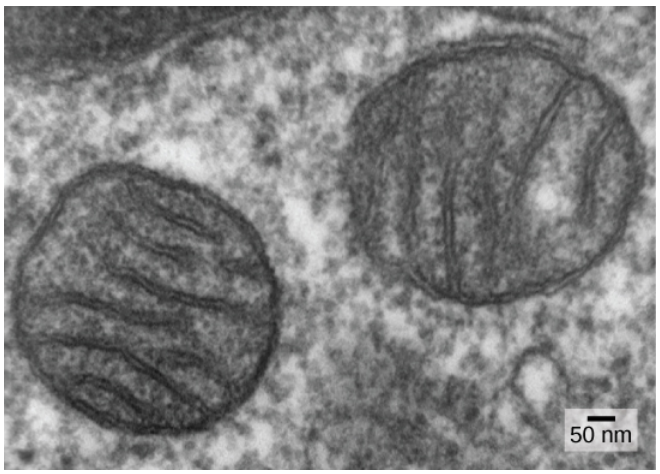


Figure 28.1.1: In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section. (credit: Louise Howard)

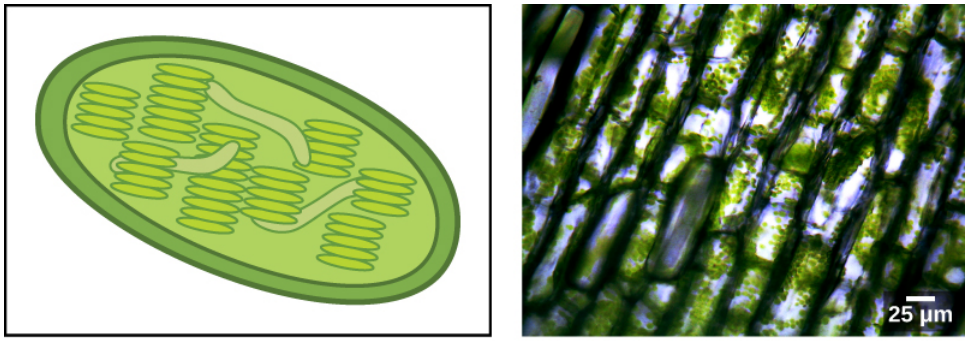
Mitochondria divide independently by a process that resembles binary fission in prokaryotes. Specifically, mitochondria are not formed from scratch (de novo) by the eukaryotic cell; they reproduce within it and are distributed with the cytoplasm when a cell divides or two cells fuse. Therefore, although these organelles are highly integrated into the eukaryotic cell, they still reproduce as if they are independent organisms within the cell. However, their reproduction is synchronized with the activity and division of the cell. Mitochondria have their own (usually) circular DNA chromosome that is stabilized by attachments to the inner membrane and carries genes similar to genes expressed by alpha-proteobacteria. Mitochondria also have special ribosomes and transfer RNAs that resemble these components in prokaryotes. These features all support that mitochondria were once free-living prokaryotes.

Mitochondria that carry out aerobic respiration have their own genomes, with genes similar to those in alpha-proteobacteria. However, many of the genes for respiratory proteins are located in the nucleus. When these genes are compared to those of other organisms, they appear to be of alpha-proteobacterial origin. Additionally, in some eukaryotic groups, such genes are found in the mitochondria, whereas in other groups, they are found in the nucleus. This has been interpreted as evidence that genes have been transferred from the endosymbiont chromosome to the host genome. This loss of genes by the endosymbiont is probably one explanation why mitochondria cannot live without a host.

Some living eukaryotes are anaerobic and cannot survive in the presence of too much oxygen. Some appear to lack organelles that could be recognized as mitochondria. In the 1970s to the early 1990s, many biologists suggested that some of these eukaryotes were descended from ancestors whose lineages had diverged from the lineage of mitochondrion-containing eukaryotes before endosymbiosis occurred. However, later findings suggest that reduced organelles are found in most, if not all, anaerobic eukaryotes, and that all eukaryotes appear to carry some genes in their nuclei that are of mitochondrial origin. In addition to the aerobic generation of ATP, mitochondria have several other metabolic functions. One of these functions is to generate clusters of iron and sulfur that are important cofactors of many enzymes. Such functions are often associated with the reduced mitochondrion-derived organelles of anaerobic eukaryotes. Therefore, most biologists accept that the last common ancestor of eukaryotes had mitochondria.

Plastids

Some groups of eukaryotes are photosynthetic. Their cells contain, in addition to the standard eukaryotic organelles, another kind of organelle called a plastid. When such cells are carrying out photosynthesis, their plastids are rich in the pigment chlorophyll *a* and a range of other pigments, called accessory pigments, which are involved in harvesting energy from light. Photosynthetic plastids are called chloroplasts (Figure **28.1.2**).



(a) (b)

Figure **28.1.2**: (a) This chloroplast cross-section illustrates its elaborate inner membrane organization. Stacks of thylakoid membranes compartmentalize photosynthetic enzymes and provide scaffolding for chloroplast DNA. (b) In this micrograph of *Elodea* sp., the chloroplasts can be seen as small green spheres. (credit b: modification of work by Brandon Zierer; scale-bar data from Matt Russell)

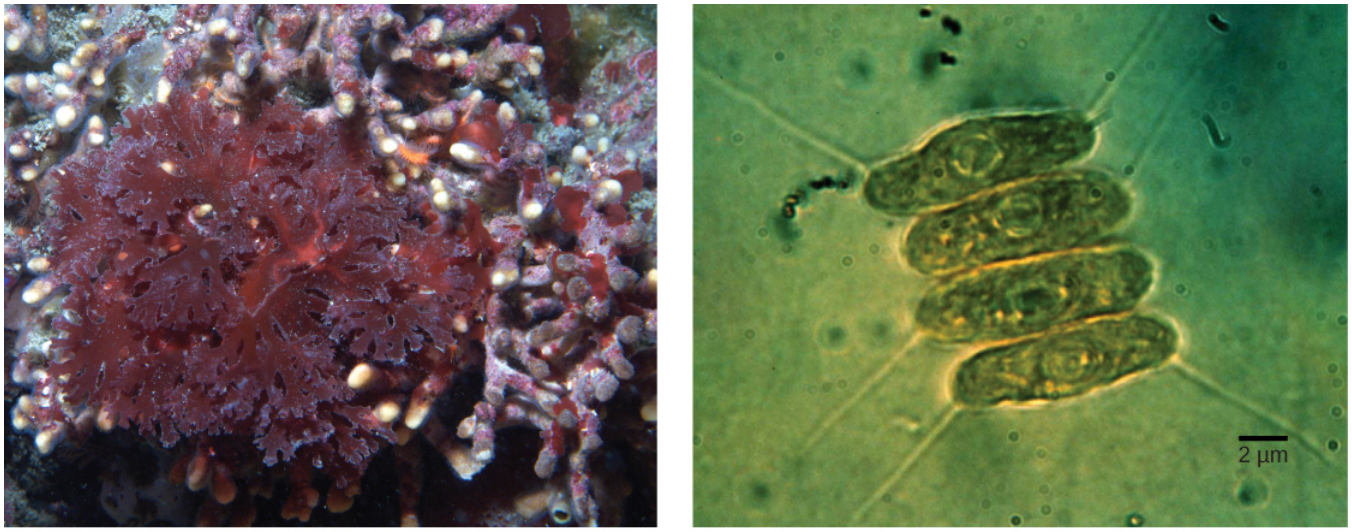
Like mitochondria, plastids appear to have an endosymbiotic origin. This hypothesis was also championed by Lynn Margulis. Plastids are derived from cyanobacteria that lived inside the cells of an ancestral, aerobic, heterotrophic eukaryote. This is called primary endosymbiosis, and plastids of primary origin are surrounded by two membranes. The best evidence is that this has happened twice in the history of eukaryotes. In one case, the common ancestor of the major lineage/supergroup Archaeplastida took on a cyanobacterial endosymbiont; in the other, the ancestor of the small amoeboid rhizarian taxon, *Paulinella*, took on a different cyanobacterial endosymbiont. Almost all photosynthetic eukaryotes are descended from the first event, and only a couple of species are derived from the other.

Cyanobacteria are a group of Gram-negative bacteria with all the conventional structures of the group. However, unlike most prokaryotes, they have extensive, internal membrane-bound sacs called thylakoids. Chlorophyll is a component of these membranes, as are many of the proteins of the light reactions of photosynthesis. Cyanobacteria also have the peptidoglycan wall and lipopolysaccharide layer associated with Gram-negative bacteria.

Chloroplasts of primary origin have thylakoids, a circular DNA chromosome, and ribosomes similar to those of cyanobacteria. Each chloroplast is surrounded by two membranes. In the group of Archaeplastida called the glaucophytes and in *Paulinella*, a thin peptidoglycan layer is present between the outer and inner plastid membranes. All other plastids lack this relictual cyanobacterial wall. The outer membrane surrounding the plastid is thought to be derived from the vacuole in the host, and the inner membrane is thought to be derived from the plasma membrane of the symbiont.

There is also, as with the case of mitochondria, strong evidence that many of the genes of the endosymbiont were transferred to the nucleus. Plastids, like mitochondria, cannot live independently outside the host. In addition, like mitochondria, plastids are derived from the division of other plastids and never built from scratch. Researchers have suggested that the endosymbiotic event that led to Archaeplastida occurred 1 to 1.5 billion years ago, at least 5 hundred million years after the fossil record suggests that eukaryotes were present.

Not all plastids in eukaryotes are derived directly from primary endosymbiosis. Some of the major groups of algae became photosynthetic by secondary endosymbiosis, that is, by taking in either green algae or red algae (both from Archaeplastida) as endosymbionts (Figure **28.1.3**). Numerous microscopic and genetic studies have supported this conclusion. Secondary plastids are surrounded by three or more membranes, and some secondary plastids even have clear remnants of the nucleus of endosymbiotic alga. Others have not “kept” any remnants. There are cases where tertiary or higher-order endosymbiotic events are the best explanations for plastids in some eukaryotes.



(a) (b)

Figure **28.1.3**: (a) Red algae and (b) green algae (visualized by light microscopy) share similar DNA sequences with photosynthetic cyanobacteria. Scientists speculate that, in a process called endosymbiosis, an ancestral prokaryote engulfed a photosynthetic cyanobacterium that evolved into modern-day chloroplasts. (credit a: modification of work by Ed Bierman; credit b: modification of work by G. Fahnenstiel, NOAA; scale-bar data from Matt Russell)

Art Connection

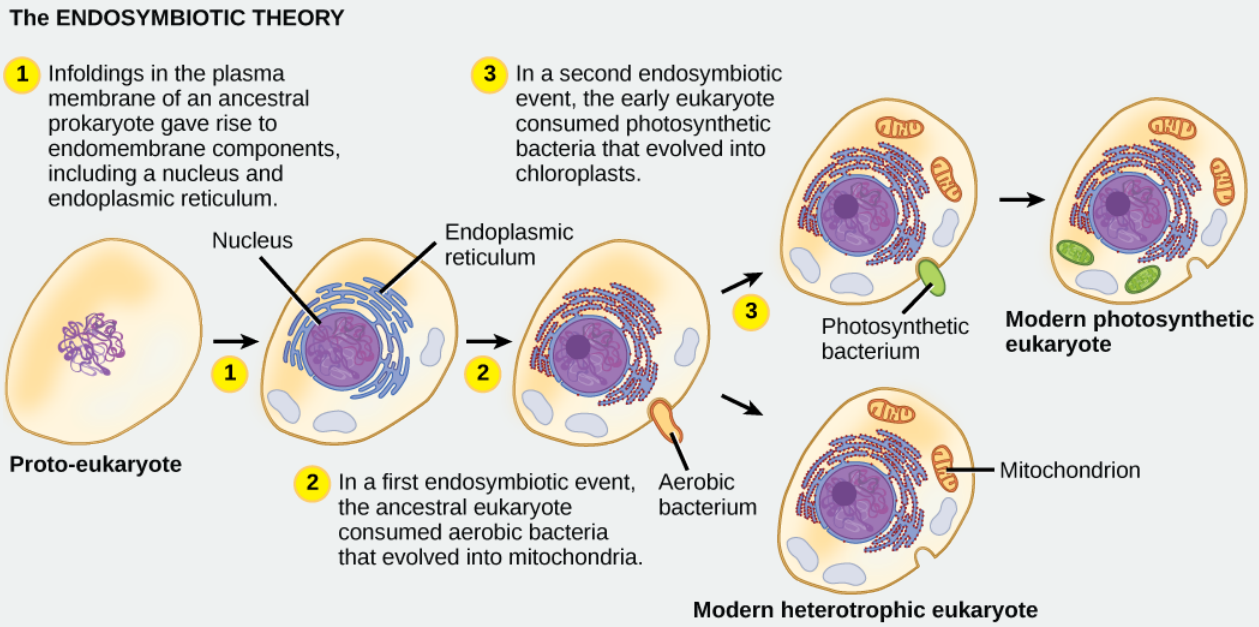


Figure **28.1.4**: The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote, and, in some cases, a photosynthetic prokaryote, to form mitochondria and chloroplasts, respectively.

What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Evolution Connection: Secondary Endosymbiosis in Chlorarachniophytes

Endosymbiosis involves one cell engulfing another to produce, over time, a coevolved relationship in which neither cell could survive alone. The chloroplasts of red and green algae, for instance, are derived from the engulfment of a photosynthetic cyanobacterium by an early prokaryote.

This leads to the question of the possibility of a cell containing an endosymbiont to itself become engulfed, resulting in a secondary endosymbiosis. Molecular and morphological evidence suggest that the chlorarachniophyte protists are derived from a secondary endosymbiotic event. Chlorarachniophytes are rare algae indigenous to tropical seas and sand that can be classified into the rhizarian supergroup. Chlorarachniophytes extend thin cytoplasmic strands, interconnecting themselves with other chlorarachniophytes, in a cytoplasmic network. These protists are thought to have originated when a eukaryote engulfed a green alga, the latter of which had already established an endosymbiotic relationship with a photosynthetic cyanobacterium (Figure **28.1.5**).

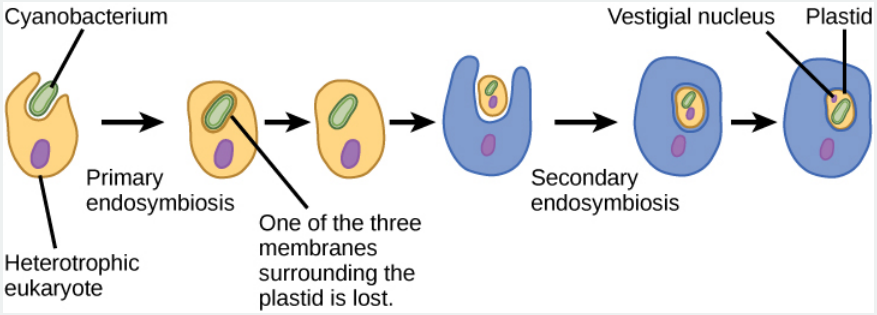


Figure **28.1.5**: The hypothesized process of endosymbiotic events leading to the evolution of chlorarachniophytes is shown. In a primary endosymbiotic event, a heterotrophic eukaryote consumed a cyanobacterium. In a secondary endosymbiotic event, the cell resulting from primary endosymbiosis was consumed by a second cell. The resulting organelle became a plastid in modern chlorarachniophytes.

Several lines of evidence support that chlorarachniophytes evolved from secondary endosymbiosis. The chloroplasts contained within the green algal endosymbionts still are capable of photosynthesis, making chlorarachniophytes photosynthetic. The green algal endosymbiont also exhibits a stunted vestigial nucleus. In fact, it appears that chlorarachniophytes are the products of an evolutionarily recent secondary endosymbiotic event. The plastids of chlorarachniophytes are surrounded by four membranes: The first two correspond to the inner and outer membranes of the photosynthetic cyanobacterium, the third corresponds to the green alga, and the fourth corresponds to the vacuole that surrounded the green alga when it was engulfed by the chlorarachniophyte ancestor. In other lineages that involved secondary endosymbiosis, only three membranes can be identified around plastids. This is currently rectified as a sequential loss of a membrane during the course of evolution.

The process of secondary endosymbiosis is not unique to chlorarachniophytes. In fact, secondary endosymbiosis of green algae also led to euglenid protists, whereas secondary endosymbiosis of red algae led to the evolution of dinoflagellates, apicomplexans, and stramenopiles.

Summary

The oldest fossil evidence of eukaryotes is about 2 billion years old. Fossils older than this all appear to be prokaryotes. It is probable that today's eukaryotes are descended from an ancestor that had a prokaryotic organization. The last common ancestor of today's Eukarya had several characteristics, including cells with nuclei that divided mitotically and contained linear chromosomes where the DNA was associated with histones, a cytoskeleton and endomembrane system, and the ability to make cilia/flagella during at least part of its life cycle. It was aerobic because it had mitochondria that were the result of an aerobic alpha-proteobacterium that lived inside a host cell. Whether this host had a nucleus at the time of the initial symbiosis remains unknown. The last common ancestor may have had a cell wall for at least part of its life cycle, but more data are needed to confirm this hypothesis. Today's eukaryotes are very diverse in their shapes, organization, life cycles, and number of cells per individual.

Art Connections

Figure **28.1.4**: What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Answer

All eukaryotic cells have mitochondria, but not all eukaryotic cells have chloroplasts.

Glossary

endosymbiosis
: engulfment of one cell within another such that the engulfed cell survives, and both cells benefit; the process responsible for the evolution of mitochondria and chloroplasts in eukaryotes

endosymbiotic theory
: theory that states that eukaryotes may have been a product of one cell engulfing another, one living within another, and evolving over time until the separate cells were no longer recognizable as such

plastid
: one of a group of related organelles in plant cells that are involved in the storage of starches, fats, proteins, and pigments

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28.2: Overview of Protists

Skills to Develop

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called **convergent evolution**, is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six "supergroups" that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor (Figure 28.2.1). The supergroups are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

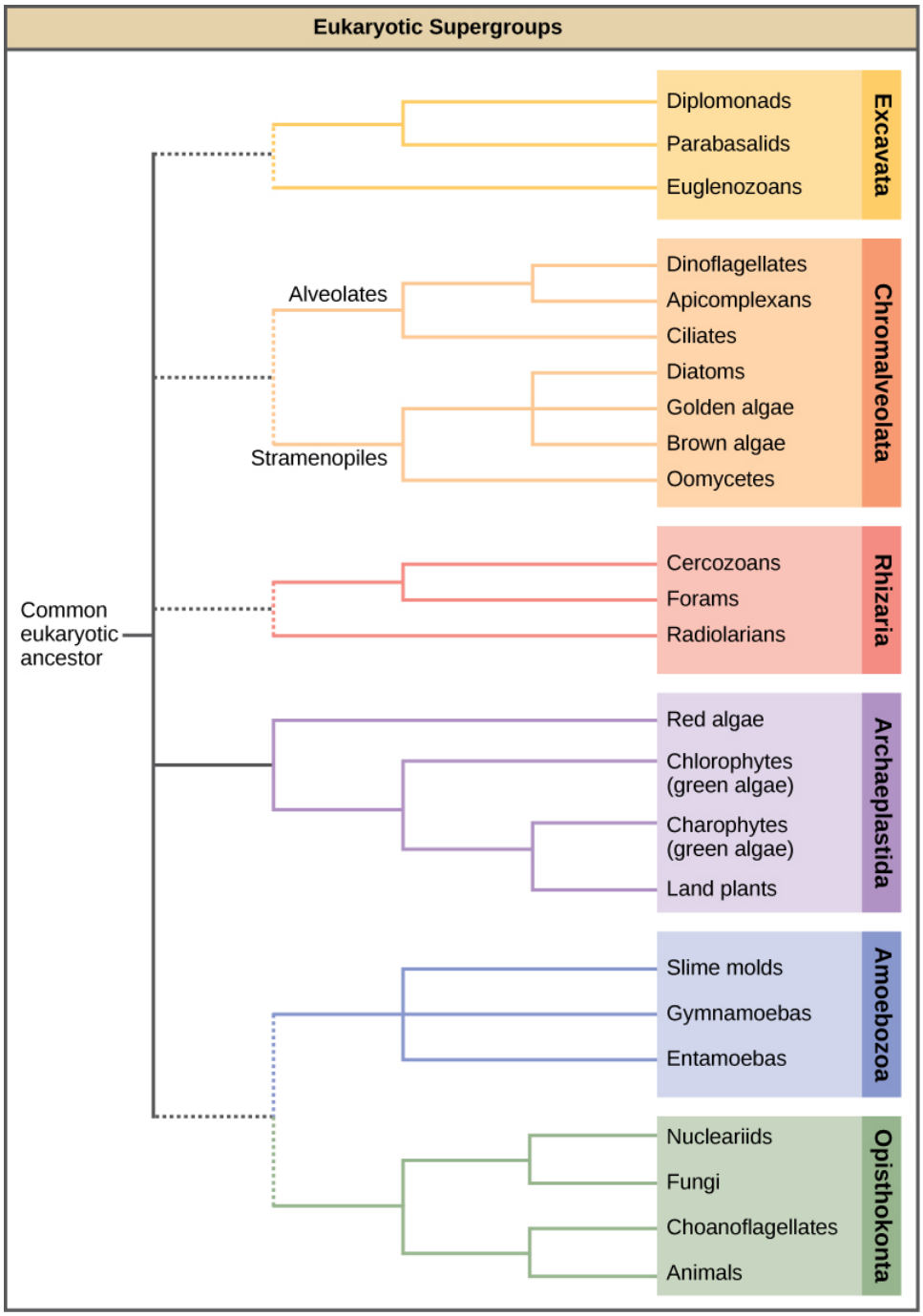


Figure **28.2.1**: This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia* (Figure **28.2.2**). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called mitosomes, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.



Figure **28.2.2**: The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell)

Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called hydrogenosomes because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichamoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the kinetoplast, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human

or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.

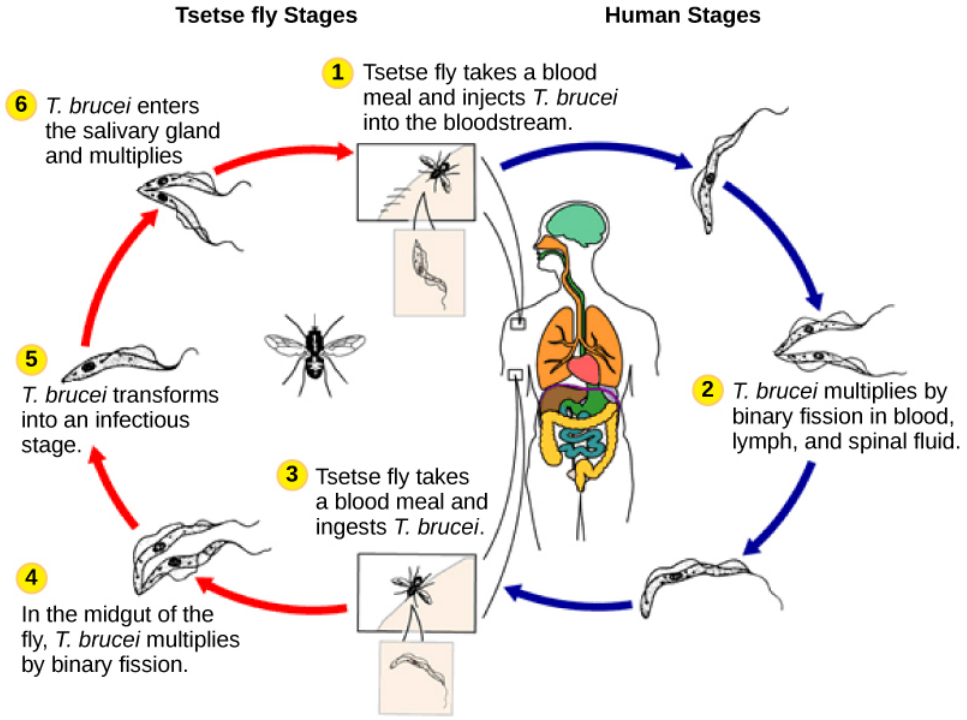


Figure **28.2.3**: *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Trypanosoma brucei



Watch this video to see *T. brucei* swimming. https://youtu.be/EnsydwITLYk

Chromalveolata

Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether.

Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexians, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate (Figure **28.2.4**). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of plankton, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.

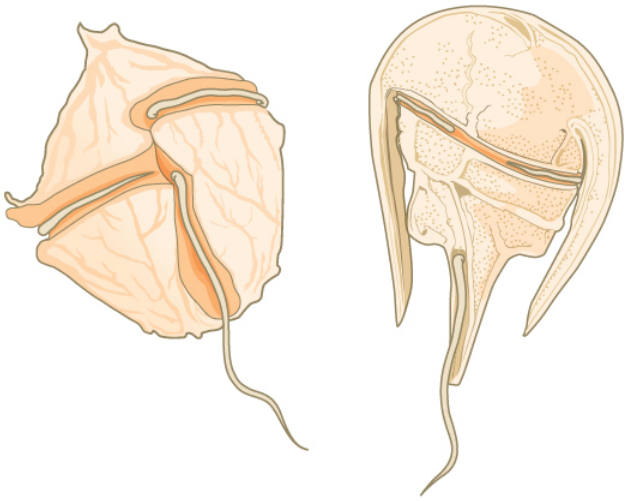


Figure **28.2.4**: The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

Some dinoflagellates generate light, called bioluminescence, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color (Figure **28.2.5**). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



Figure 28.2.5: Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: "catalano82"/Flickr)

The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex (Figure 28.2.6). The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

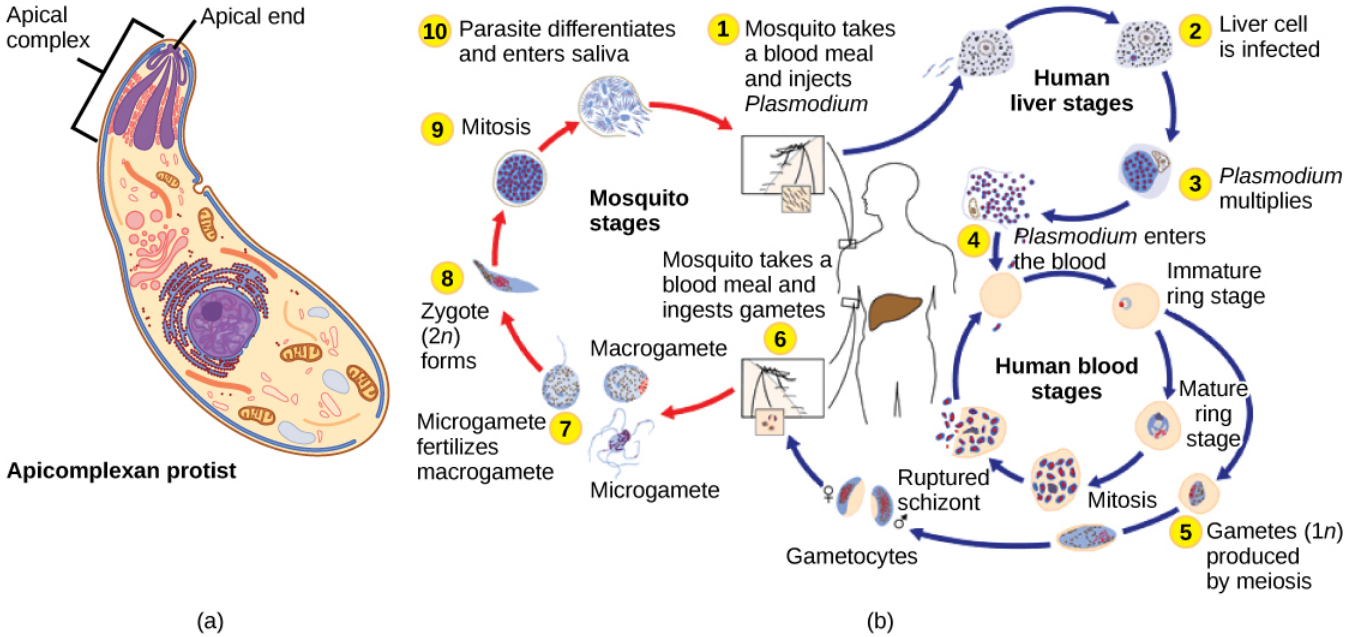


Figure 28.2.6: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria (Figure 28.2.7). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses contractile vacuoles, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.

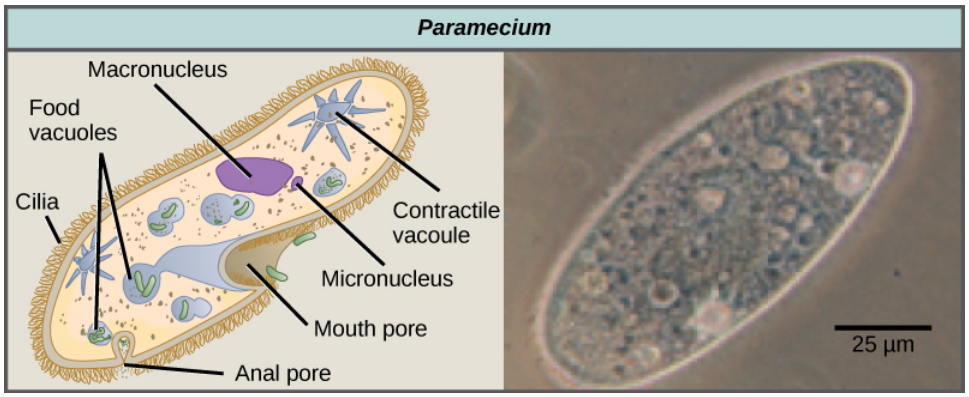
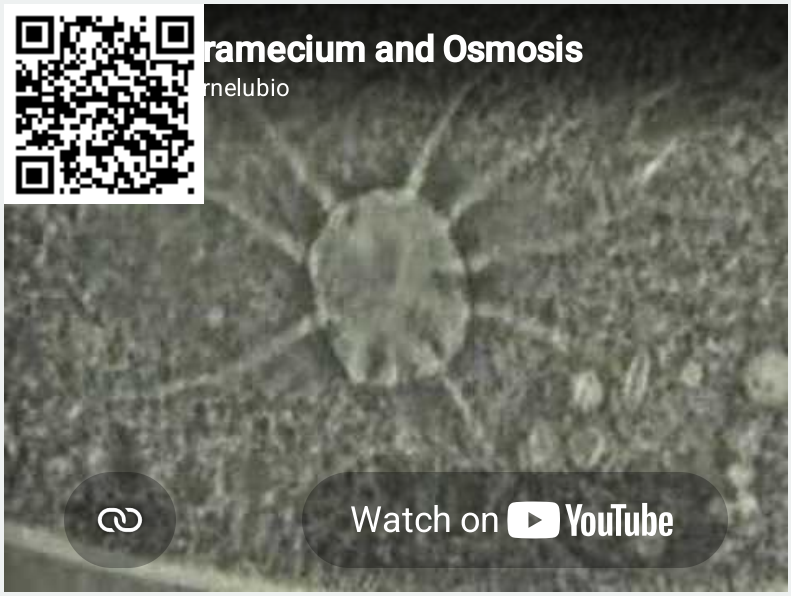


Figure 28.2.7: *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt Russell)

Link to Learning



Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge (Figure 28.2.8). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

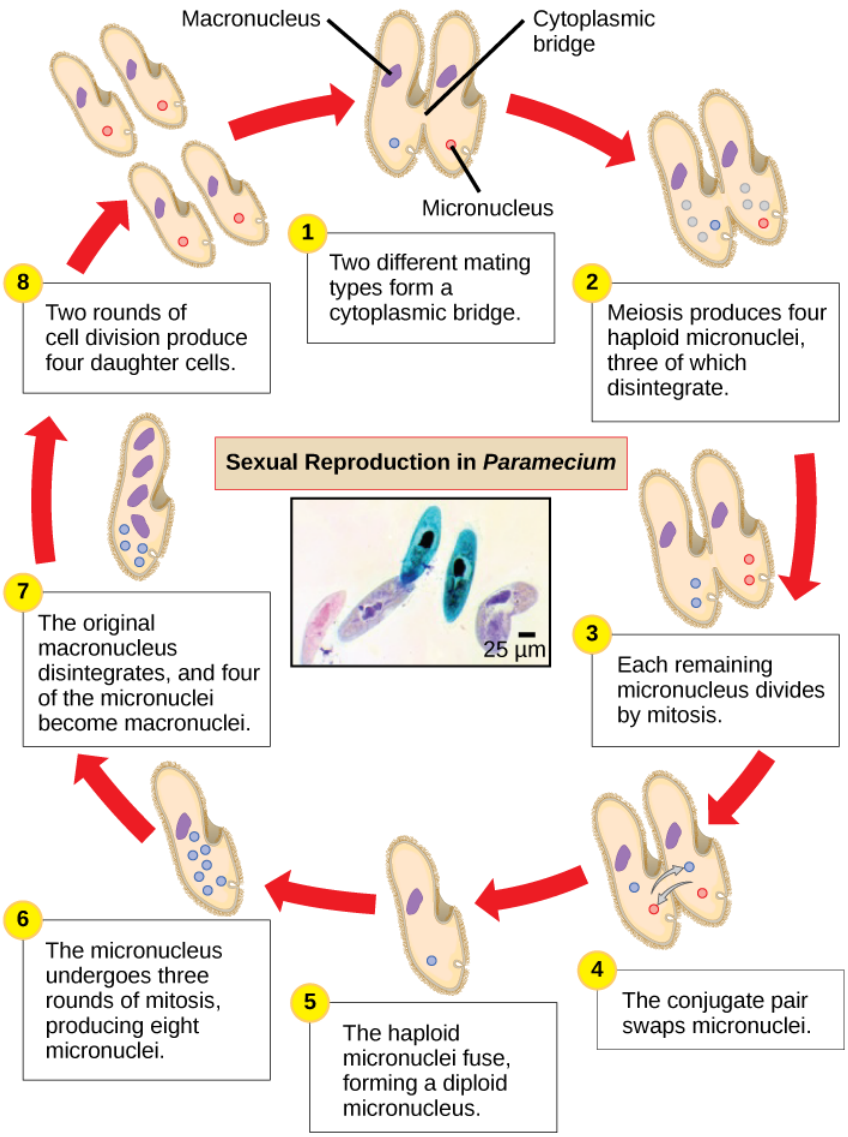


Figure 28.2.8: The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work by Ian Sutton; scale-bar data from Matt Russell)

Exercise

Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronucleii.
D. Each parent produces four daughter cells.

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or "hairy," flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections (Figure 28.2.9). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

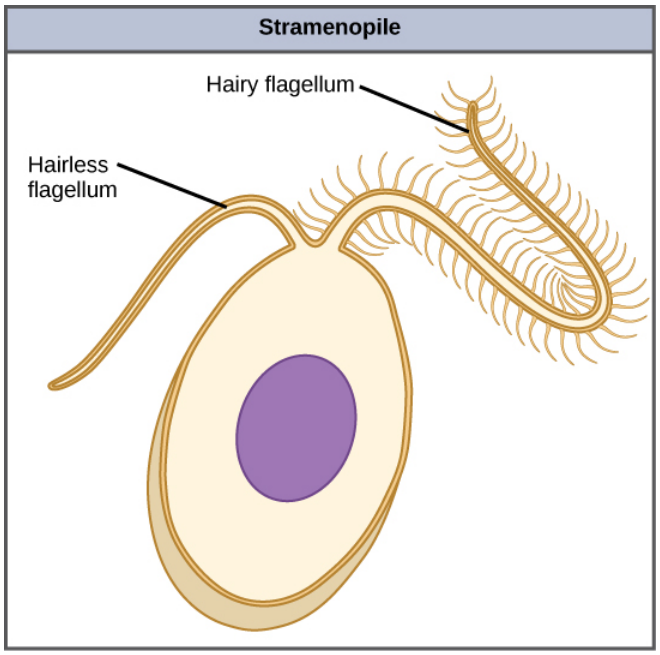


Figure **28.2.9**: This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles (Figure **28.2.10**). These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell, called a raphe. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

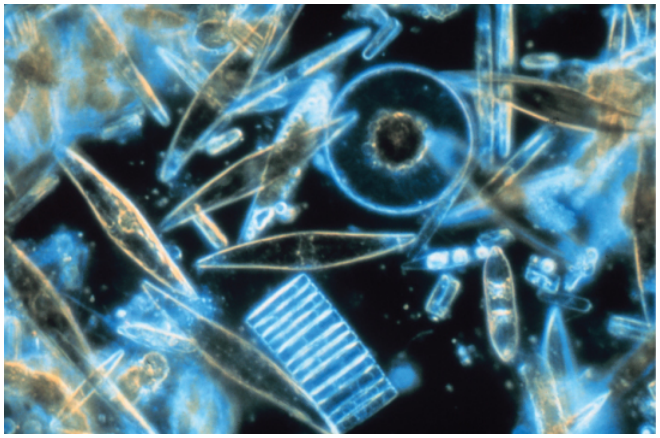


Figure **28.2.10**: Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the biological carbon pump, because carbon is “pumped” to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form (Figure **28.2.11**). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

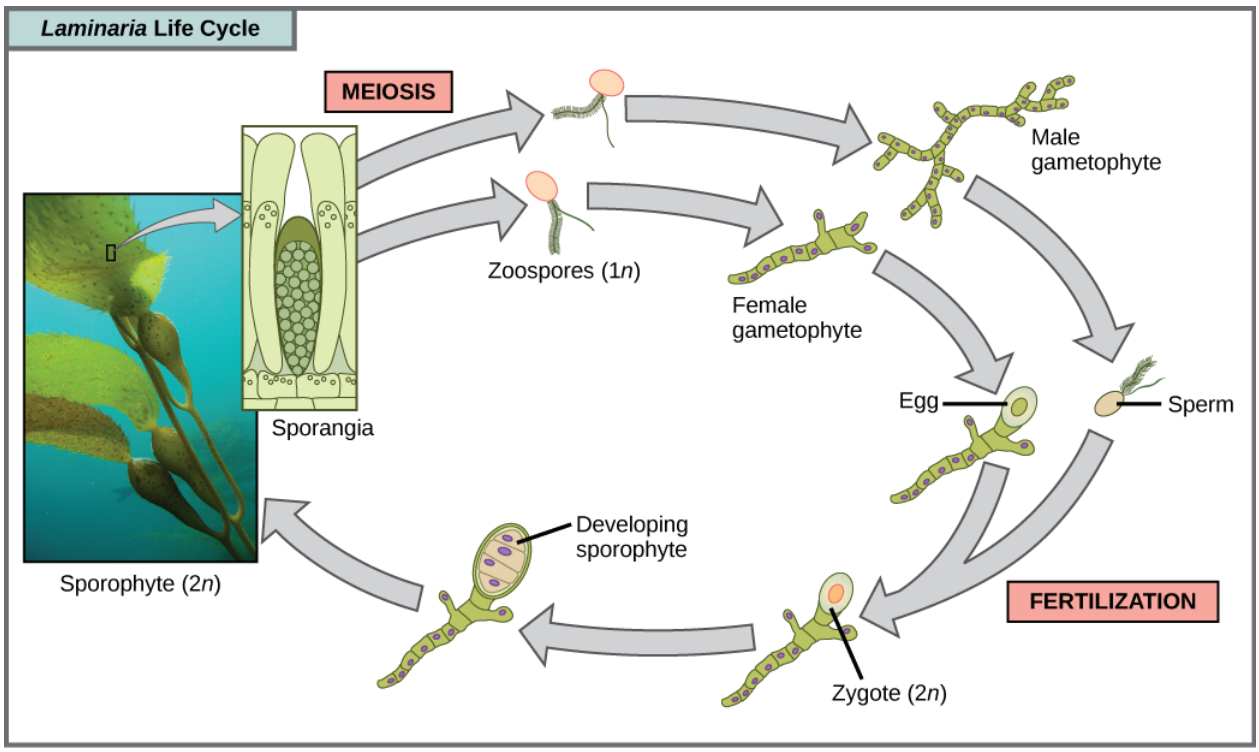


Figure **28.2.11**: Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit "laminaria photograph": modification of work by Claire Fackler, CINMS, NOAA Photo Library)

Exercise

Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.
B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

The water molds, oomycetes ("egg fungus"), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms (Figure **28.2.12**). Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.



Figure 28.2.12: A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (Figure 28.2.13). Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called cytoplasmic streaming, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.

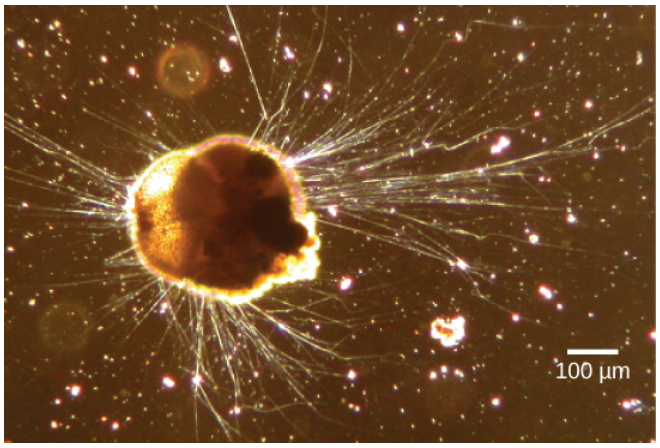


Figure 28.2.13: *Ammonia tepida*, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia. (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

Link to Learning



Take a look at this video to see cytoplasmic streaming in a green alga.

Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails (Figure 28.2.14). As a group, the forams exhibit porous shells, called tests that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.

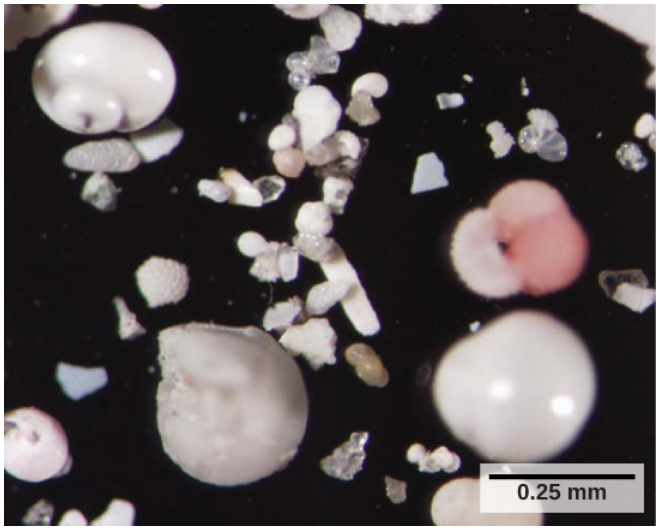


Figure 28.2.14: These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER)

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry (Figure 28.2.15). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

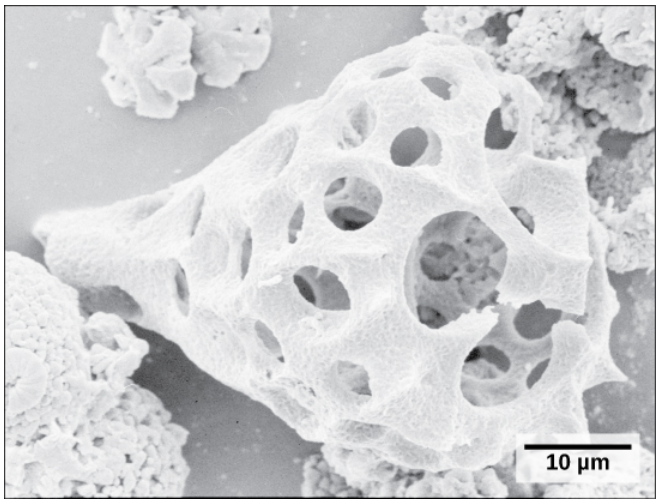


Figure 28.2.15: This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism (Figure 28.2.16). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



Figure **28.2.16**: *Volvox aureus* is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters (Figure **28.2.17**). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure **28.2.17**: *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Amoebozoa

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba (Figure **28.2.18**). The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.

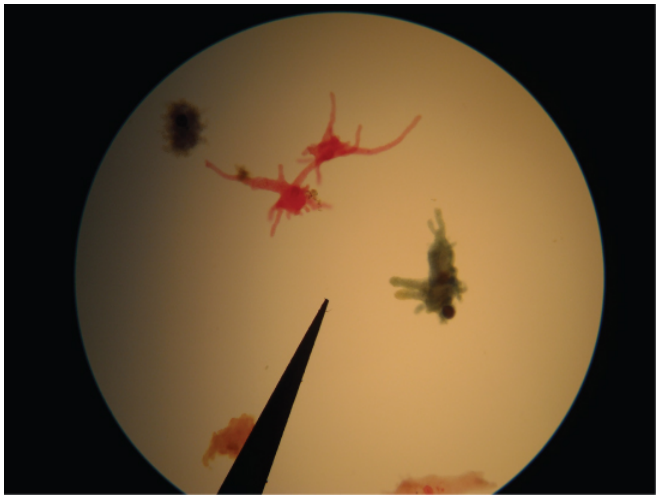


Figure **28.2.18**: Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage (Figure **28.2.19**). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

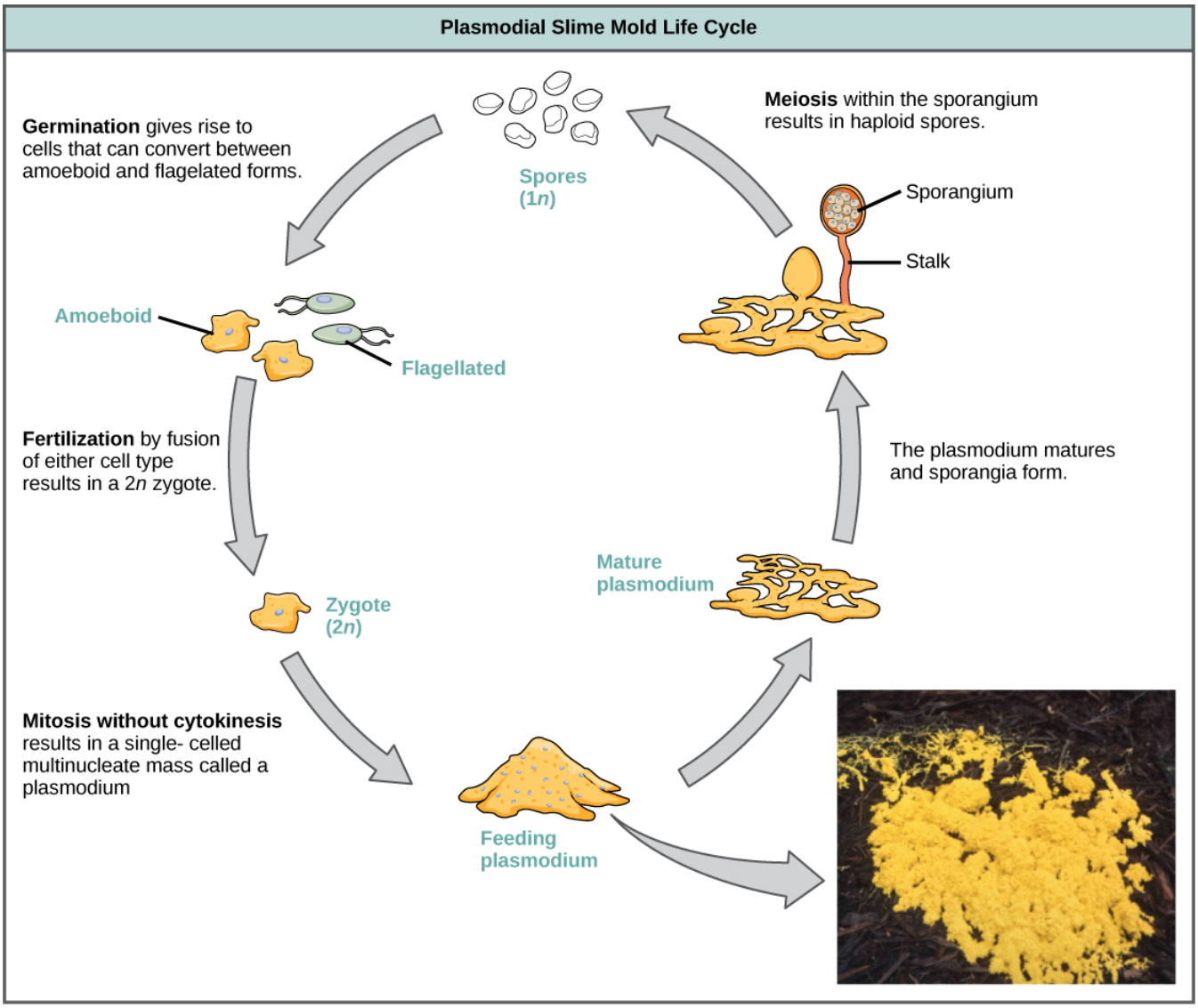


Figure 28.2.19: The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant (Figure 28.2.20). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

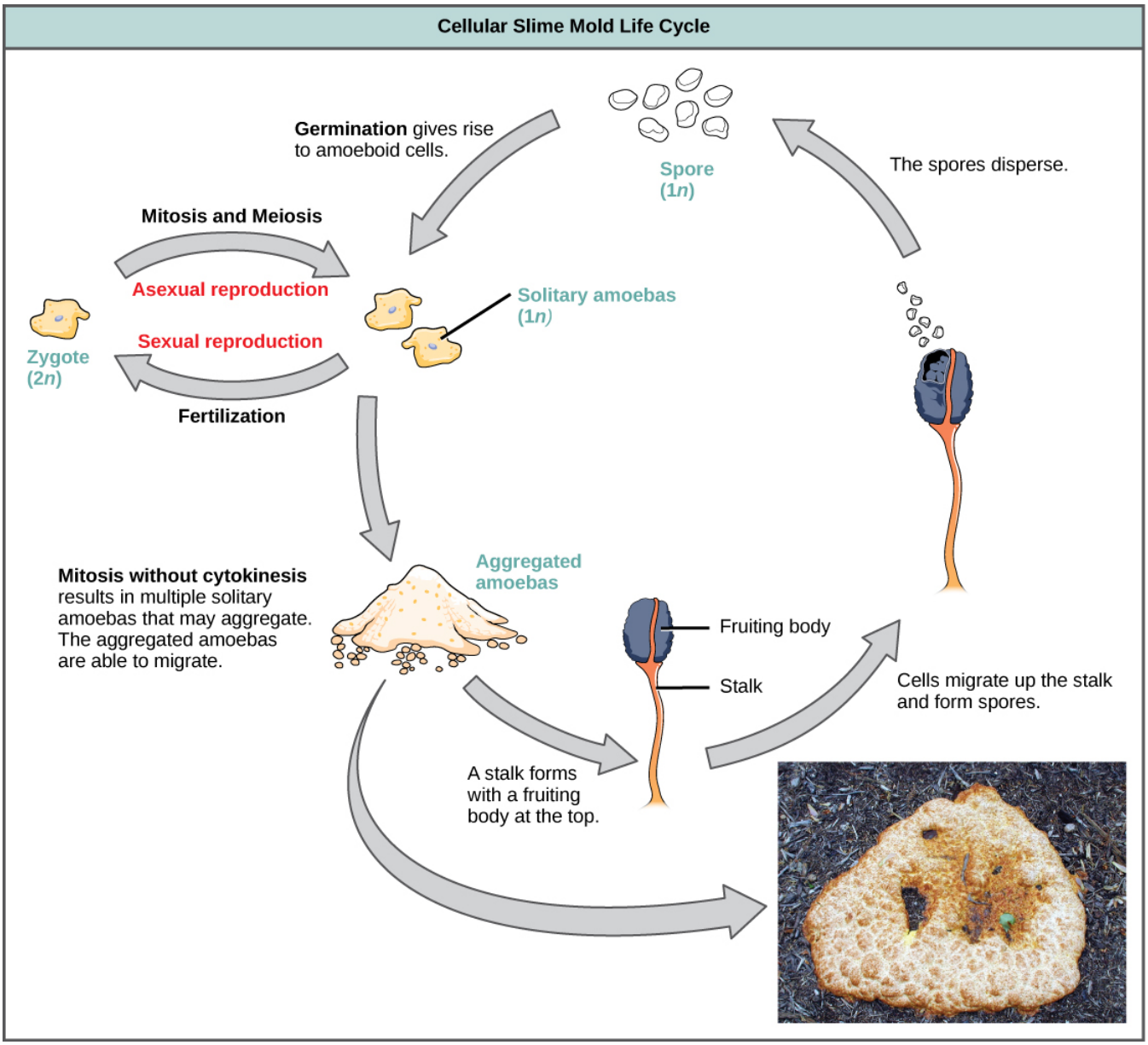


Figure **28.2.20**: Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

Link to Learning



View this site to see the formation of a fruiting body by a cellular slime mold.

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

The Mesomycetozoa form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood. These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology.

Summary

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Amoebozoa, and Opisthokonta. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor. At present, the monophyly of some of the supergroups are better supported by genetic data than others. Although tremendous variation exists within the supergroups, commonalities at the morphological, physiological, and ecological levels can be identified.

Art Connections

Figure **28.2.8**: Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronuclei.
D. Each parent produces four daughter cells.

Answer

C

Figure **28.2.11**: Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.

B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

Answer

C

Glossary

biological carbon pump
process by which inorganic carbon is fixed by photosynthetic species that then die and fall to the sea floor where they cannot be reached by saprobes and their carbon dioxide consumption cannot be returned to the atmosphere

bioluminescence
generation and emission of light by an organism, as in dinoflagellates

contractile vacuole
vesicle that fills with water (as it enters the cell by osmosis) and then contracts to squeeze water from the cell; an osmoregulatory vesicle

cytoplasmic streaming
movement of cytoplasm into an extended pseudopod such that the entire cell is transported to the site of the pseudopod

hydrogenosome
organelle carried by parabasalids (Excavata) that functions anaerobically and outputs hydrogen gas as a byproduct; likely evolved from mitochondria

kinetoplast
mass of DNA carried within the single, oversized mitochondrion, characteristic of kinetoplastids (phylum: Euglenozoa)

mitosome
nonfunctional organelle carried in the cells of diplomonads (Excavata) that likely evolved from a mitochondrion

plankton
diverse group of mostly microscopic organisms that drift in marine and freshwater systems and serve as a food source for larger aquatic organisms

raphe
slit in the silica shell of diatoms through which the protist secretes a stream of mucopolysaccharides for locomotion and attachment to substrates

test
porous shell of a foram that is built from various organic materials and typically hardened with calcium carbonate

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28.3: Characteristics of Excavata

Skills to Develop

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called **convergent evolution**, is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six "supergroups" that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor (Figure 28.3.1). The supergroups are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

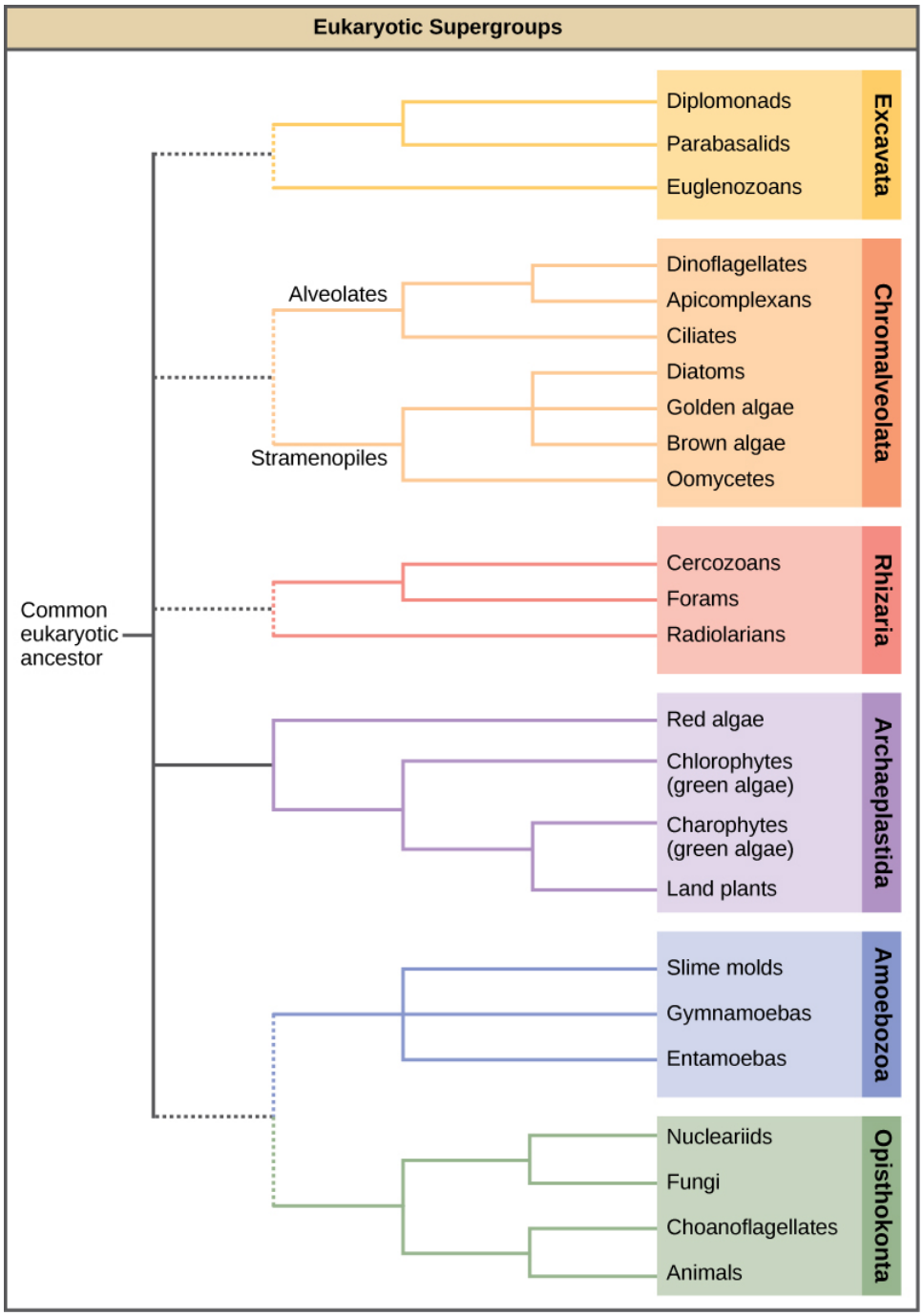


Figure **28.3.1**: This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia* (Figure **28.3.2**). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called mitosomes, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.



Figure **28.3.2**: The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell)

Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called hydrogenosomes because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichamoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the kinetoplast, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human

or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.

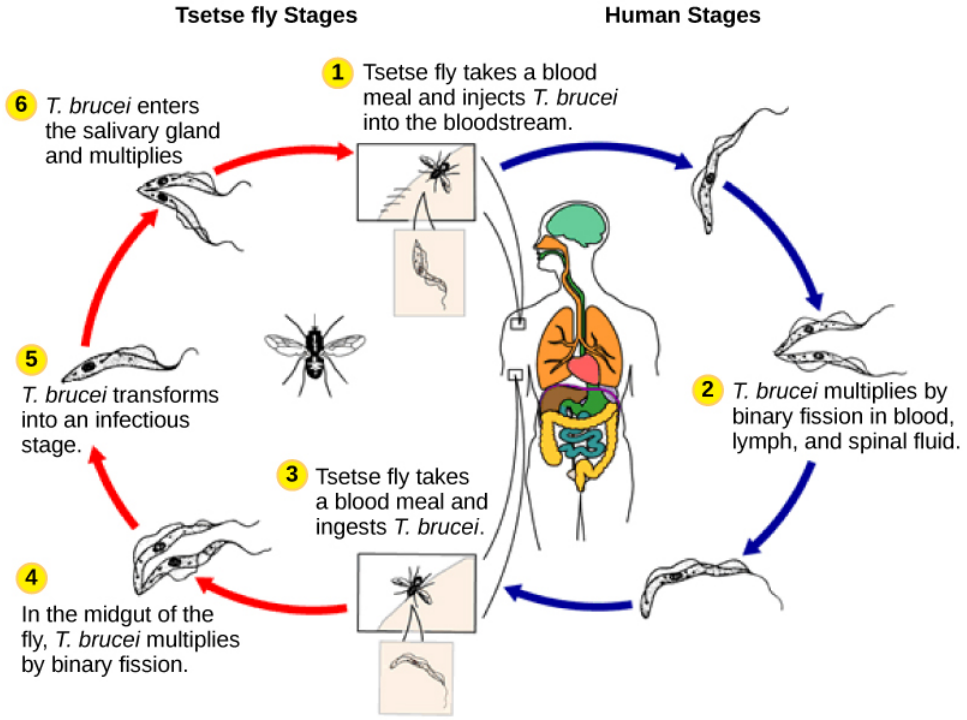


Figure **28.3.3**: *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Trypanosoma brucei



Watch this video to see *T. brucei* swimming. https://youtu.be/EnsydwITLYk

Chromalveolata

Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether.

Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexians, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate (Figure **28.3.4**). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of plankton, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.

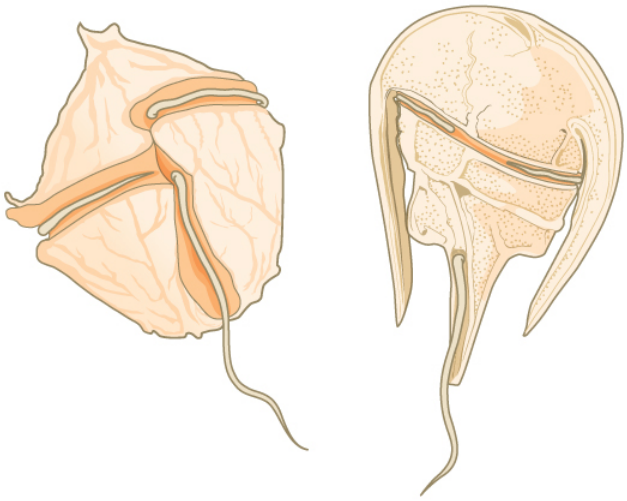


Figure **28.3.4**: The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

Some dinoflagellates generate light, called bioluminescence, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color (Figure **28.3.5**). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



Figure 28.3.5: Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: "catalano82"/Flickr)

The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex (Figure 28.3.6). The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

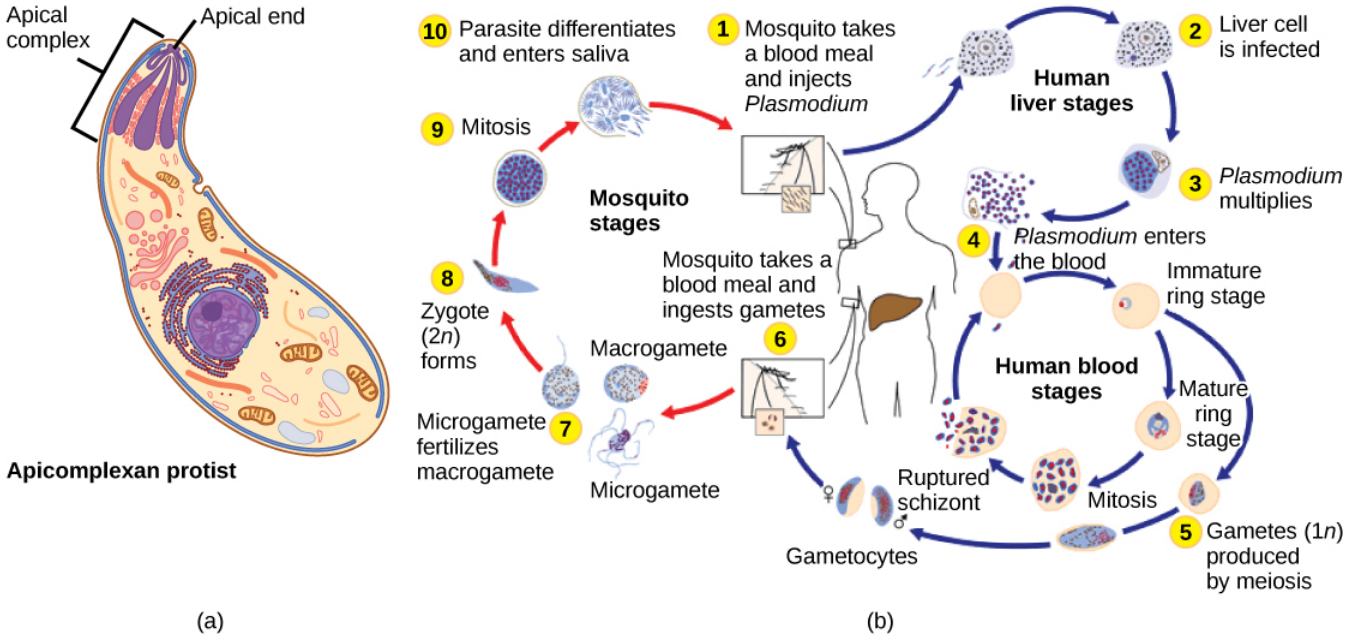


Figure 28.3.6: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria (Figure 28.3.7). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses contractile vacuoles, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.

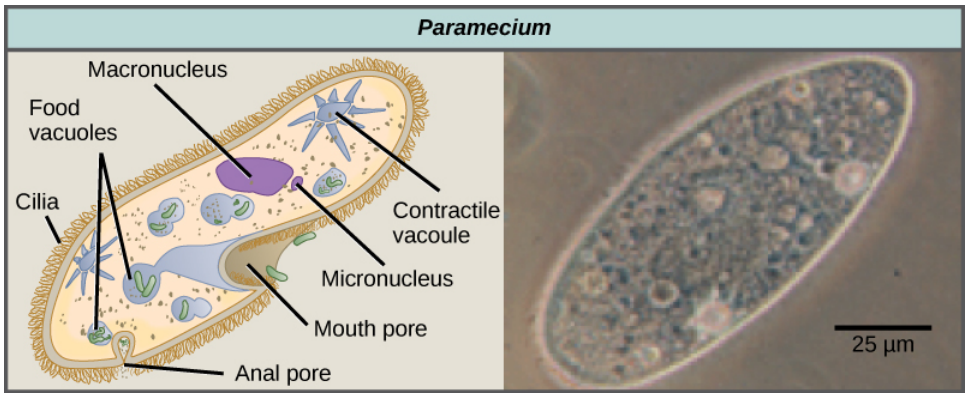
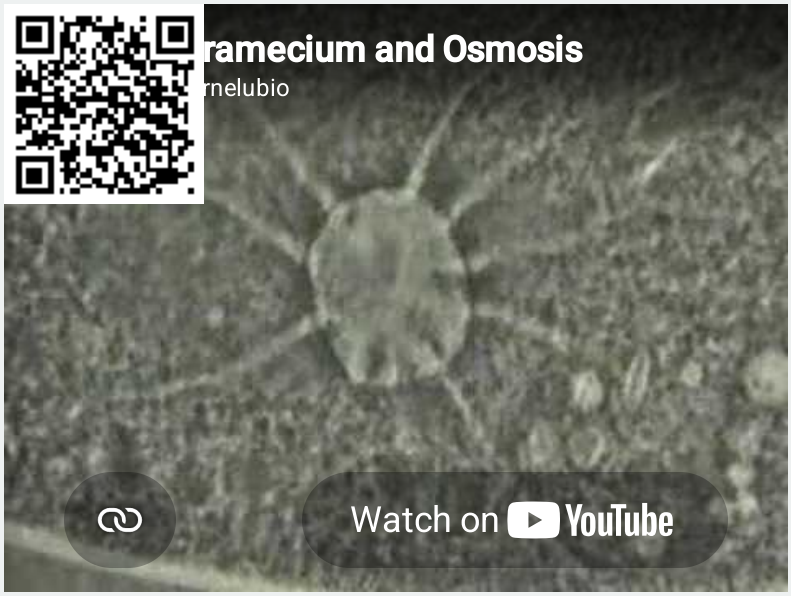


Figure 28.3.7: *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt Russell)

Link to Learning



Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge (Figure 28.3.8). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

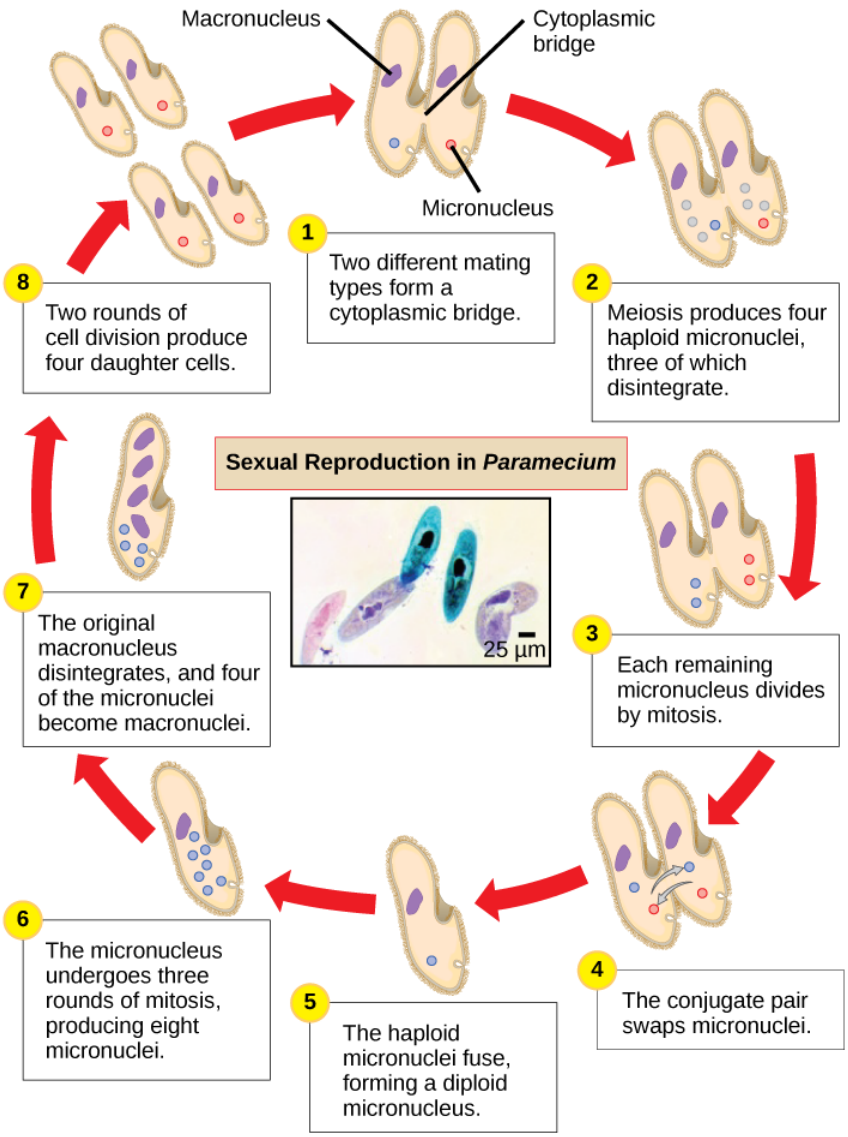


Figure 28.3.8: The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work by Ian Sutton; scale-bar data from Matt Russell)

Exercise

Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronucleii.
D. Each parent produces four daughter cells.

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or "hairy," flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections (Figure 28.3.9). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

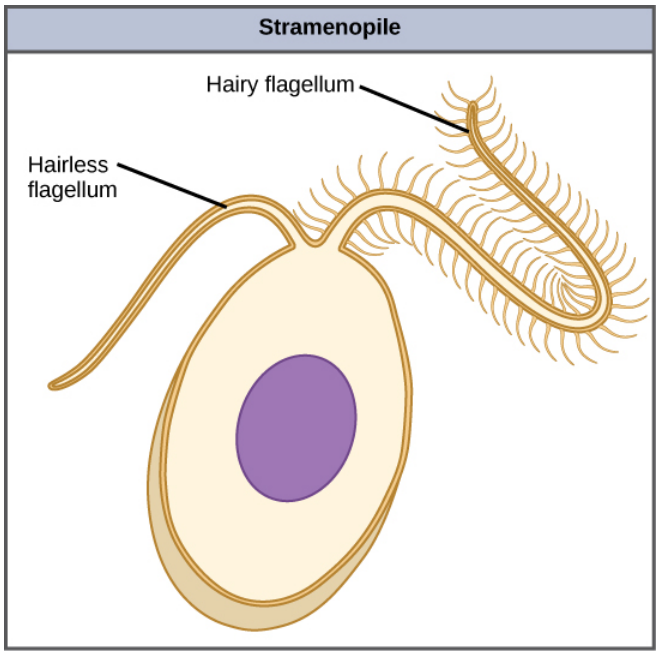


Figure **28.3.9**: This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles (Figure **28.3.10**). These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell, called a raphe. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

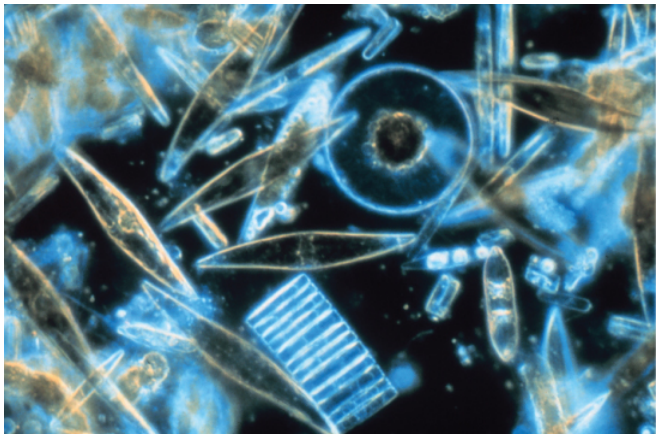


Figure **28.3.10**: Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the biological carbon pump, because carbon is “pumped” to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form (Figure **28.3.11**). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

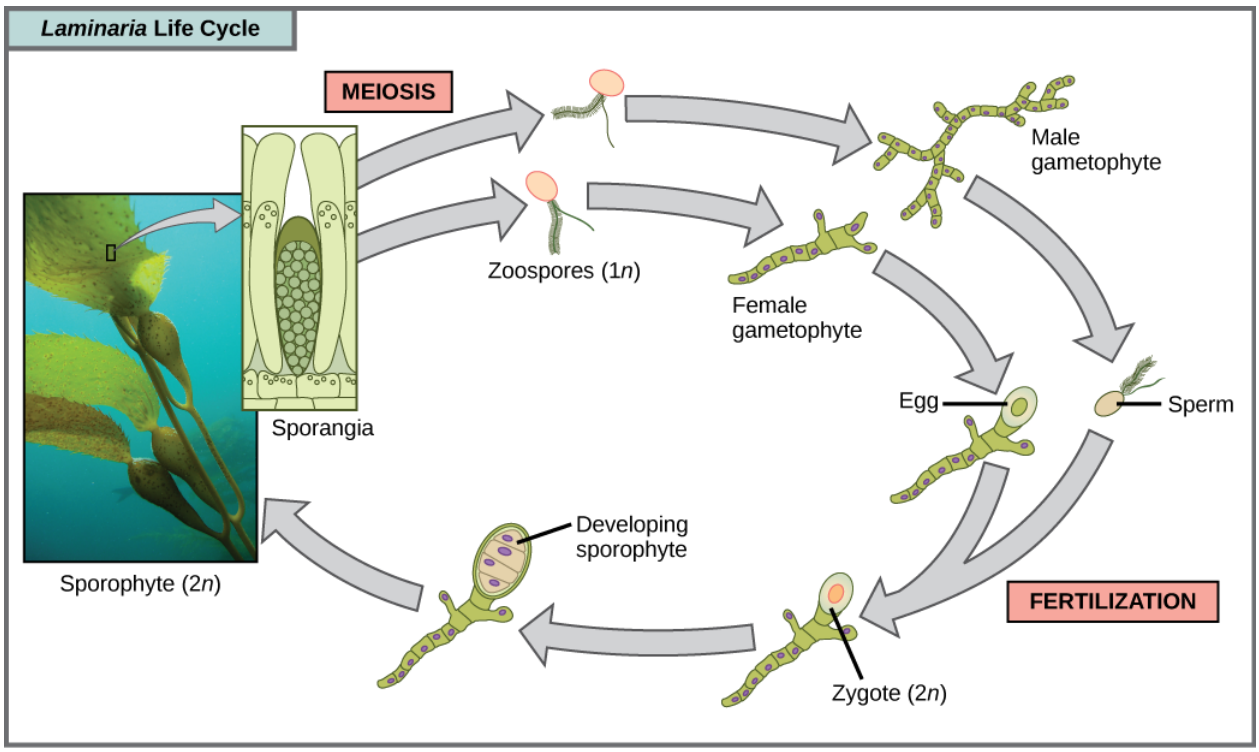


Figure **28.3.11**: Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit "laminaria photograph": modification of work by Claire Fackler, CINMS, NOAA Photo Library)

Exercise

Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.
B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

The water molds, oomycetes ("egg fungus"), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms (Figure **28.3.12**). Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.



Figure 28.3.12: A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (Figure 28.3.13). Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called cytoplasmic streaming, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.

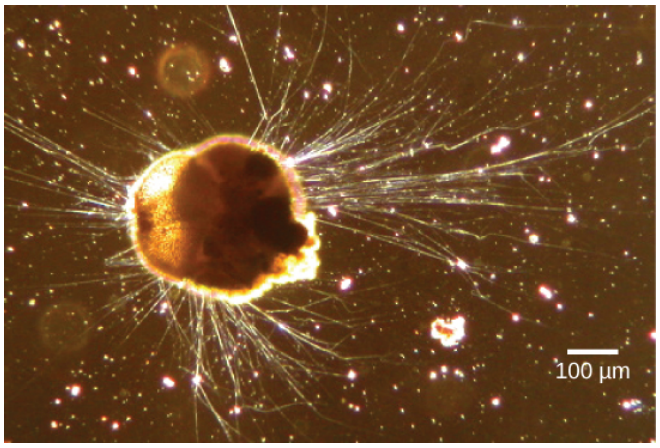


Figure 28.3.13: *Ammonia tepida*, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia. (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

Link to Learning



Take a look at this video to see cytoplasmic streaming in a green alga.

Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails (Figure 28.3.14). As a group, the forams exhibit porous shells, called tests that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.

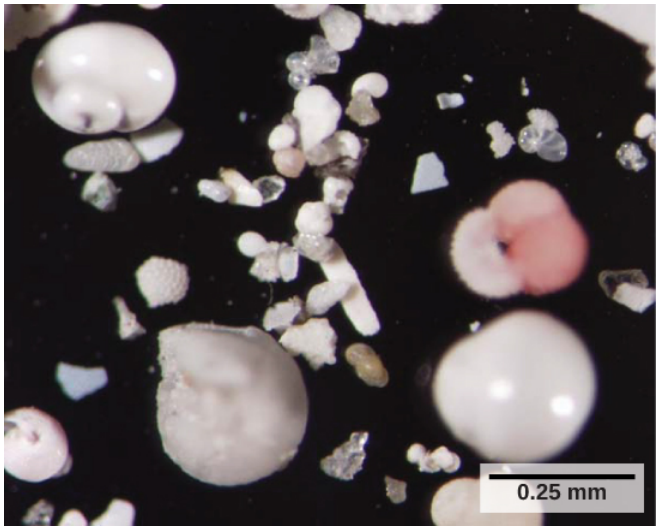


Figure 28.3.14: These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER)

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry (Figure 28.3.15). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

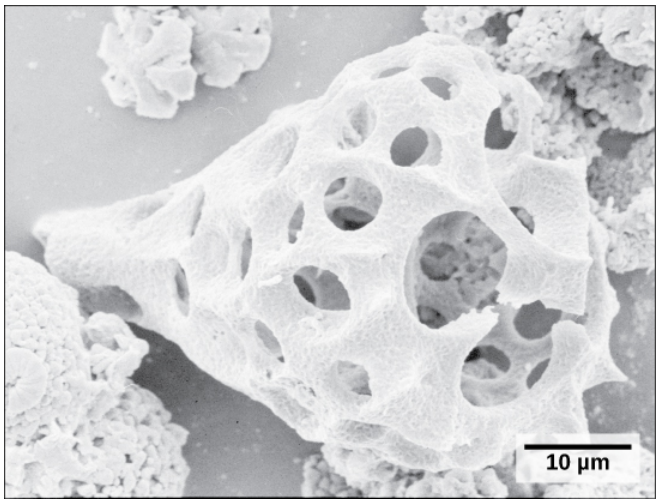


Figure 28.3.15: This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism (Figure 28.3.16). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



Figure **28.3.16**: *Volvox aureus* is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters (Figure **28.3.17**). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure **28.3.17**: *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Amoebozoa

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba (Figure **28.3.18**). The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.

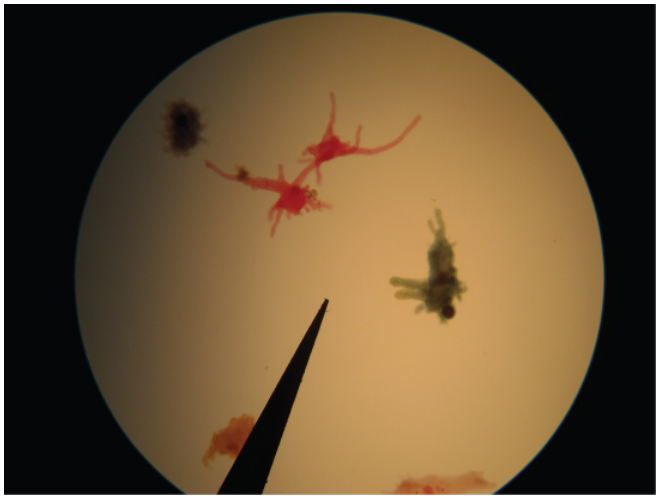


Figure **28.3.18**: Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage (Figure **28.3.19**). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

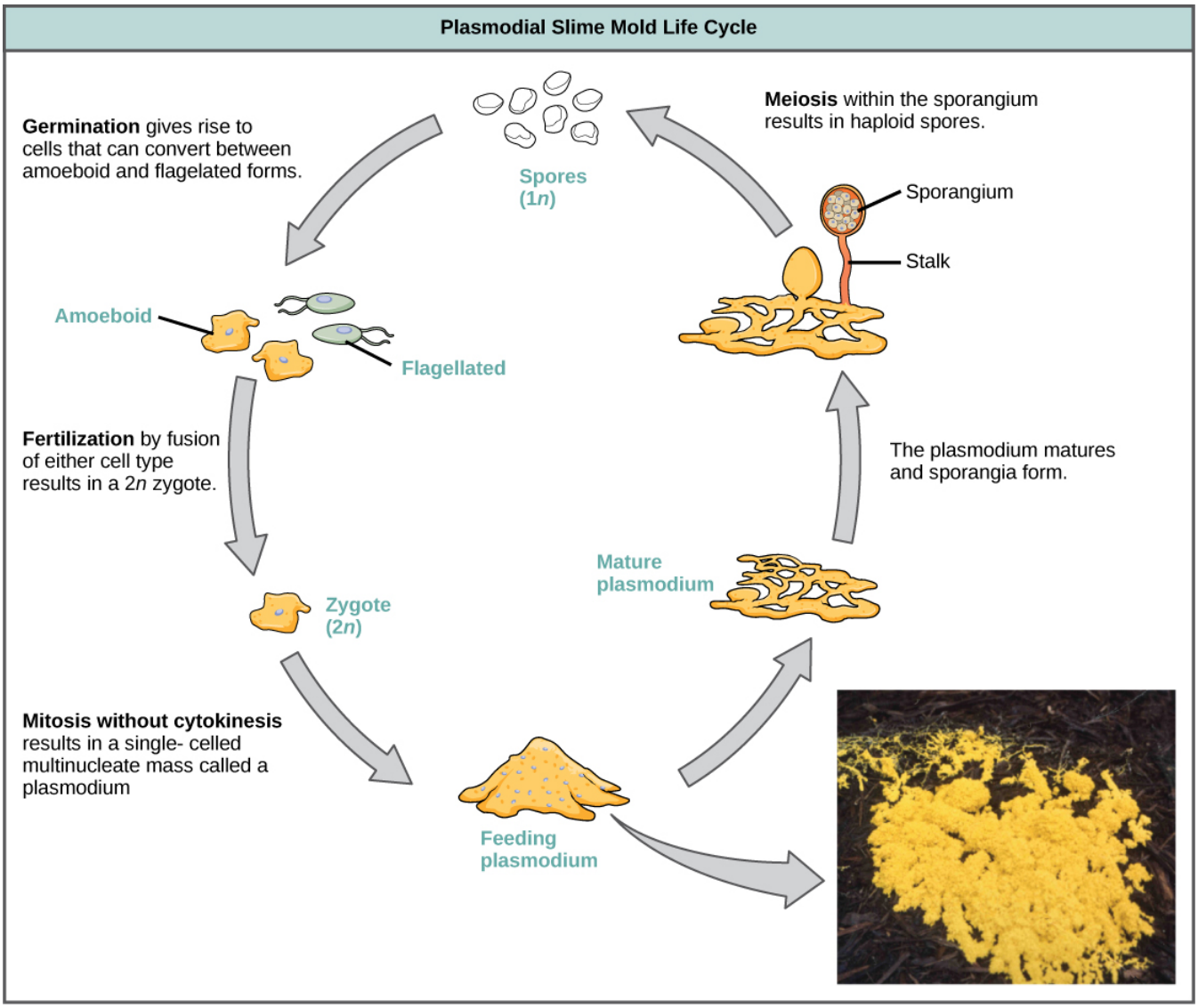


Figure 28.3.19: The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant (Figure 28.3.20). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

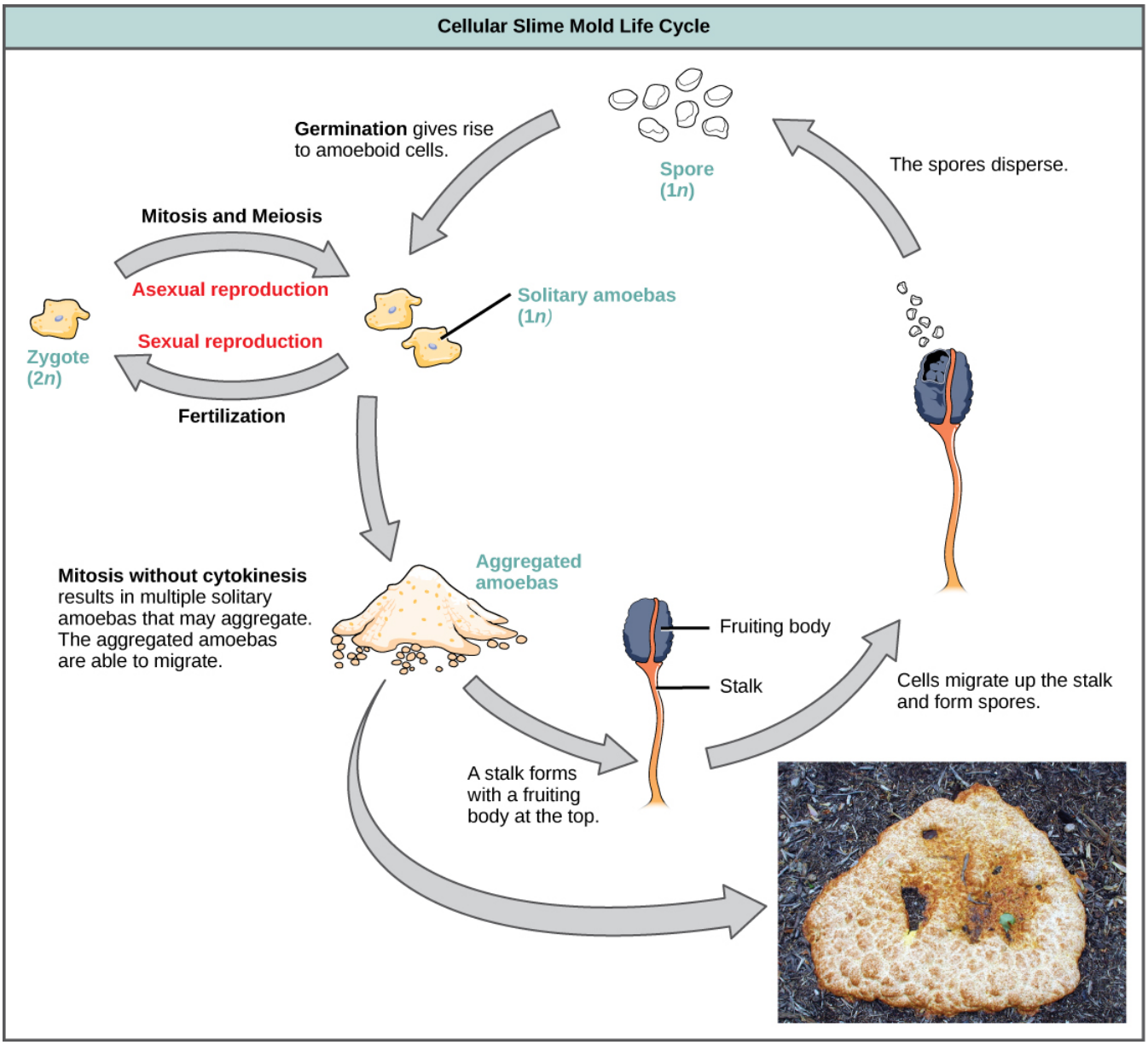


Figure **28.3.20**: Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

Link to Learning

https://bio.libretexts.org/@go/page/74270



View this site to see the formation of a fruiting body by a cellular slime mold.

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

The Mesomycetozoa form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood. These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology.

Summary

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Amoebozoa, and Opisthokonta. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor. At present, the monophyly of some of the supergroups are better supported by genetic data than others. Although tremendous variation exists within the supergroups, commonalities at the morphological, physiological, and ecological levels can be identified.

Art Connections

Figure **28.3.8**: Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronuclei.
D. Each parent produces four daughter cells.

Answer

C

Figure **28.3.11**: Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.

B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

Answer

C

Glossary

biological carbon pump
process by which inorganic carbon is fixed by photosynthetic species that then die and fall to the sea floor where they cannot be reached by saprobes and their carbon dioxide consumption cannot be returned to the atmosphere

bioluminescence
generation and emission of light by an organism, as in dinoflagellates

contractile vacuole
vesicle that fills with water (as it enters the cell by osmosis) and then contracts to squeeze water from the cell; an osmoregulatory vesicle

cytoplasmic streaming
movement of cytoplasm into an extended pseudopod such that the entire cell is transported to the site of the pseudopod

hydrogenosome
organelle carried by parabasalids (Excavata) that functions anaerobically and outputs hydrogen gas as a byproduct; likely evolved from mitochondria

kinetoplast
mass of DNA carried within the single, oversized mitochondrion, characteristic of kinetoplastids (phylum: Euglenozoa)

mitosome
nonfunctional organelle carried in the cells of diplomonads (Excavata) that likely evolved from a mitochondrion

plankton
diverse group of mostly microscopic organisms that drift in marine and freshwater systems and serve as a food source for larger aquatic organisms

raphe
slit in the silica shell of diatoms through which the protist secretes a stream of mucopolysaccharides for locomotion and attachment to substrates

test
porous shell of a foram that is built from various organic materials and typically hardened with calcium carbonate

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28.4: Characteristics of Chromalveolata

Skills to Develop

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called **convergent evolution**, is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six "supergroups" that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor (Figure 28.4.1). The supergroups are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

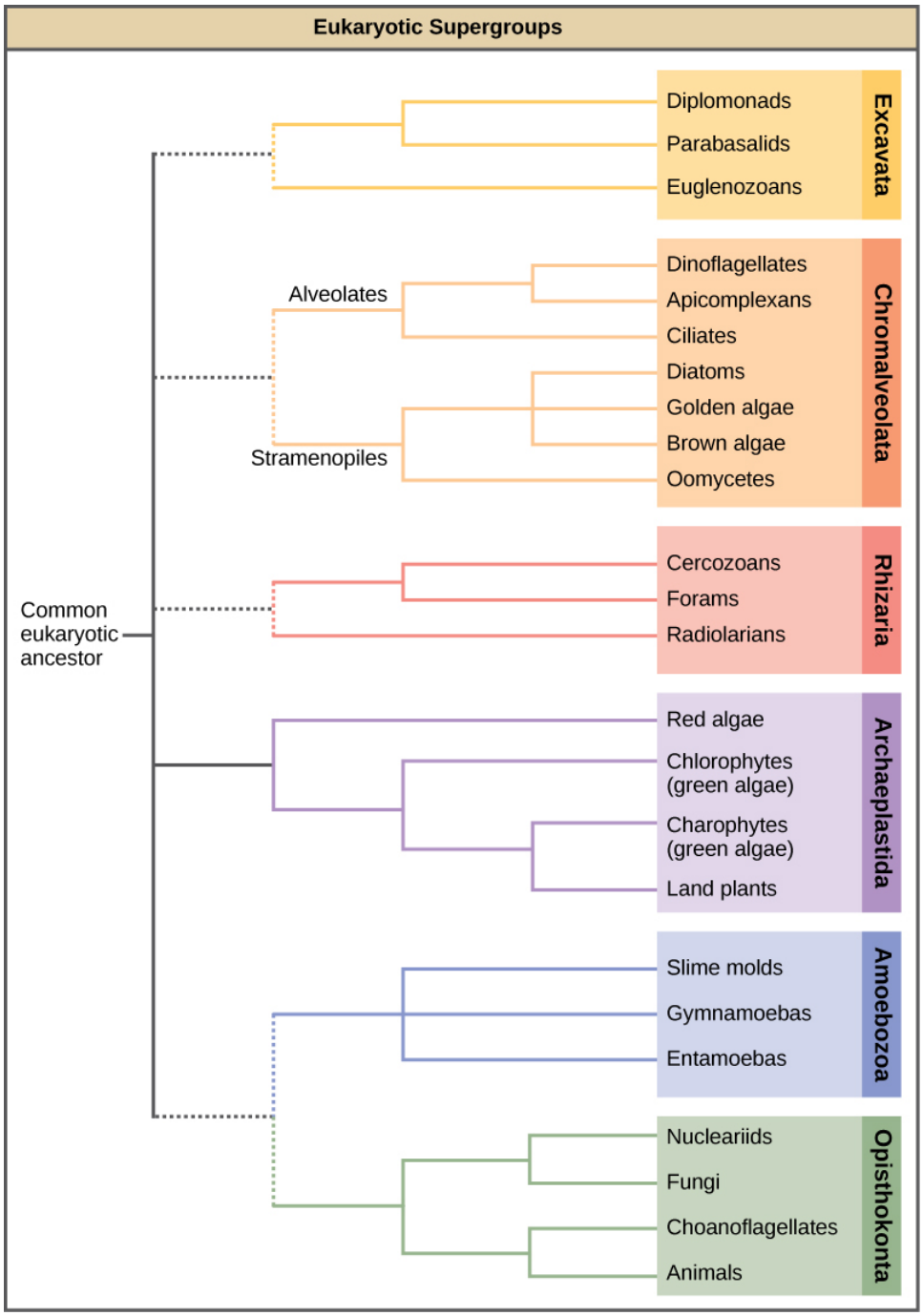


Figure **28.4.1**: This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia* (Figure 28.4.2). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called mitosomes, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.



Figure 28.4.2: The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell)

Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called hydrogenosomes because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichamoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the kinetoplast, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human

or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.

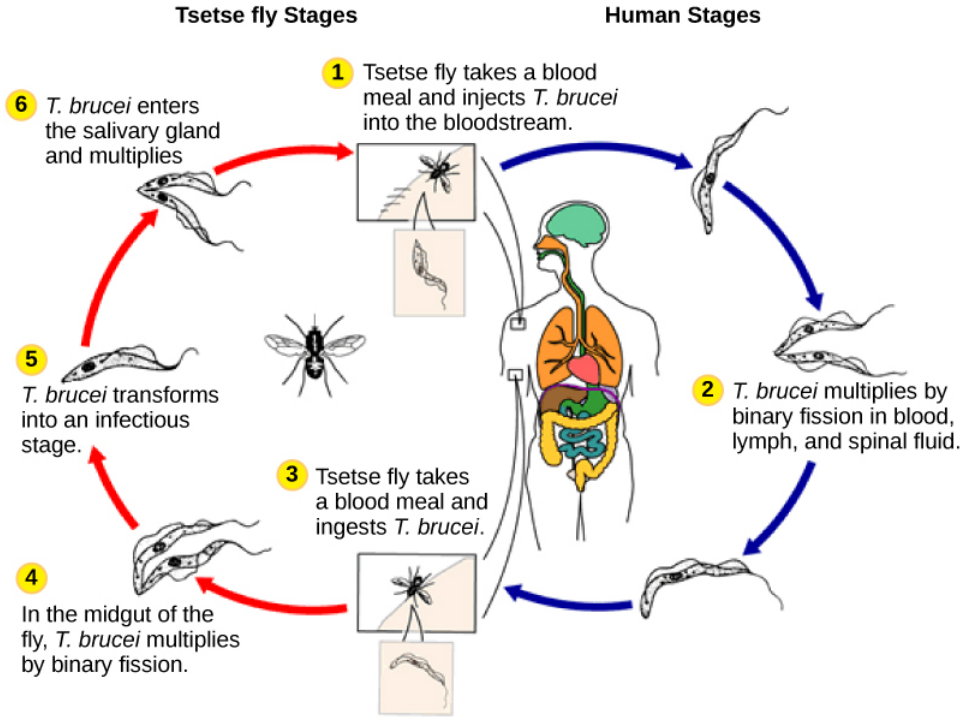


Figure **28.4.3**: *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Trypanosoma brucei



Watch this video to see *T. brucei* swimming. https://youtu.be/EnsydwITLYk

Chromalveolata

Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether.

Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexians, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate (Figure **28.4.4**). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of plankton, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.

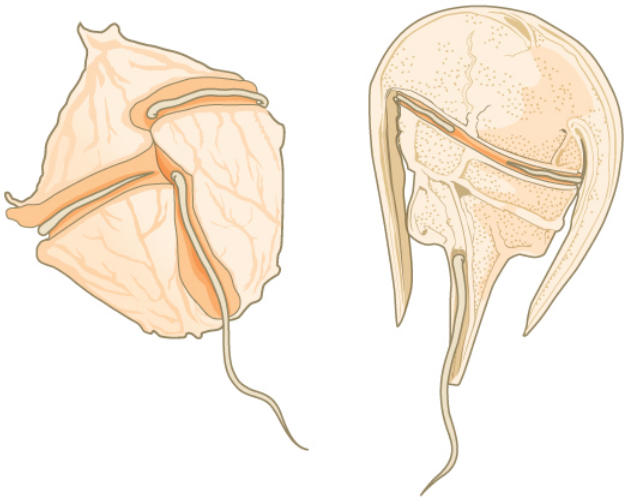


Figure **28.4.4**: The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

Some dinoflagellates generate light, called bioluminescence, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color (Figure **28.4.5**). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



Figure 28.4.5: Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: "catalano82"/Flickr)

The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex (Figure 28.4.6). The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

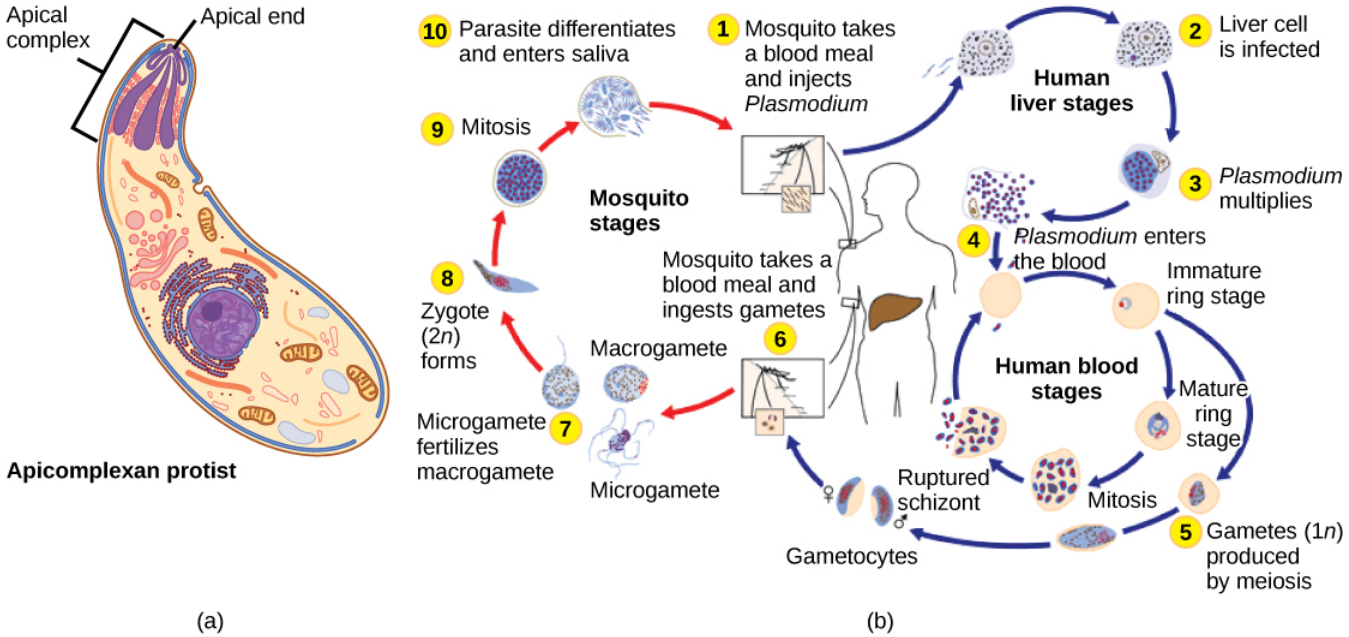


Figure 28.4.6: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria (Figure 28.4.7). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses contractile vacuoles, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.

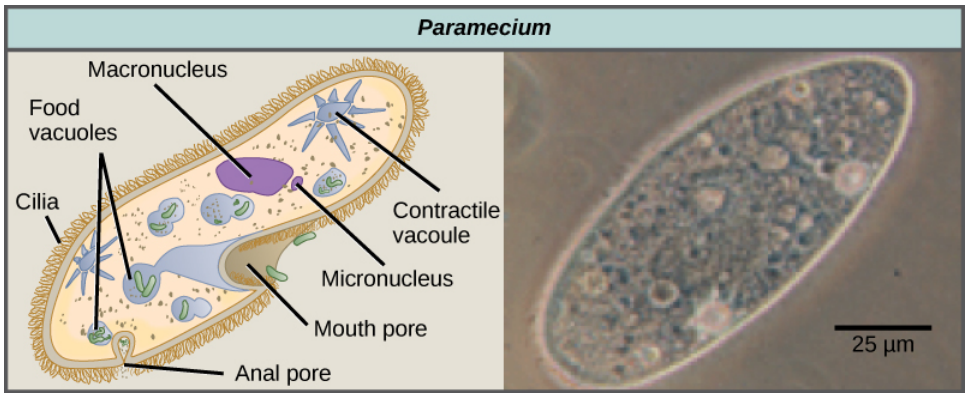
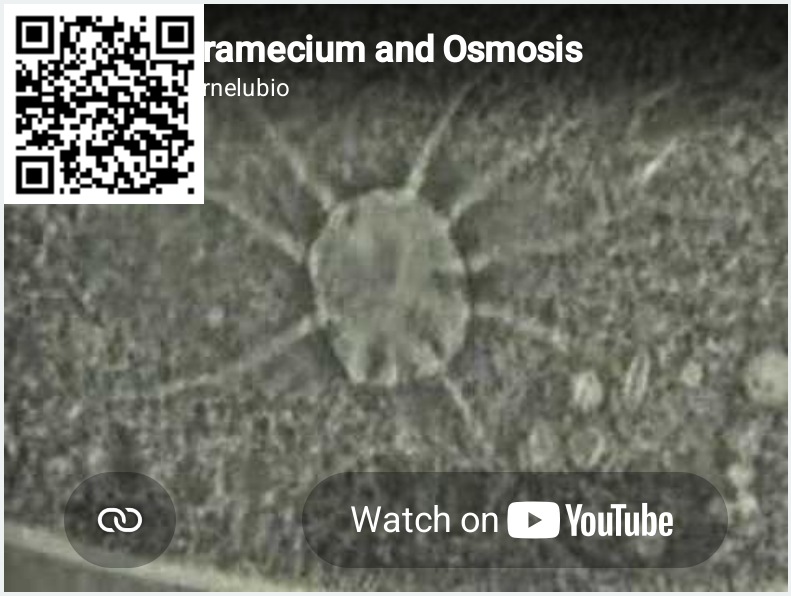


Figure 28.4.7: *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt Russell)

Link to Learning



Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge (Figure 28.4.8). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

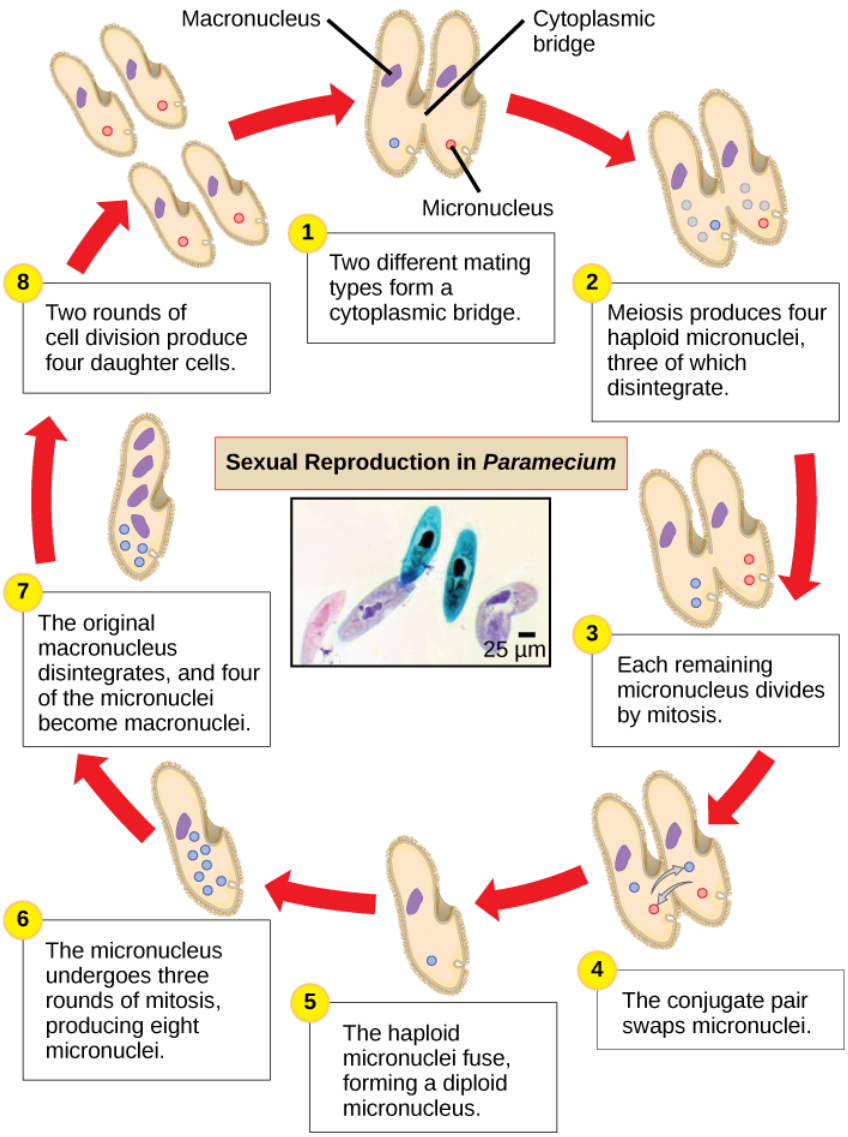


Figure 28.4.8: The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work by Ian Sutton; scale-bar data from Matt Russell)

Exercise

Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronucleii.
D. Each parent produces four daughter cells.

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or "hairy," flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections (Figure 28.4.9). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

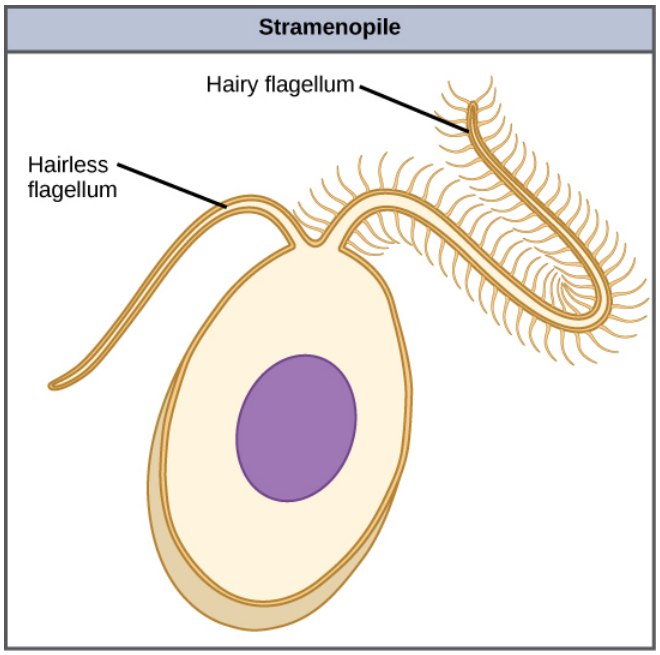


Figure **28.4.9**: This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles (Figure **28.4.10**). These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell, called a raphe. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

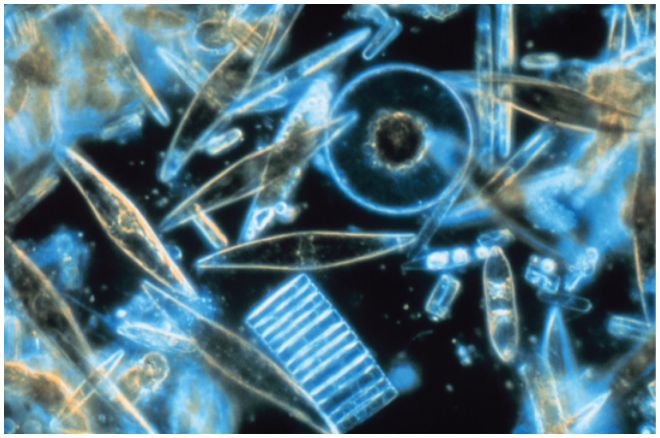


Figure **28.4.10**: Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the biological carbon pump, because carbon is “pumped” to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form (Figure **28.4.11**). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

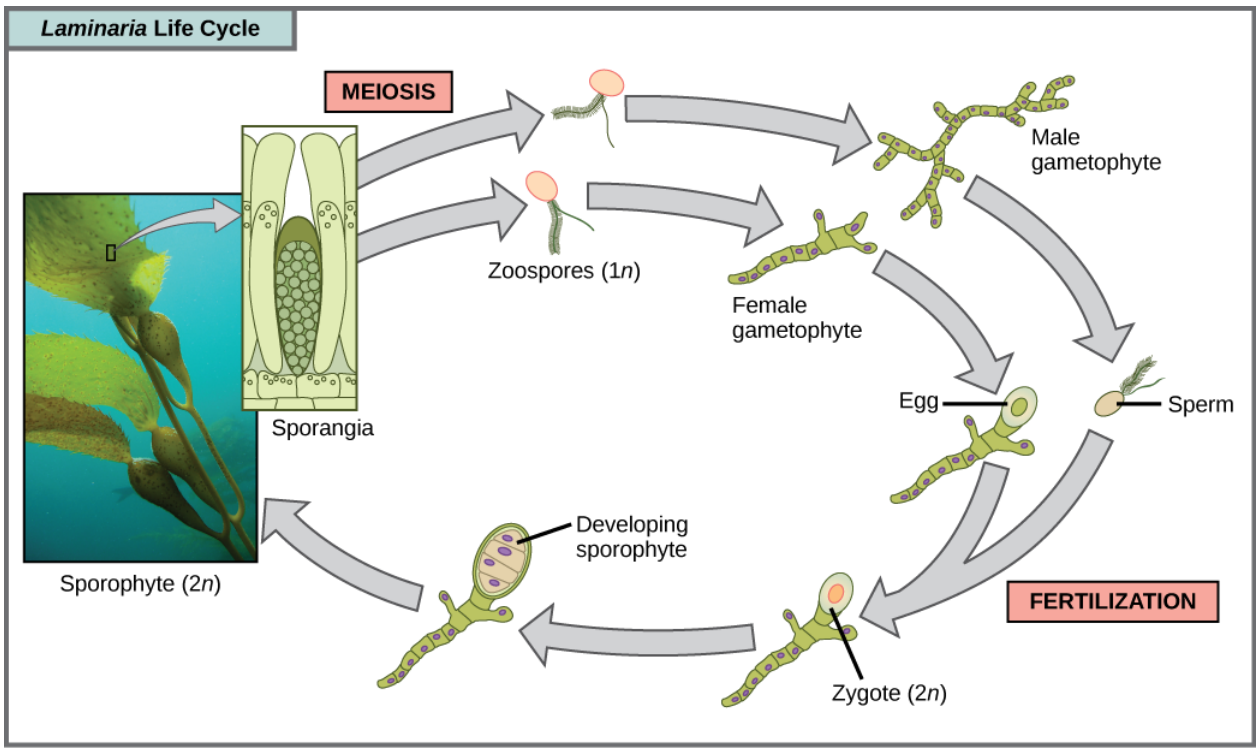


Figure **28.4.11**: Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit "laminaria photograph": modification of work by Claire Fackler, CINMS, NOAA Photo Library)

Exercise

Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.
B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

The water molds, oomycetes ("egg fungus"), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms (Figure **28.4.12**). Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.



Figure 28.4.12: A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (Figure 28.4.13). Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called cytoplasmic streaming, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.

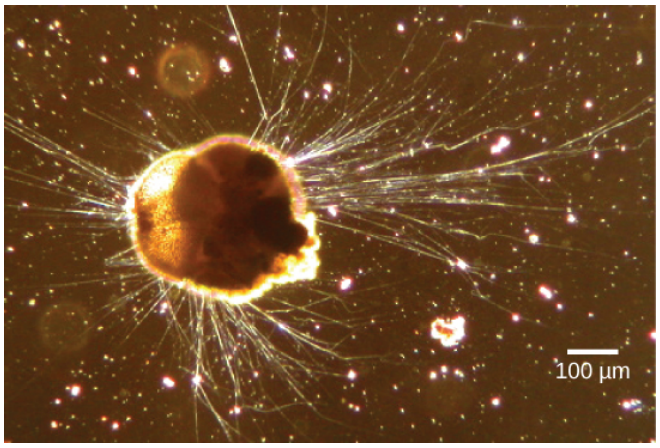


Figure 28.4.13: *Ammonia tepida*, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia. (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

Link to Learning



Take a look at this video to see cytoplasmic streaming in a green alga.

Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails (Figure 28.4.14). As a group, the forams exhibit porous shells, called tests that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.

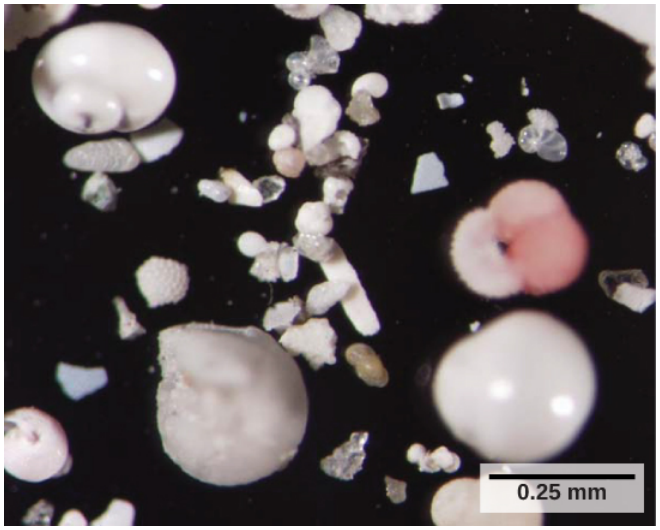


Figure 28.4.14: These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER)

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry (Figure 28.4.15). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

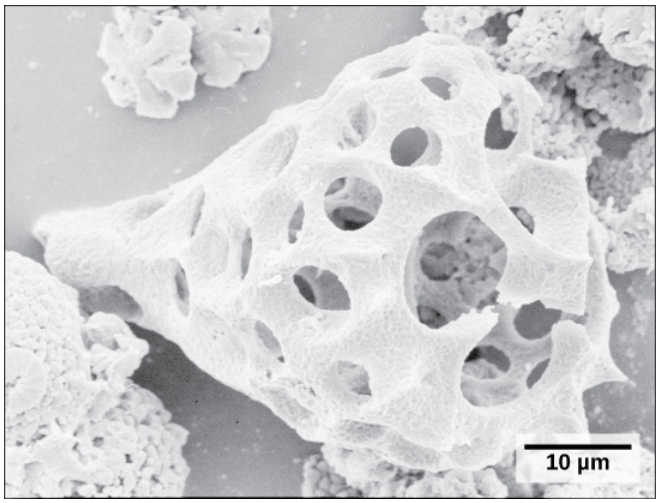


Figure 28.4.15: This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism (Figure 28.4.16). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



Figure 28.4.16: *Volvox aureus* is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters (Figure 28.4.17). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure 28.4.17: *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Amoebozoa

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba (Figure 28.4.18). The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.

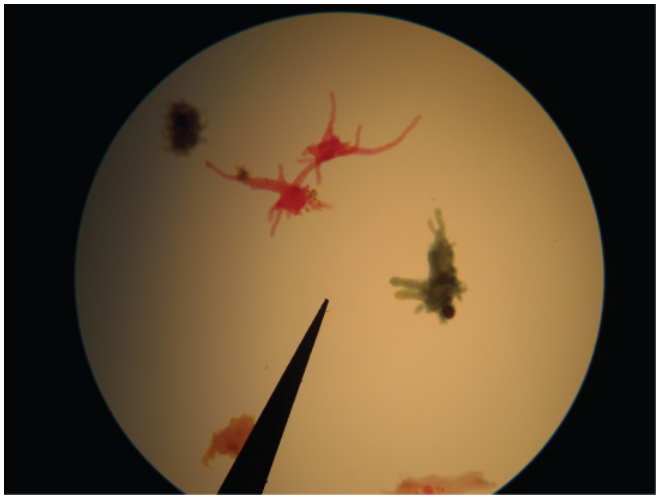


Figure **28.4.18**: Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage (Figure **28.4.19**). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

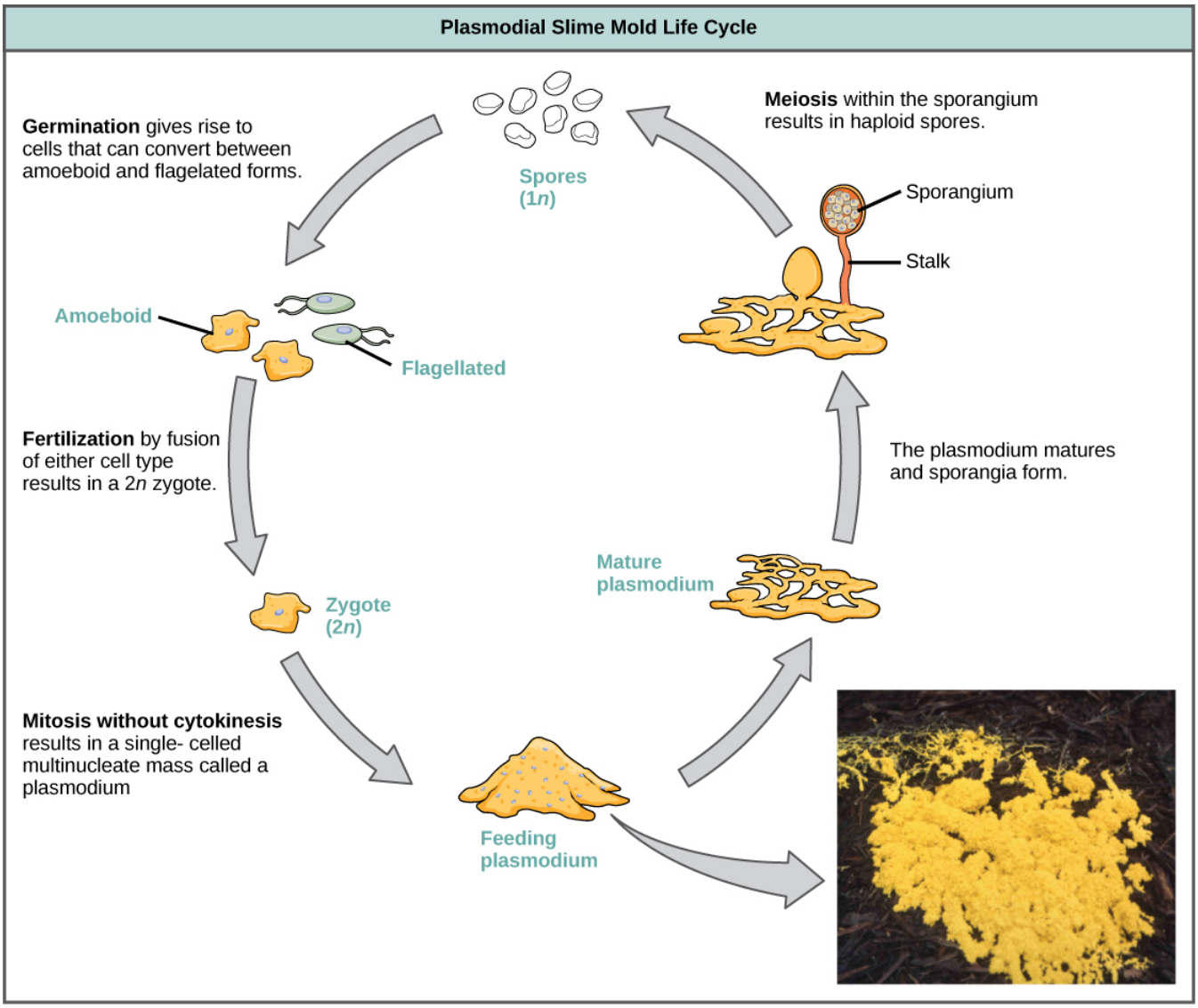


Figure 28.4.19: The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant (Figure 28.4.20). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

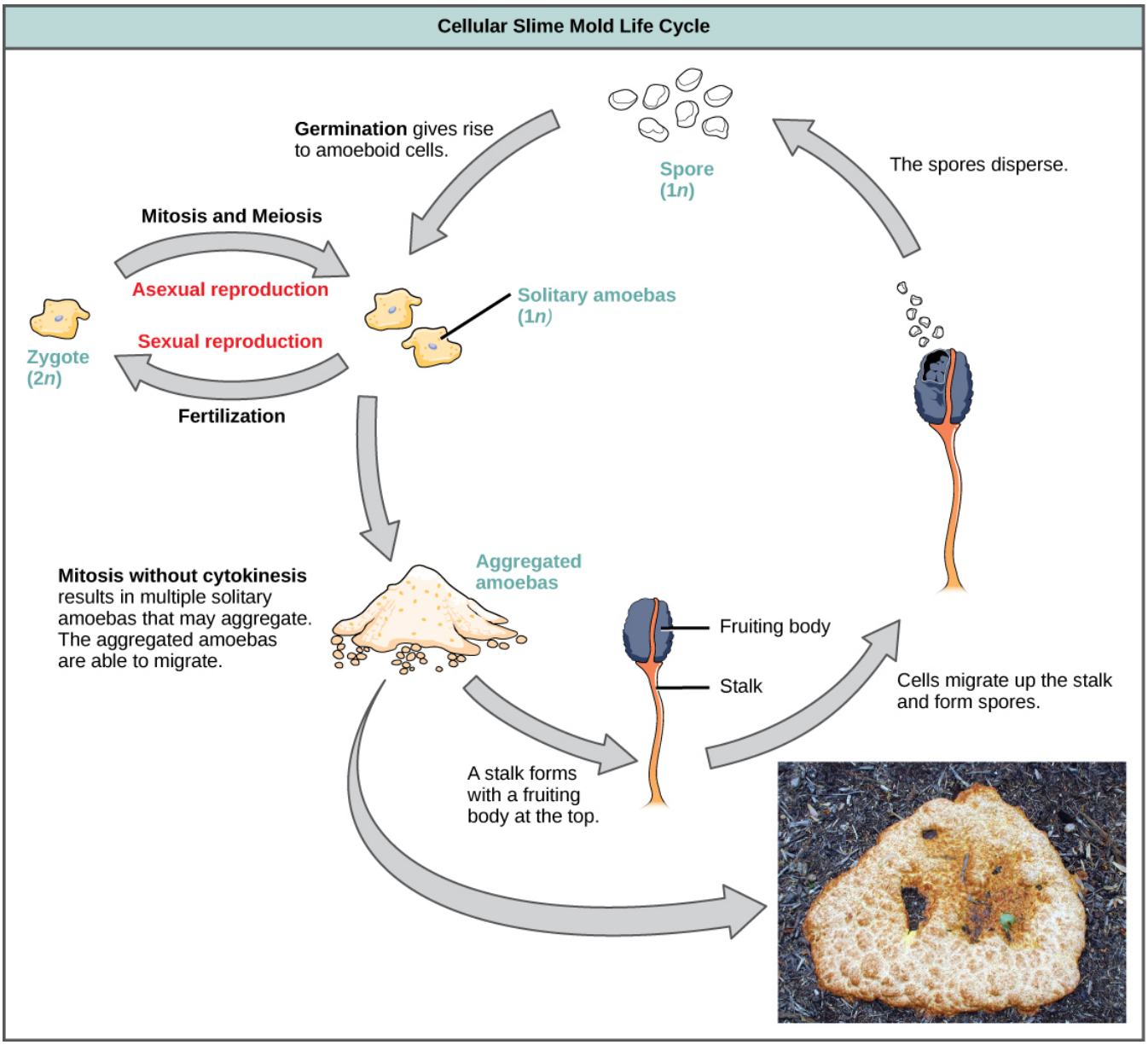


Figure 28.4.20: Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

Link to Learning

https://bio.libretexts.org/@go/page/74271



View this site to see the formation of a fruiting body by a cellular slime mold.

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

The Mesomycetozoa form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood. These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology.

Summary

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Amoebozoa, and Opisthokonta. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor. At present, the monophyly of some of the supergroups are better supported by genetic data than others. Although tremendous variation exists within the supergroups, commonalities at the morphological, physiological, and ecological levels can be identified.

Art Connections

Figure **28.4.8**: Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronuclei.
D. Each parent produces four daughter cells.

Answer

C

Figure **28.4.11**: Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.

B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

Answer

C

Glossary

biological carbon pump
process by which inorganic carbon is fixed by photosynthetic species that then die and fall to the sea floor where they cannot be reached by saprobes and their carbon dioxide consumption cannot be returned to the atmosphere

bioluminescence
generation and emission of light by an organism, as in dinoflagellates

contractile vacuole
vesicle that fills with water (as it enters the cell by osmosis) and then contracts to squeeze water from the cell; an osmoregulatory vesicle

cytoplasmic streaming
movement of cytoplasm into an extended pseudopod such that the entire cell is transported to the site of the pseudopod

hydrogenosome
organelle carried by parabasalids (Excavata) that functions anaerobically and outputs hydrogen gas as a byproduct; likely evolved from mitochondria

kinetoplast
mass of DNA carried within the single, oversized mitochondrion, characteristic of kinetoplastids (phylum: Euglenozoa)

mitosome
nonfunctional organelle carried in the cells of diplomonads (Excavata) that likely evolved from a mitochondrion

plankton
diverse group of mostly microscopic organisms that drift in marine and freshwater systems and serve as a food source for larger aquatic organisms

raphe
slit in the silica shell of diatoms through which the protist secretes a stream of mucopolysaccharides for locomotion and attachment to substrates

test
porous shell of a foram that is built from various organic materials and typically hardened with calcium carbonate

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28.5: Characteristics of Rhizaria

Skills to Develop

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called **convergent evolution**, is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six "supergroups" that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor (Figure 28.5.1). The supergroups are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

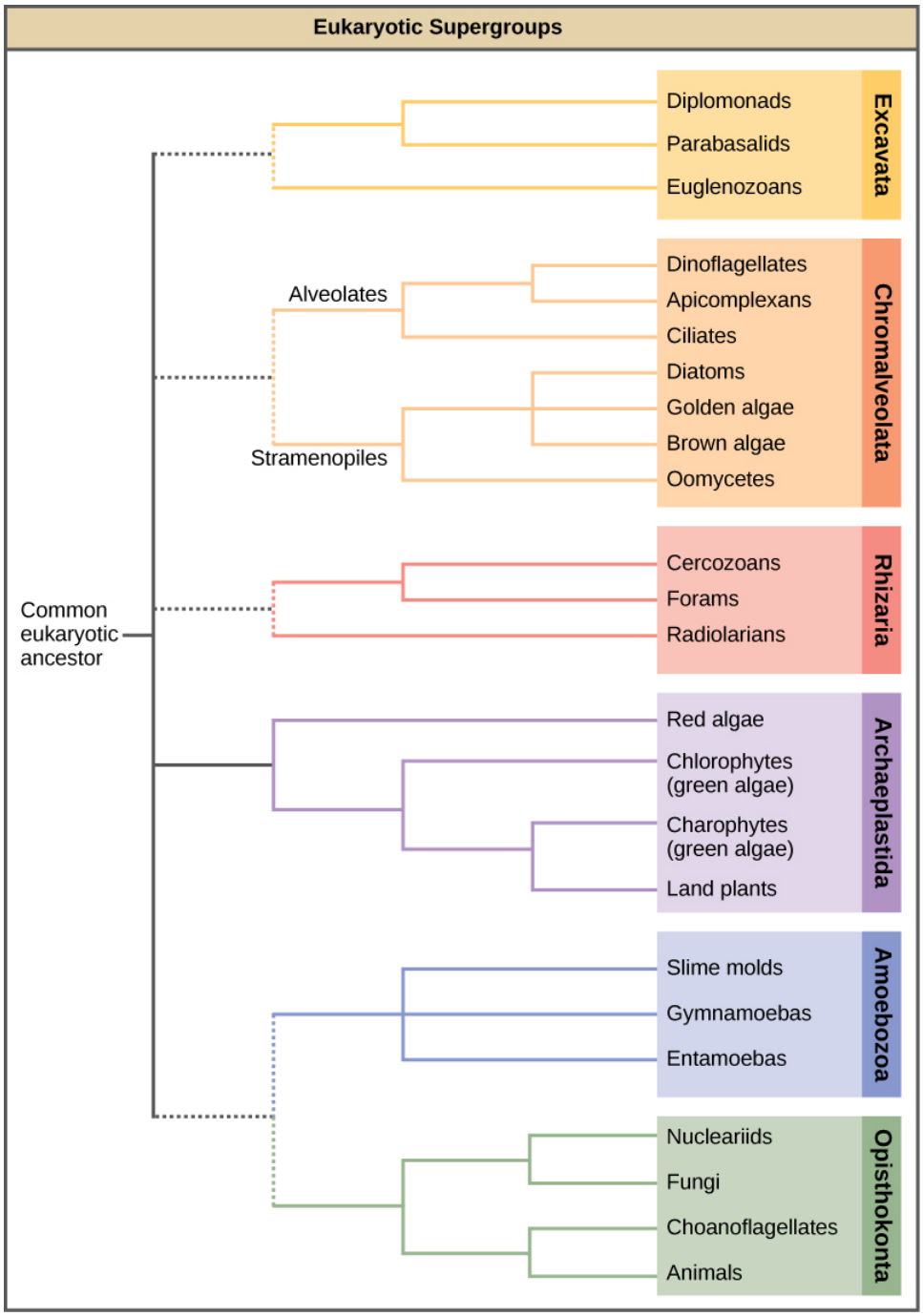


Figure **28.5.1**: This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia* (Figure **28.5.2**). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called mitosomes, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.



Figure **28.5.2**: The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell)

Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called hydrogenosomes because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichamoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the kinetoplast, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human

or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.

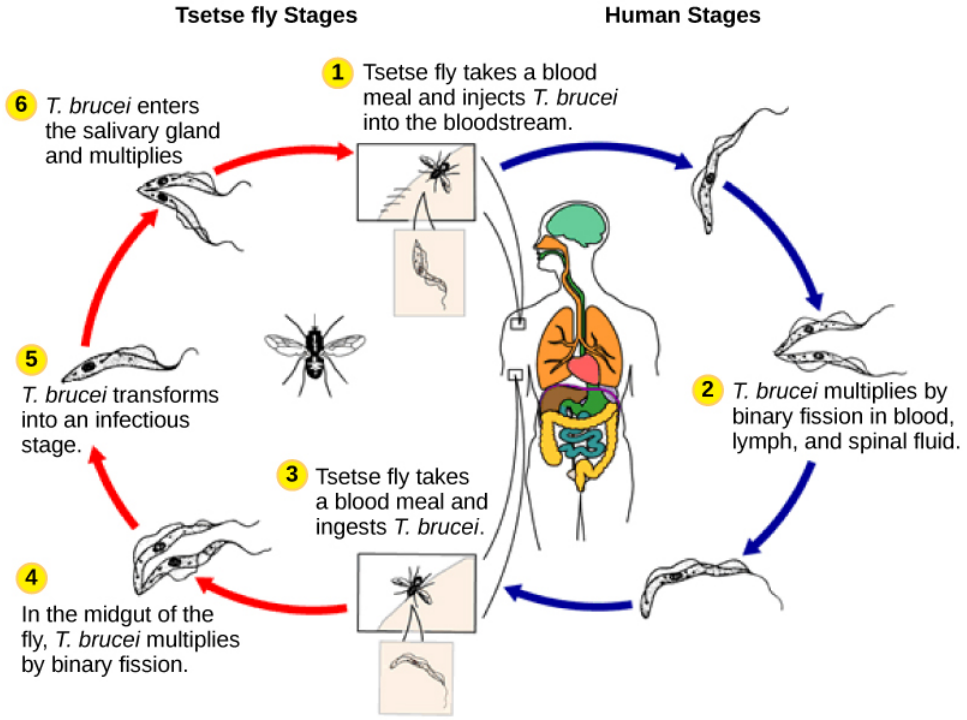


Figure **28.5.3**: *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Trypanosoma brucei



Watch this video to see *T. brucei* swimming. https://youtu.be/EnsydwITLYk

Chromalveolata

Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether.

Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexians, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate (Figure **28.5.4**). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of plankton, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.

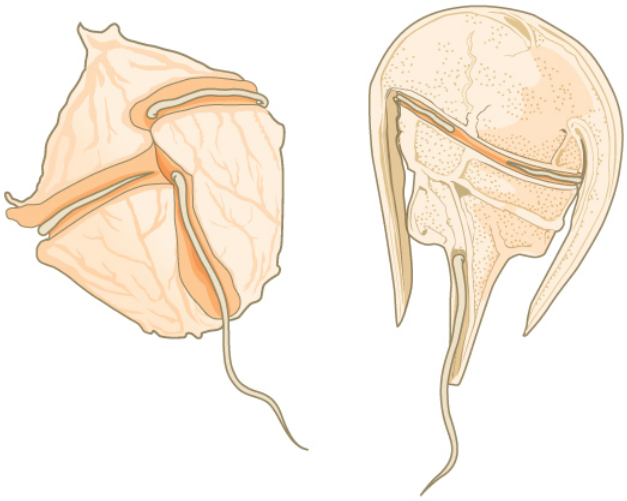


Figure **28.5.4**: The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

Some dinoflagellates generate light, called bioluminescence, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color (Figure **28.5.5**). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



Figure 28.5.5: Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: "catalano82"/Flickr)

The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex (Figure 28.5.6). The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

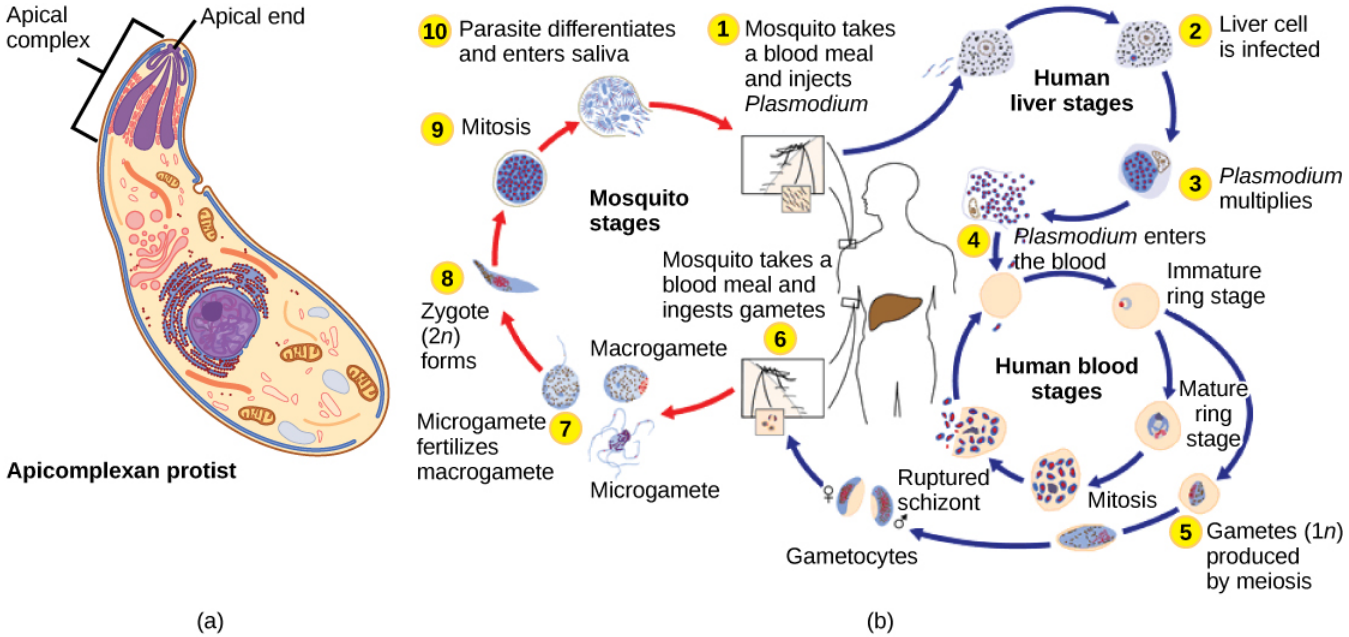


Figure 28.5.6: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria (Figure 28.5.7). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses contractile vacuoles, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.

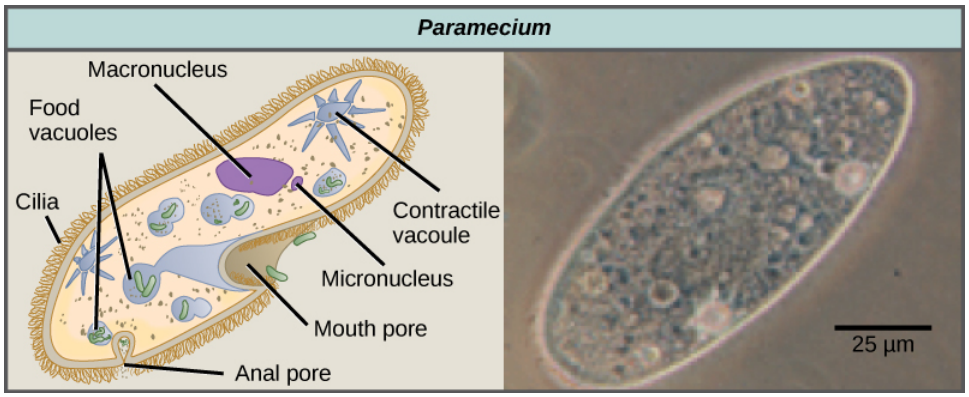
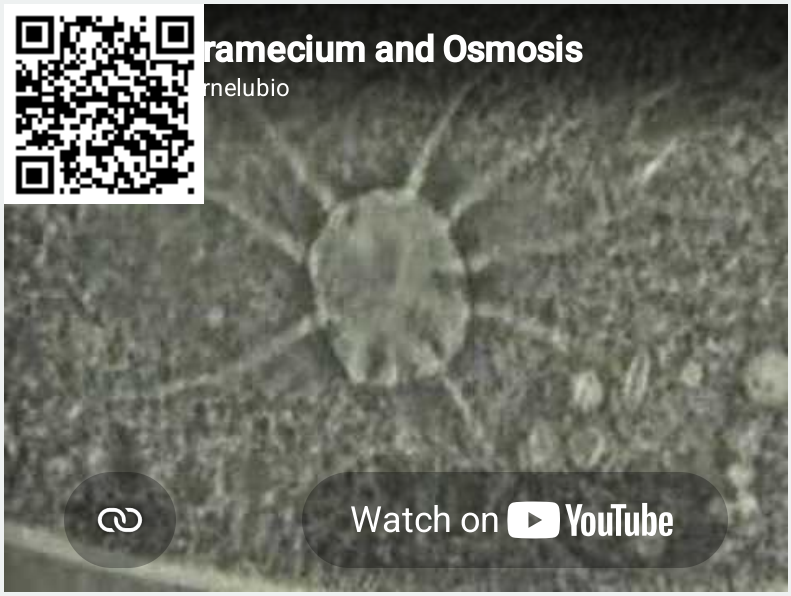


Figure 28.5.7: *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt Russell)

Link to Learning



Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge (Figure 28.5.8). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

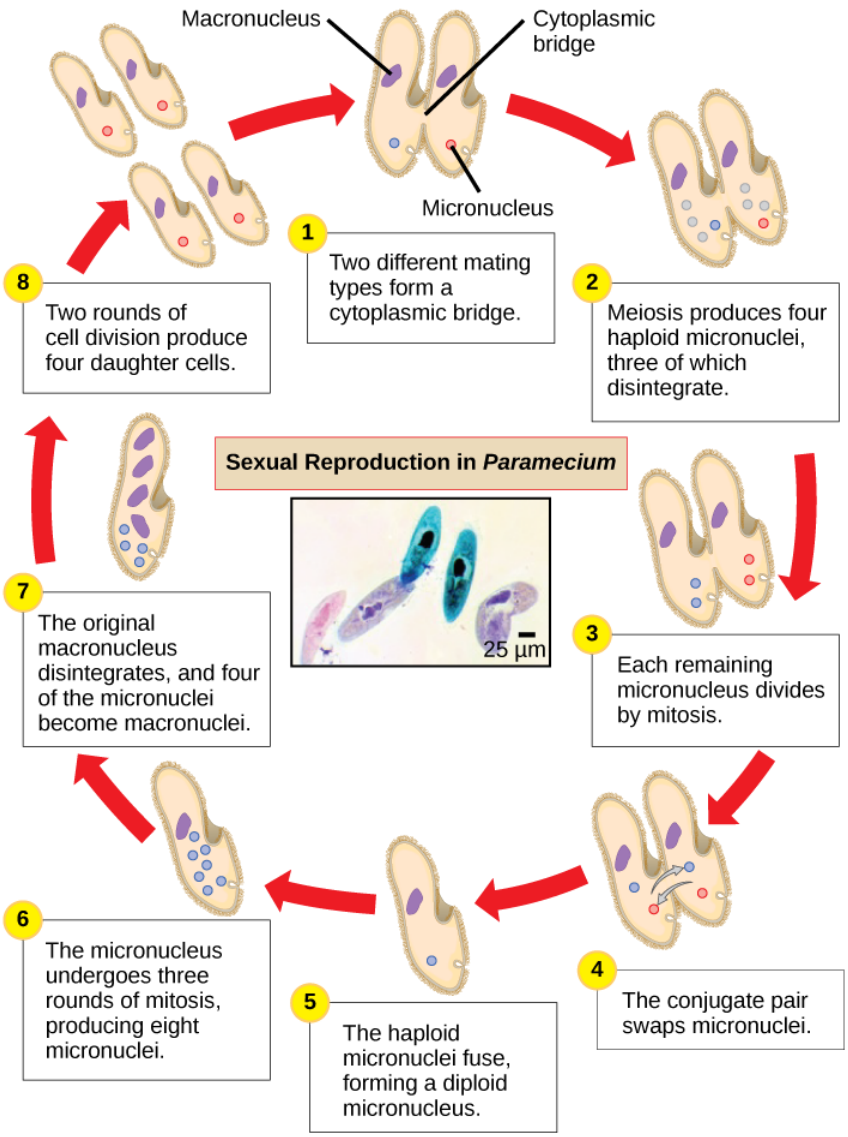


Figure 28.5.8: The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work by Ian Sutton; scale-bar data from Matt Russell)

Exercise

Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronucleii.
D. Each parent produces four daughter cells.

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or "hairy," flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections (Figure 28.5.9). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

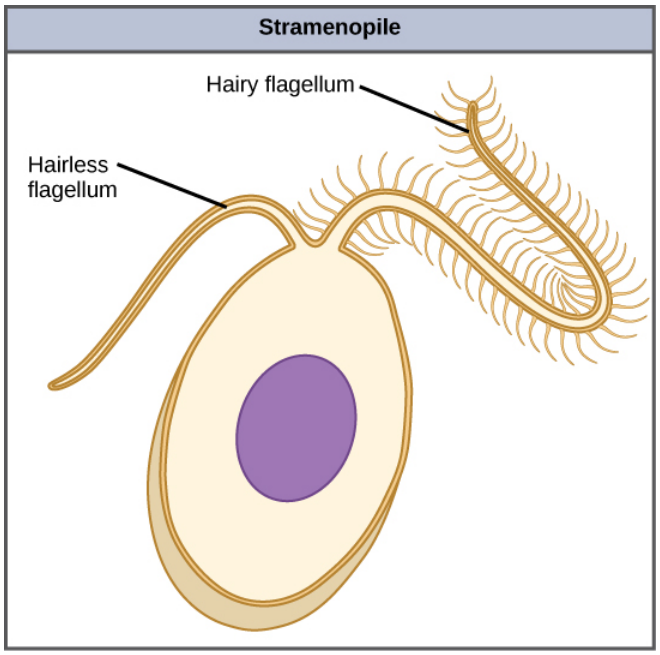


Figure **28.5.9**: This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles (Figure **28.5.10**). These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell, called a raphe. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

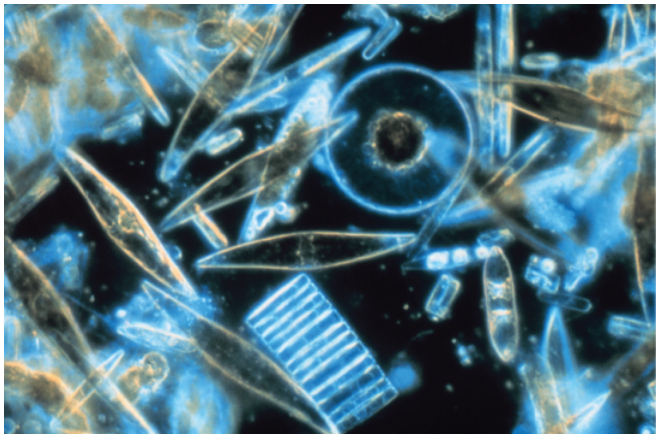


Figure **28.5.10**: Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the biological carbon pump, because carbon is “pumped” to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form (Figure **28.5.11**). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

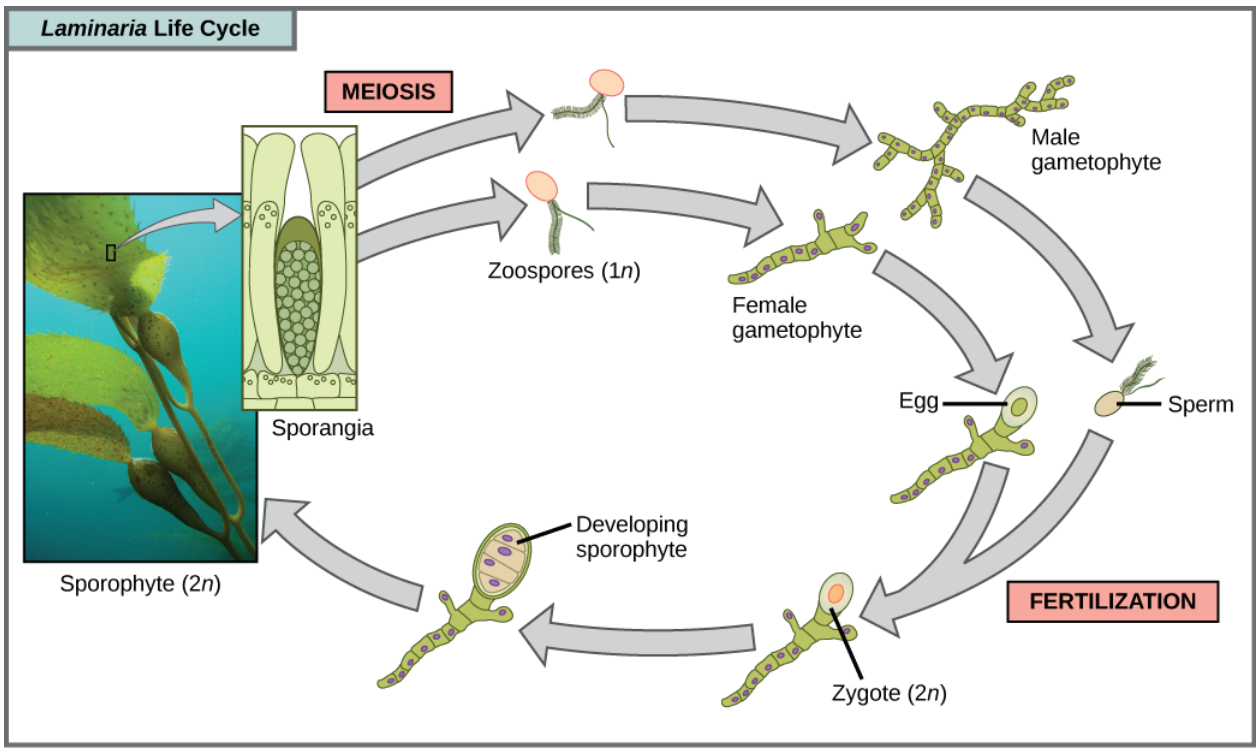


Figure **28.5.11**: Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit "laminaria photograph": modification of work by Claire Fackler, CINMS, NOAA Photo Library)

Exercise

Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.
B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

The water molds, oomycetes ("egg fungus"), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms (Figure **28.5.12**). Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.



Figure 28.5.12: A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (Figure 28.5.13). Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called cytoplasmic streaming, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.

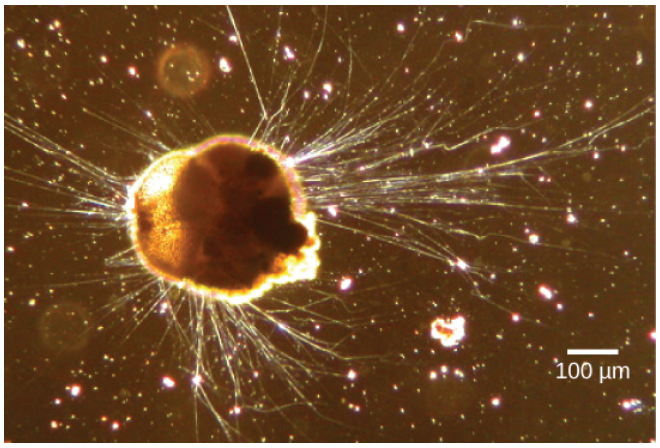


Figure 28.5.13: *Ammonia tepida*, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia. (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

Link to Learning



Take a look at this video to see cytoplasmic streaming in a green alga.

Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails (Figure 28.5.14). As a group, the forams exhibit porous shells, called tests that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.

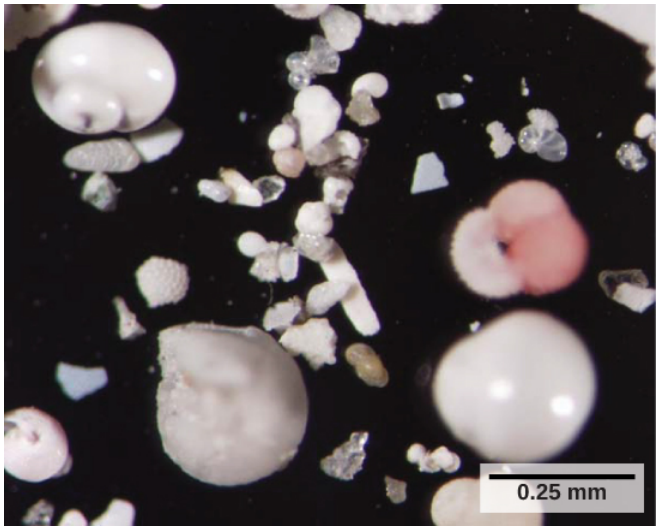


Figure 28.5.14: These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER)

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry (Figure 28.5.15). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

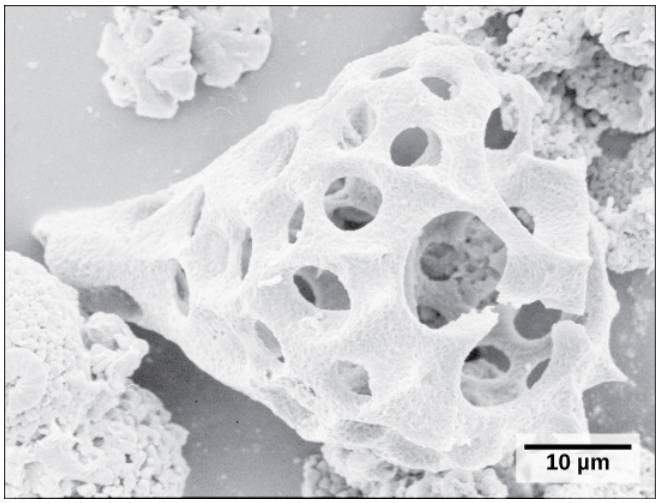


Figure 28.5.15: This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism (Figure 28.5.16). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



Figure **28.5.16**: *Volvox aureus* is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters (Figure **28.5.17**). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure **28.5.17**: *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Amoebozoa

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba (Figure **28.5.18**). The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.

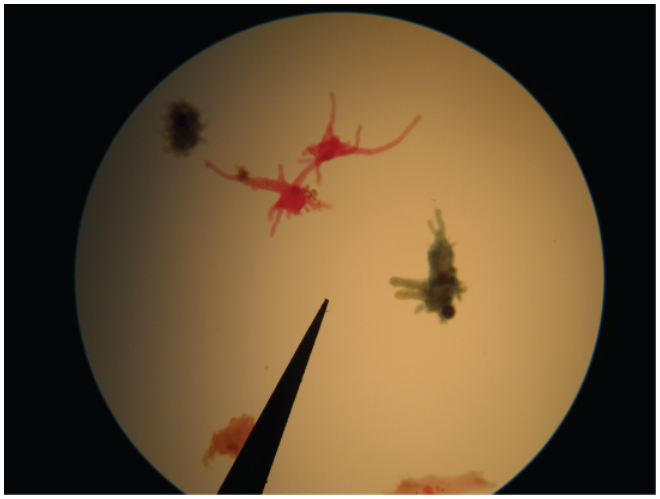


Figure **28.5.18**: Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage (Figure **28.5.19**). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

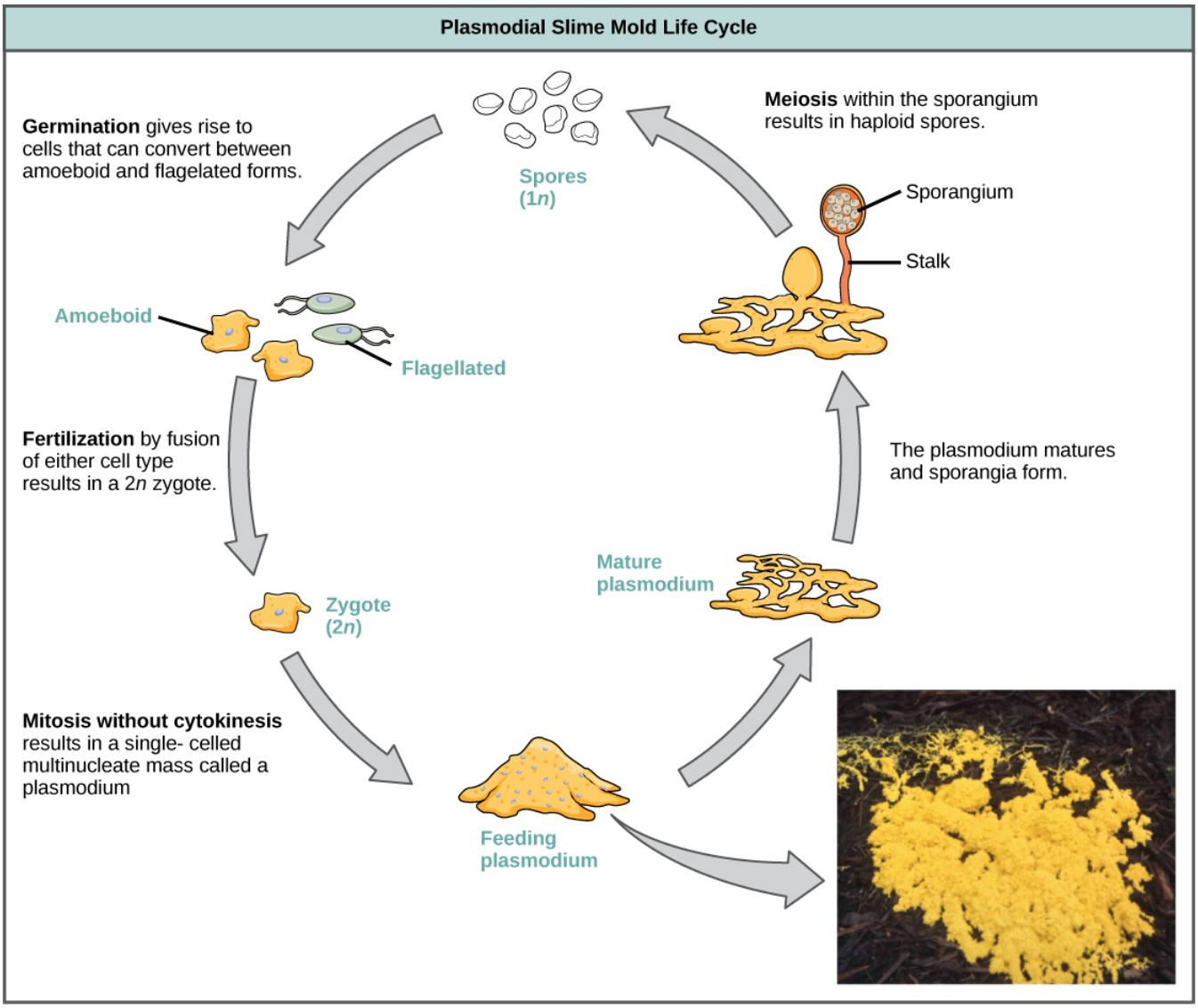


Figure 28.5.19: The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant (Figure 28.5.20). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

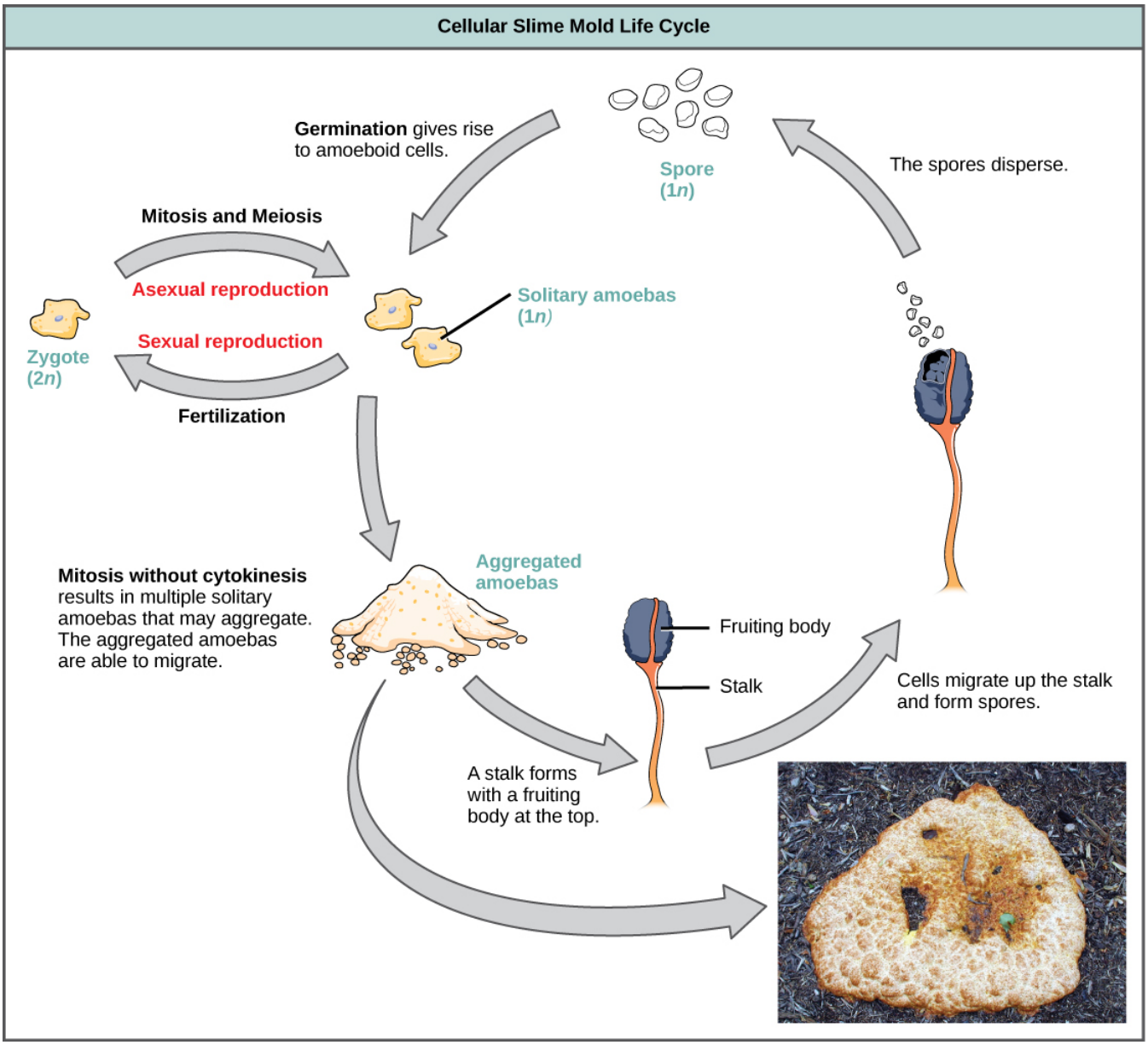


Figure **28.5.20**: Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

Link to Learning

https://bio.libretexts.org/@go/page/74272



View this site to see the formation of a fruiting body by a cellular slime mold.

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

The Mesomycetozoa form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood. These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology.

Summary

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Amoebozoa, and Opisthokonta. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor. At present, the monophyly of some of the supergroups are better supported by genetic data than others. Although tremendous variation exists within the supergroups, commonalities at the morphological, physiological, and ecological levels can be identified.

Art Connections

Figure **28.5.8**: Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronuclei.
D. Each parent produces four daughter cells.

Answer

C

Figure **28.5.11**: Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.

B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

Answer

C

Glossary

biological carbon pump
process by which inorganic carbon is fixed by photosynthetic species that then die and fall to the sea floor where they cannot be reached by saprobes and their carbon dioxide consumption cannot be returned to the atmosphere

bioluminescence
generation and emission of light by an organism, as in dinoflagellates

contractile vacuole
vesicle that fills with water (as it enters the cell by osmosis) and then contracts to squeeze water from the cell; an osmoregulatory vesicle

cytoplasmic streaming
movement of cytoplasm into an extended pseudopod such that the entire cell is transported to the site of the pseudopod

hydrogenosome
organelle carried by parabasalids (Excavata) that functions anaerobically and outputs hydrogen gas as a byproduct; likely evolved from mitochondria

kinetoplast
mass of DNA carried within the single, oversized mitochondrion, characteristic of kinetoplastids (phylum: Euglenozoa)

mitosome
nonfunctional organelle carried in the cells of diplomonads (Excavata) that likely evolved from a mitochondrion

plankton
diverse group of mostly microscopic organisms that drift in marine and freshwater systems and serve as a food source for larger aquatic organisms

raphe
slit in the silica shell of diatoms through which the protist secretes a stream of mucopolysaccharides for locomotion and attachment to substrates

test
porous shell of a foram that is built from various organic materials and typically hardened with calcium carbonate

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28.6: Characteristics of Archaeplastidia

Skills to Develop

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called **convergent evolution**, is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six "supergroups" that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor (Figure 28.6.1). The supergroups are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

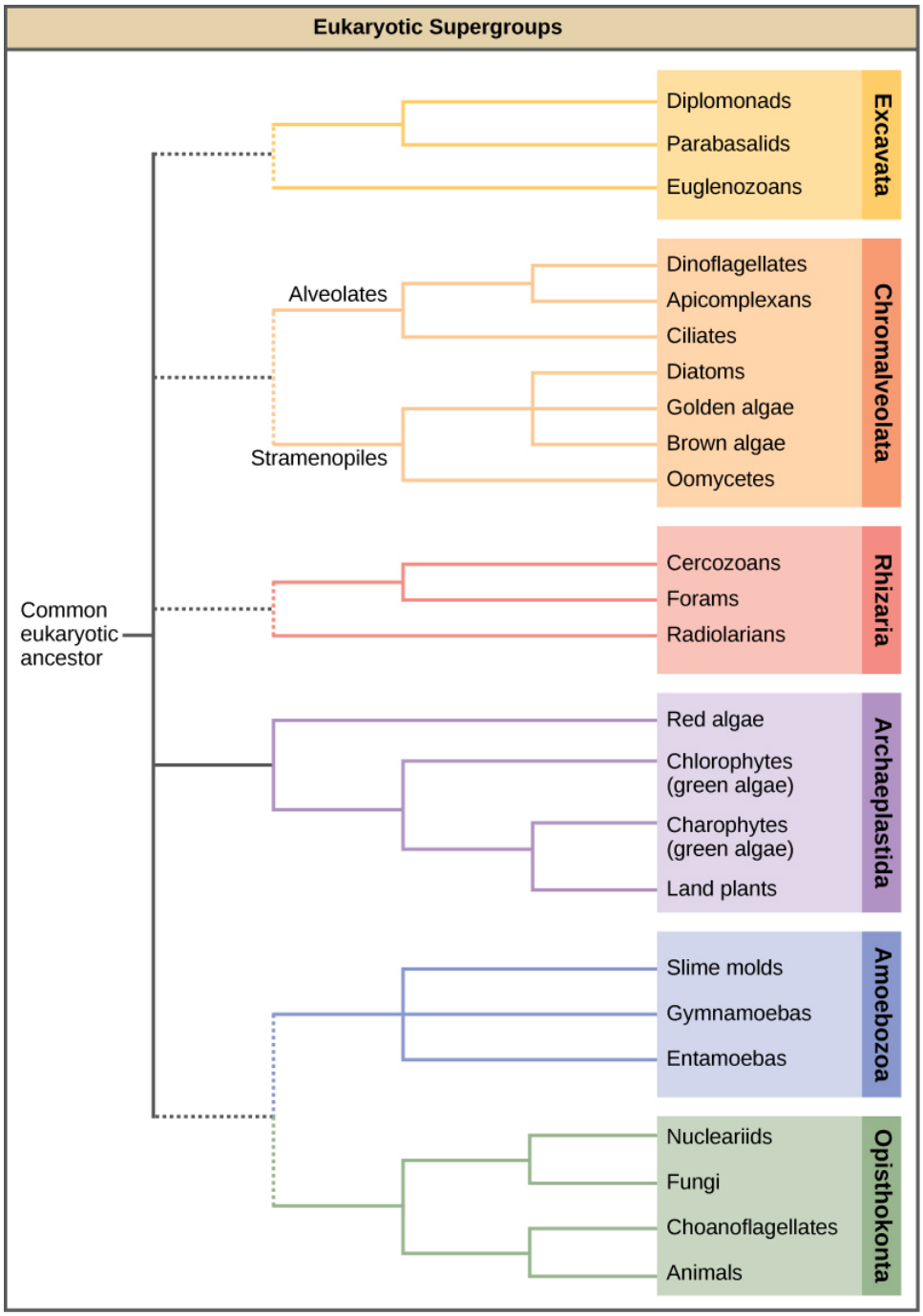


Figure **28.6.1**: This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia* (Figure **28.6.2**). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called mitosomes, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.



Figure **28.6.2**: The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell)

Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called hydrogenosomes because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichamoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the kinetoplast, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human

or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.

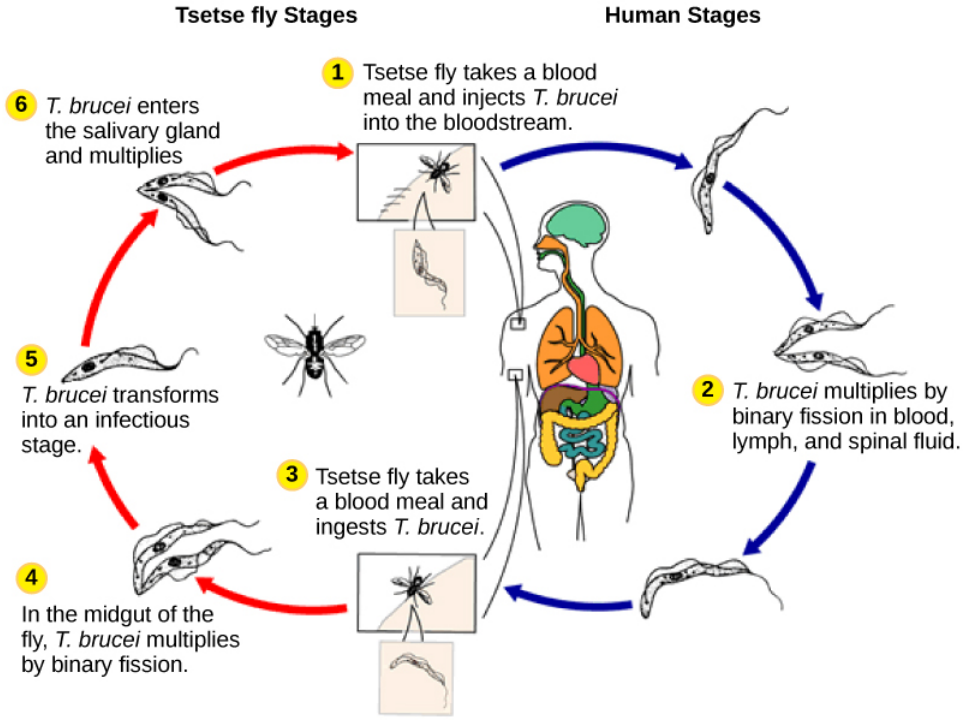


Figure **28.6.3**: *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Trypanosoma brucei



Watch this video to see *T. brucei* swimming. https://youtu.be/EnsydwITLYk

Chromalveolata

Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether.

Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexians, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate (Figure **28.6.4**). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of plankton, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.

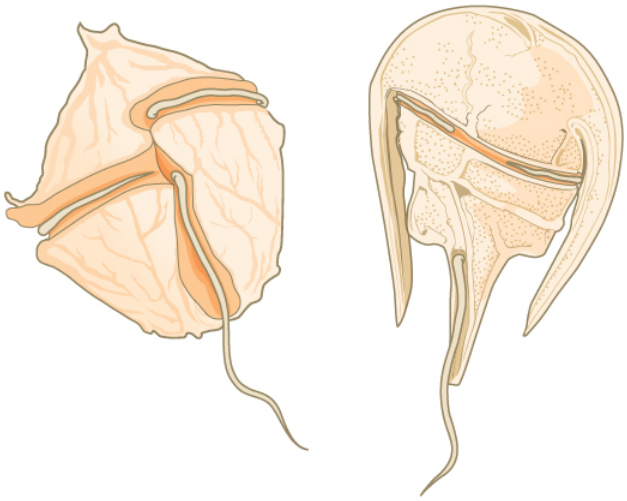


Figure **28.6.4**: The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

Some dinoflagellates generate light, called bioluminescence, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color (Figure **28.6.5**). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



Figure 28.6.5: Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: "catalano82"/Flickr)

The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex (Figure 28.6.6). The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

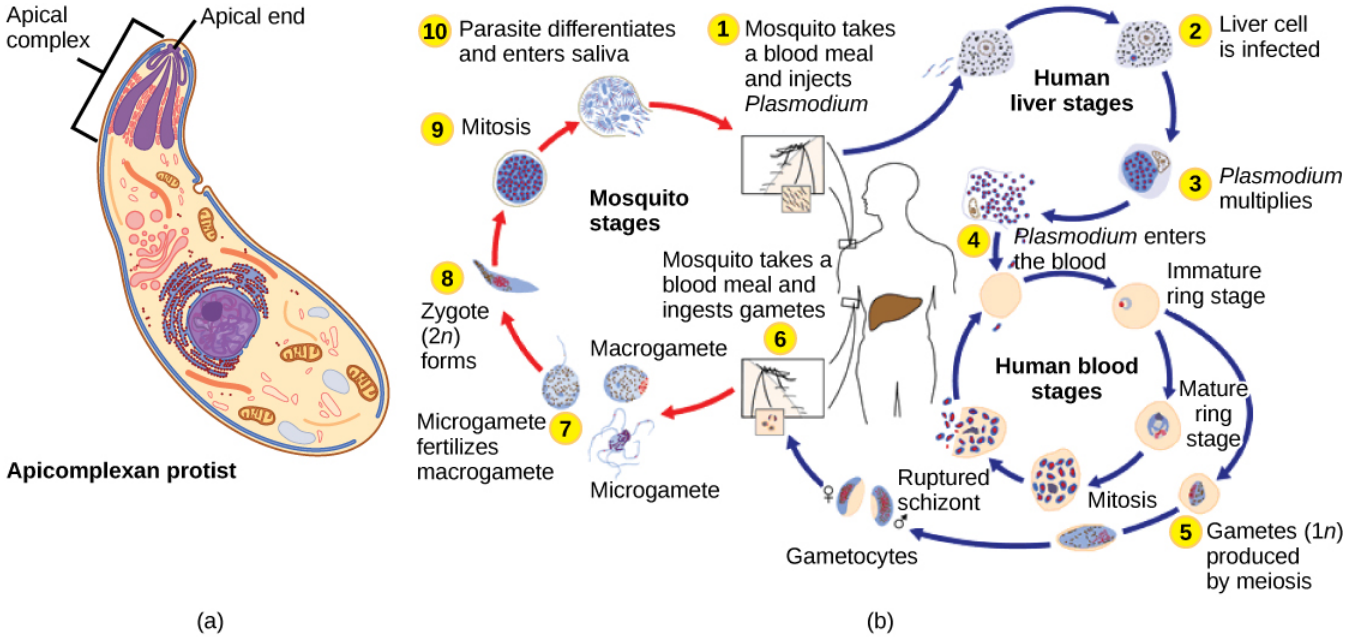


Figure 28.6.6: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria (Figure 28.6.7). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses contractile vacuoles, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.

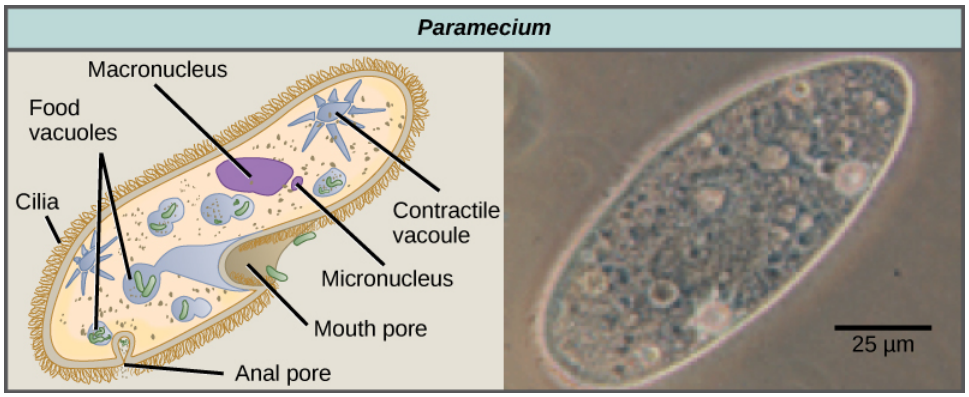
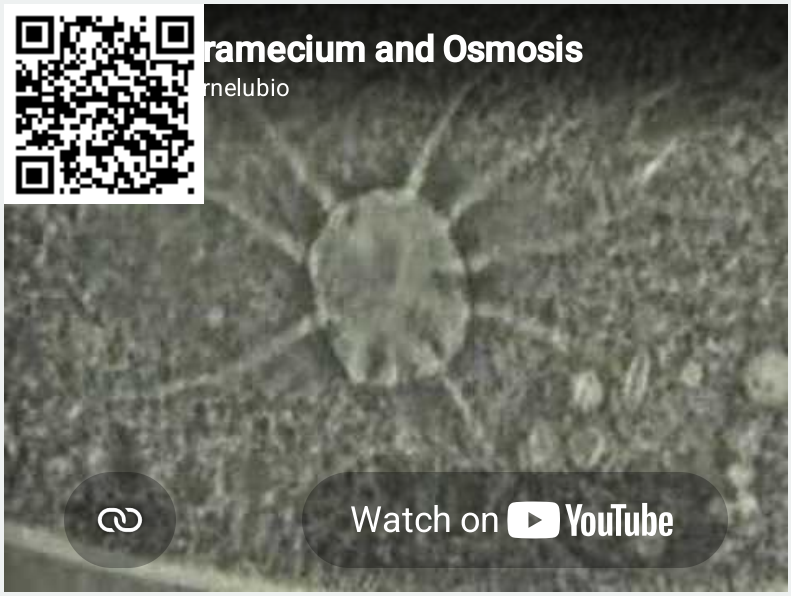


Figure 28.6.7: *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt Russell)

Link to Learning



Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge (Figure 28.6.8). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

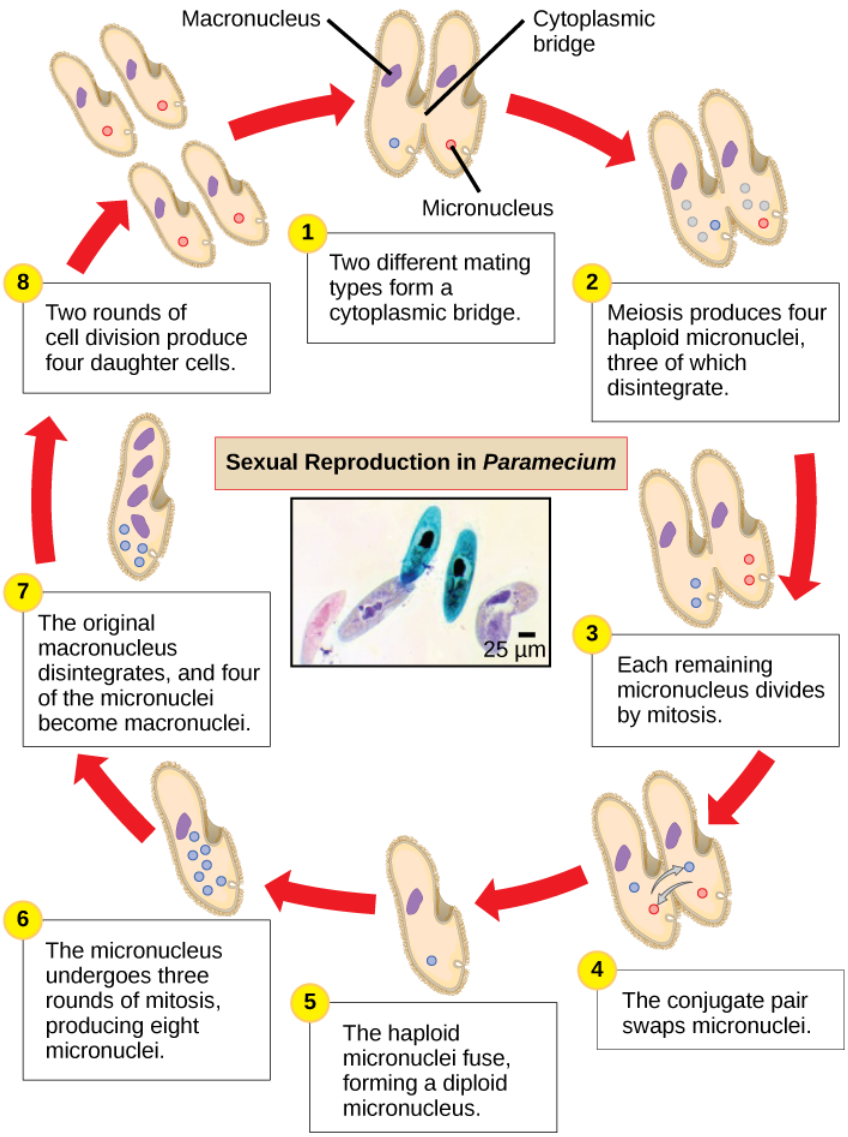


Figure 28.6.8: The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work by Ian Sutton; scale-bar data from Matt Russell)

Exercise

Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronucleii.
D. Each parent produces four daughter cells.

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or "hairy," flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections (Figure 28.6.9). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

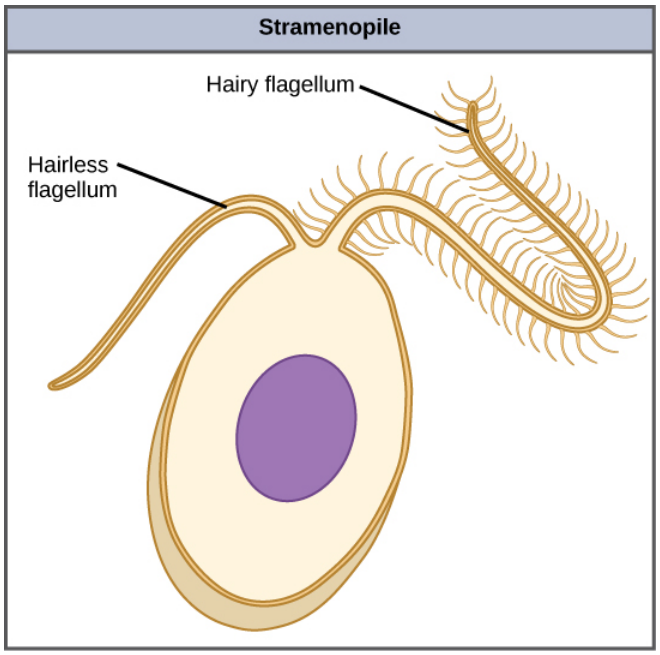


Figure **28.6.9**: This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles (Figure **28.6.10**). These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell, called a raphe. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

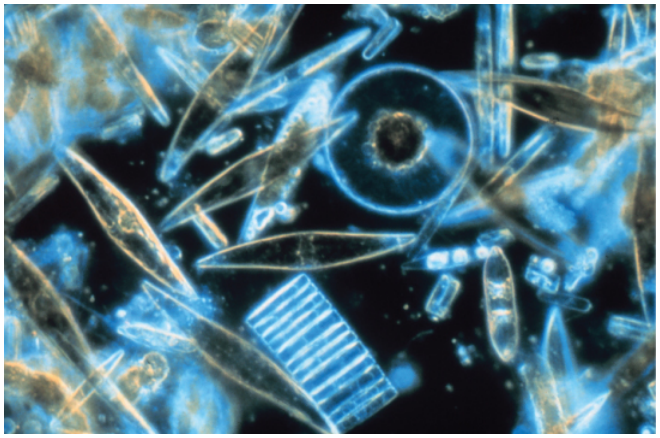


Figure **28.6.10**: Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the biological carbon pump, because carbon is “pumped” to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form (Figure **28.6.11**). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

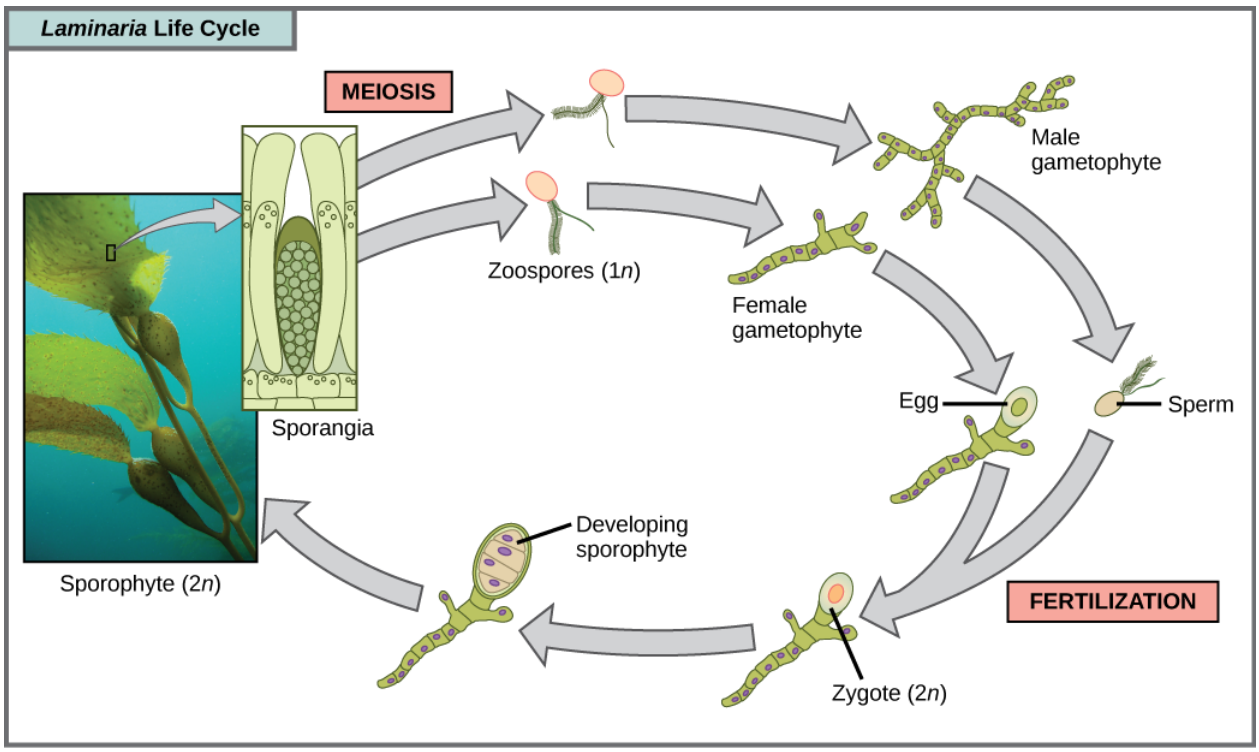


Figure **28.6.11**: Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit "laminaria photograph": modification of work by Claire Fackler, CINMS, NOAA Photo Library)

Exercise

Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.
B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

The water molds, oomycetes ("egg fungus"), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms (Figure **28.6.12**). Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.



Figure 28.6.12: A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (Figure 28.6.13). Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called cytoplasmic streaming, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.

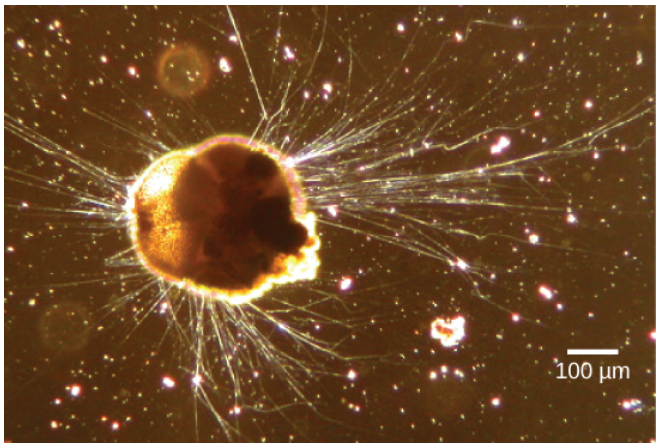


Figure 28.6.13: *Ammonia tepida*, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia. (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

Link to Learning



Take a look at this video to see cytoplasmic streaming in a green alga.

Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails (Figure 28.6.14). As a group, the forams exhibit porous shells, called tests that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.

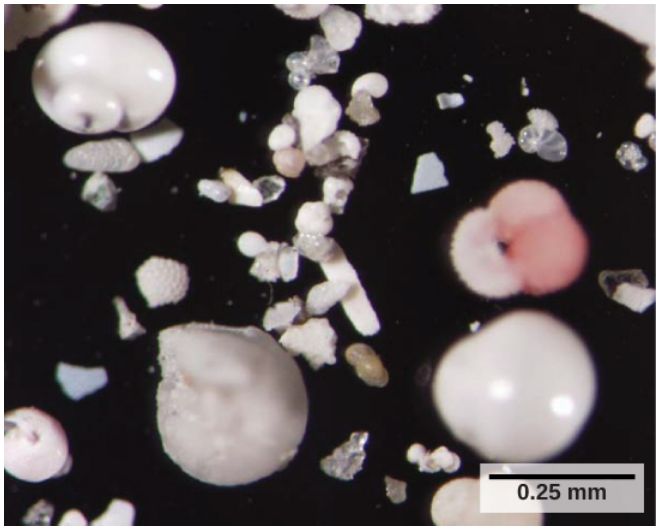


Figure 28.6.14: These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER)

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry (Figure 28.6.15). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

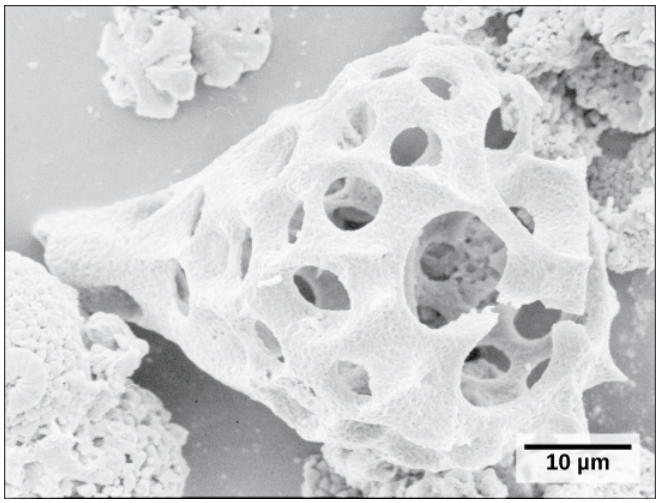


Figure 28.6.15: This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism (Figure 28.6.16). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



Figure **28.6.16**: *Volvox aureus* is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters (Figure **28.6.17**). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure **28.6.17**: *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Amoebozoa

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba (Figure **28.6.18**). The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.

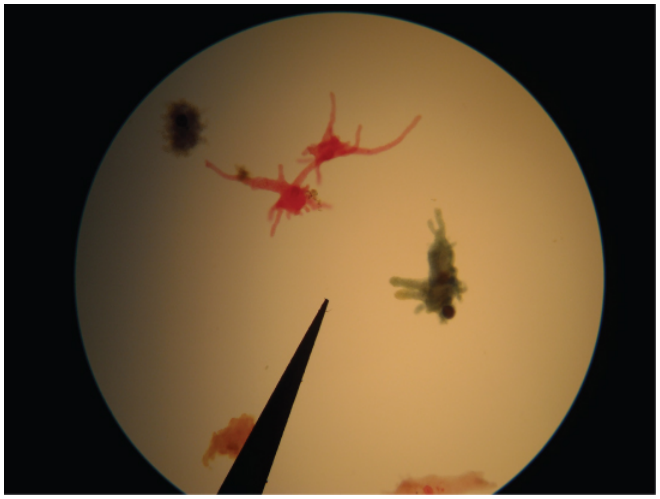


Figure **28.6.18**: Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage (Figure **28.6.19**). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

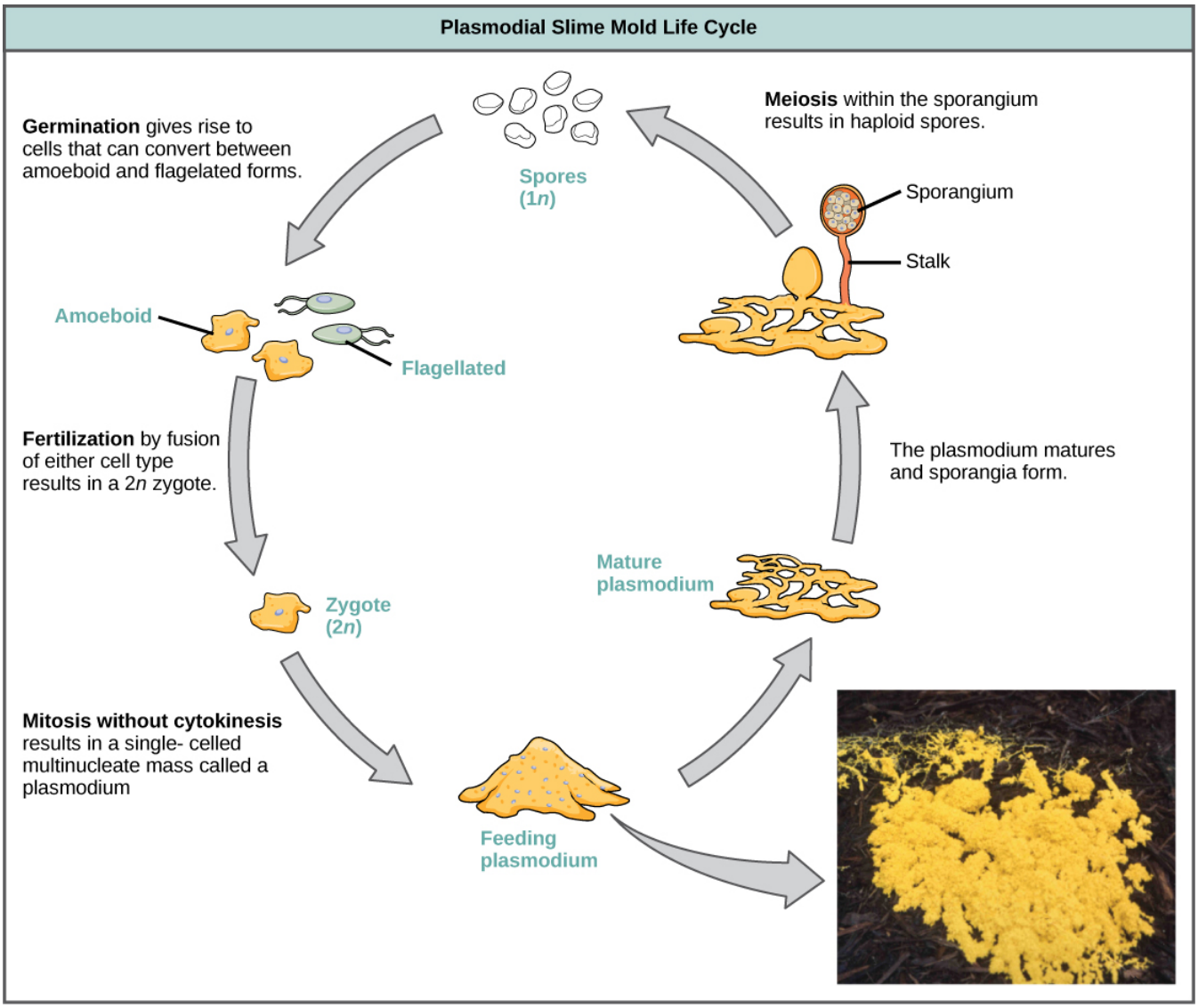


Figure 28.6.19: The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant (Figure 28.6.20). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

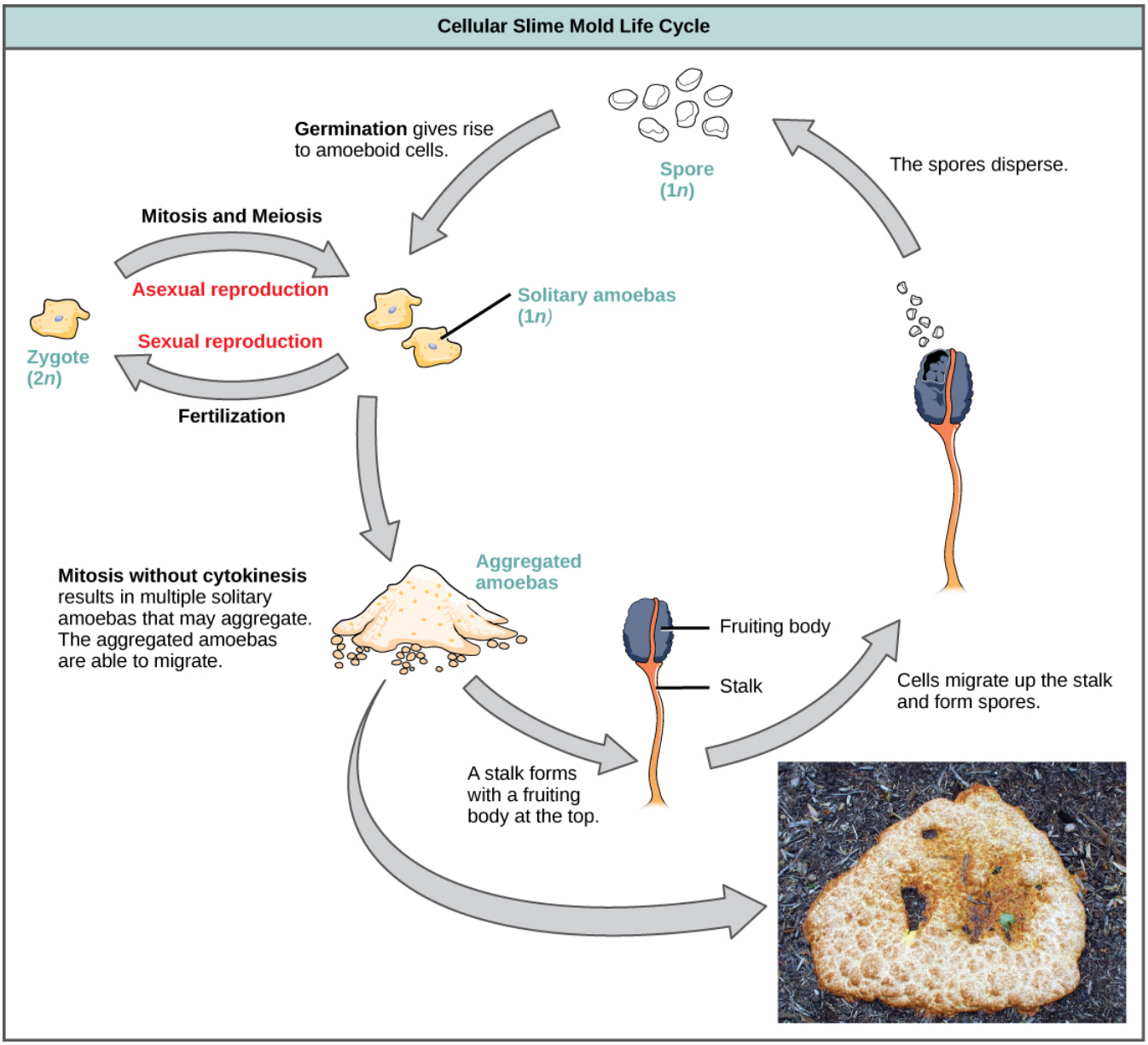


Figure **28.6.20**: Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

Link to Learning



View this site to see the formation of a fruiting body by a cellular slime mold.

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

The Mesomycetozoa form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood. These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology.

Summary

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Amoebozoa, and Opisthokonta. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor. At present, the monophyly of some of the supergroups are better supported by genetic data than others. Although tremendous variation exists within the supergroups, commonalities at the morphological, physiological, and ecological levels can be identified.

Art Connections

Figure **28.6.8**: Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronuclei.
D. Each parent produces four daughter cells.

Answer

C

Figure **28.6.11**: Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.

B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

Answer

C

Glossary

biological carbon pump
process by which inorganic carbon is fixed by photosynthetic species that then die and fall to the sea floor where they cannot be reached by saprobes and their carbon dioxide consumption cannot be returned to the atmosphere

bioluminescence
generation and emission of light by an organism, as in dinoflagellates

contractile vacuole
vesicle that fills with water (as it enters the cell by osmosis) and then contracts to squeeze water from the cell; an osmoregulatory vesicle

cytoplasmic streaming
movement of cytoplasm into an extended pseudopod such that the entire cell is transported to the site of the pseudopod

hydrogenosome
organelle carried by parabasalids (Excavata) that functions anaerobically and outputs hydrogen gas as a byproduct; likely evolved from mitochondria

kinetoplast
mass of DNA carried within the single, oversized mitochondrion, characteristic of kinetoplastids (phylum: Euglenozoa)

mitosome
nonfunctional organelle carried in the cells of diplomonads (Excavata) that likely evolved from a mitochondrion

plankton
diverse group of mostly microscopic organisms that drift in marine and freshwater systems and serve as a food source for larger aquatic organisms

raphe
slit in the silica shell of diatoms through which the protist secretes a stream of mucopolysaccharides for locomotion and attachment to substrates

test
porous shell of a foram that is built from various organic materials and typically hardened with calcium carbonate

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28.7: Characteristics of Amoebozoa

Skills to Develop

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called **convergent evolution**, is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six "supergroups" that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor (Figure 28.7.1). The supergroups are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

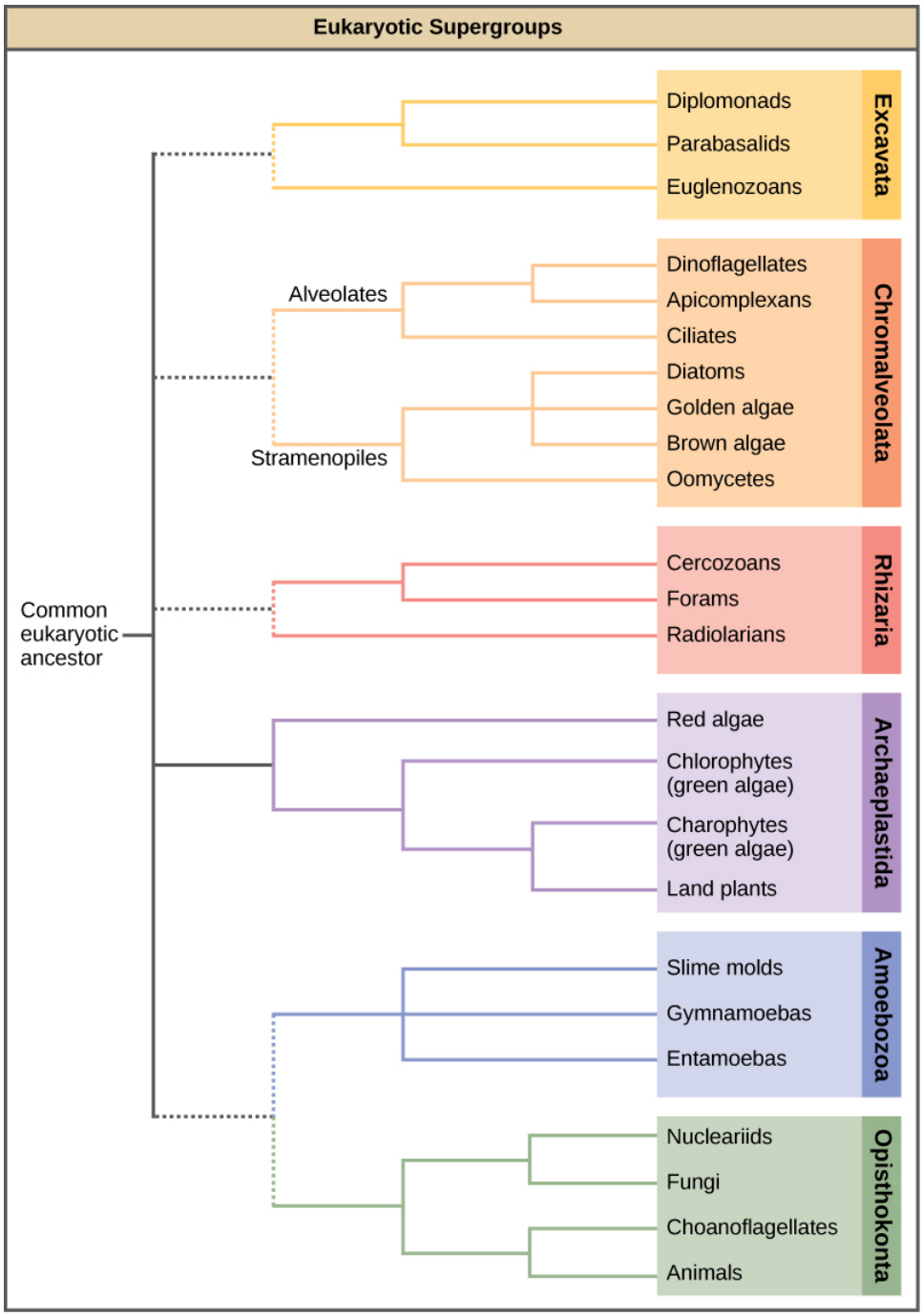


Figure **28.7.1**: This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia* (Figure **28.7.2**). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called mitosomes, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.



Figure **28.7.2**: The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell)

Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called hydrogenosomes because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichamoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the kinetoplast, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human

or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.

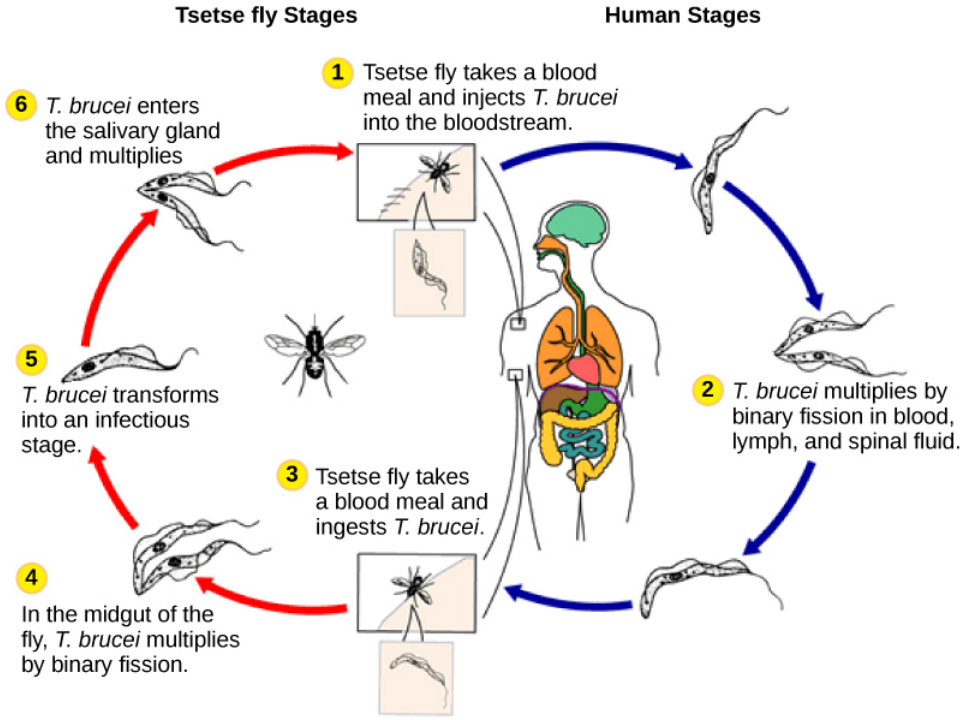


Figure **28.7.3**: *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Trypanosoma brucei



Watch this video to see *T. brucei* swimming. https://youtu.be/EnsydwITLYk

Chromalveolata

Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether.

Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexians, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate (Figure **28.7.4**). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of plankton, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.

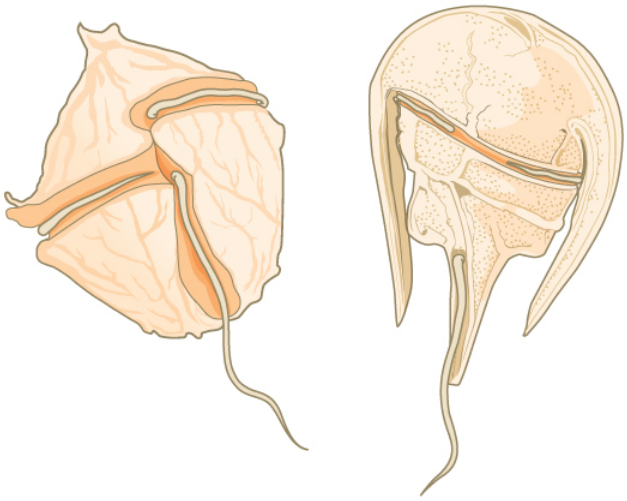


Figure **28.7.4**: The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

Some dinoflagellates generate light, called bioluminescence, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color (Figure **28.7.5**). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



Figure 28.7.5: Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: "catalano82"/Flickr)

The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex (Figure 28.7.6). The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

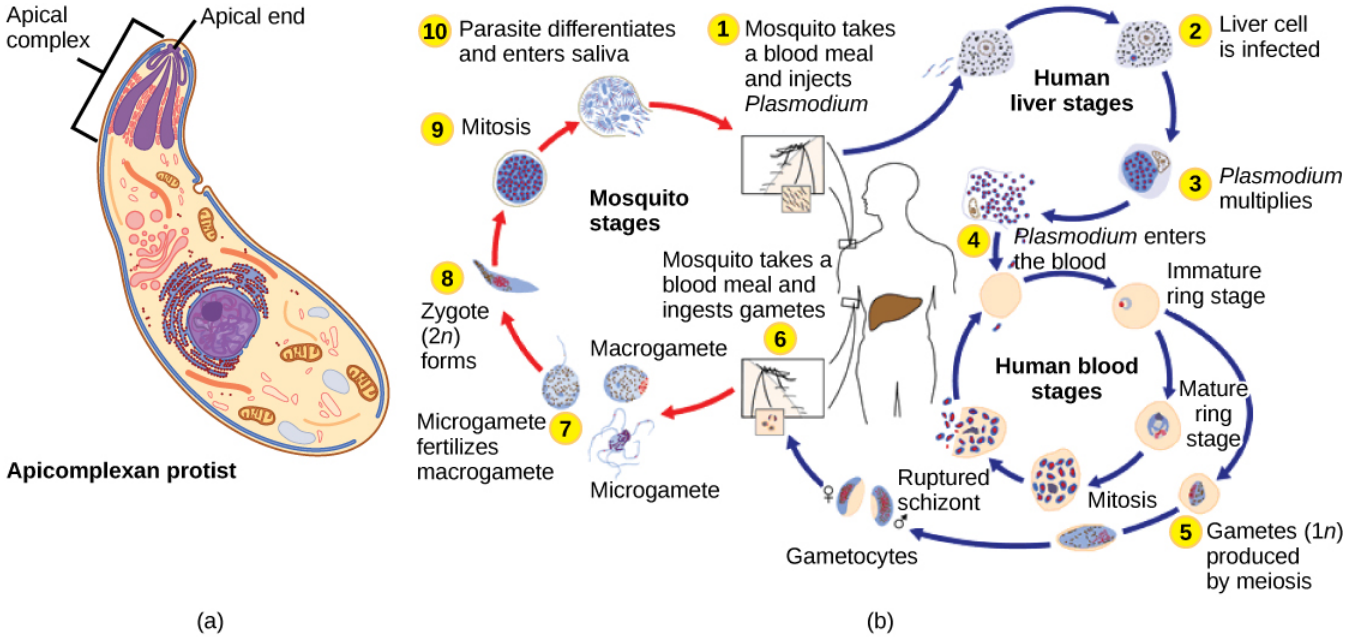


Figure 28.7.6: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria (Figure 28.7.7). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses contractile vacuoles, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.

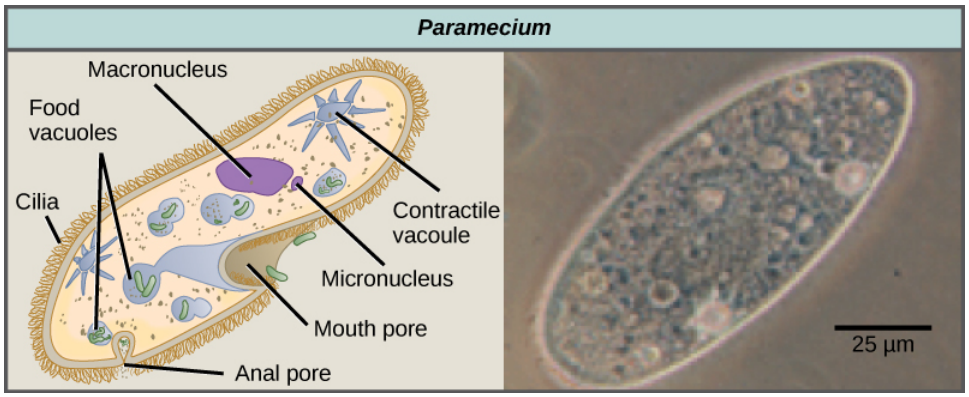
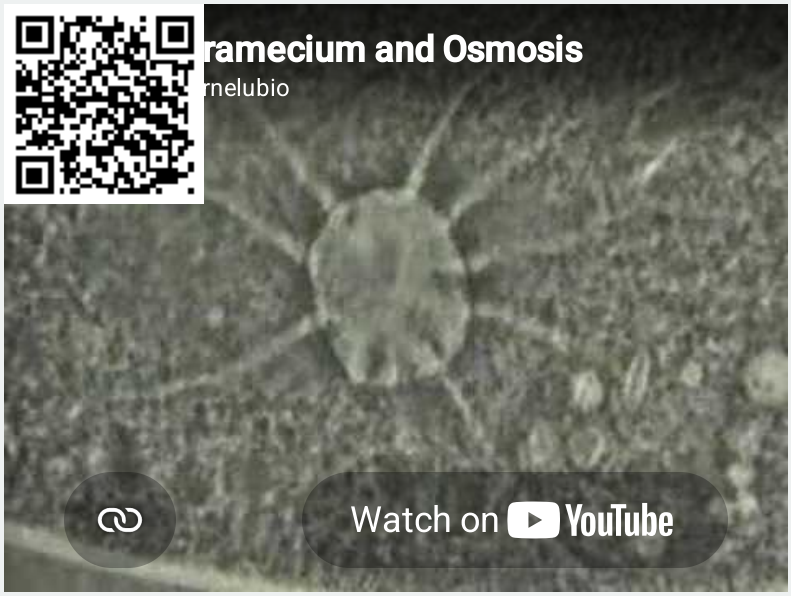


Figure 28.7.7: *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt Russell)

Link to Learning



Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge (Figure 28.7.8). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

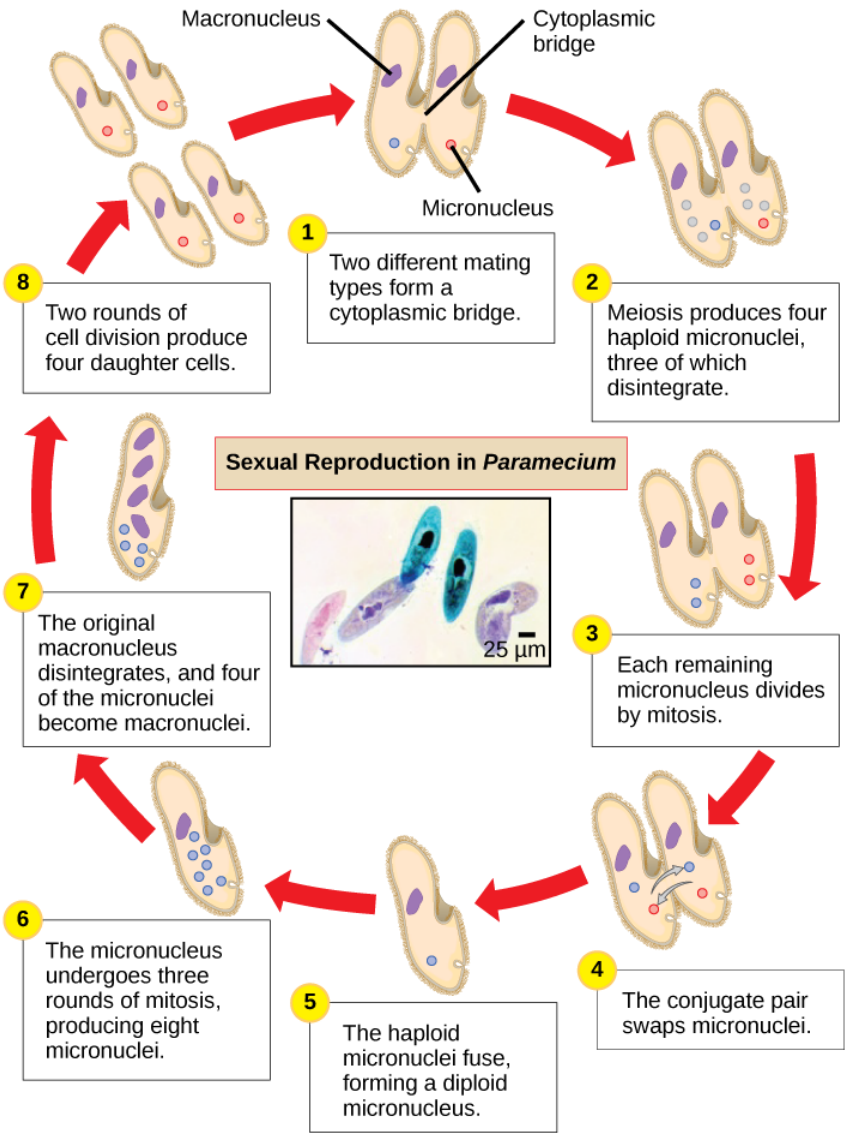


Figure 28.7.8: The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work by Ian Sutton; scale-bar data from Matt Russell)

Exercise

Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronucleii.
D. Each parent produces four daughter cells.

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or "hairy," flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections (Figure 28.7.9). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

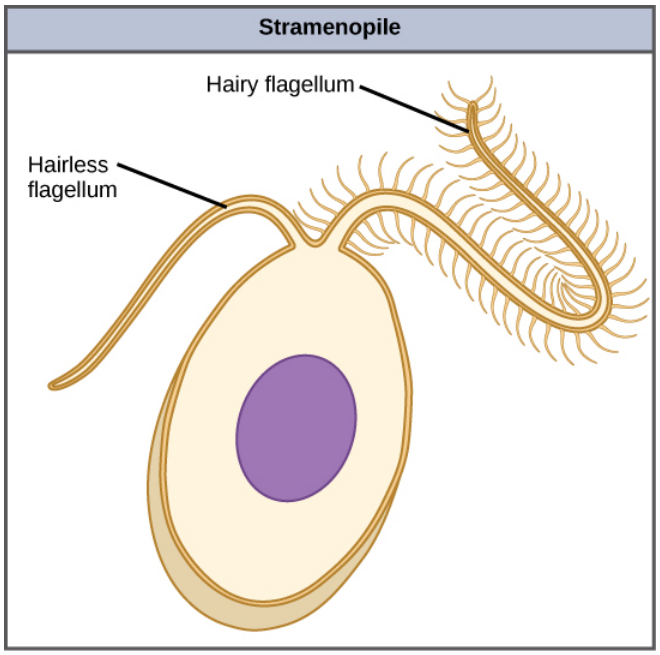


Figure **28.7.9**: This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles (Figure **28.7.10**). These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell, called a raphe. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

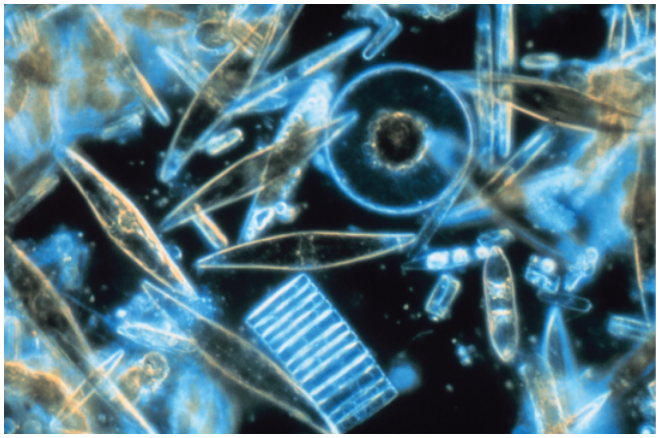


Figure **28.7.10**: Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the biological carbon pump, because carbon is “pumped” to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form (Figure **28.7.11**). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

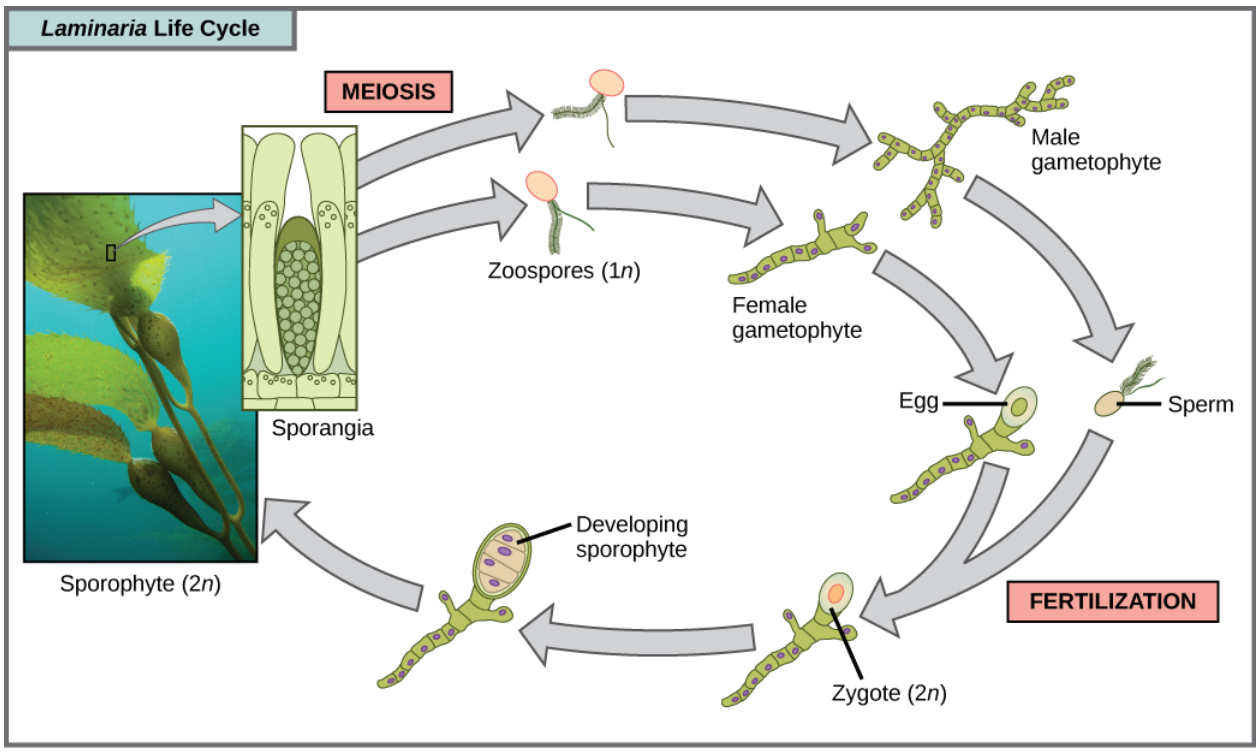


Figure **28.7.11**: Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit "laminaria photograph": modification of work by Claire Fackler, CINMS, NOAA Photo Library)

Exercise

Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.
B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

The water molds, oomycetes ("egg fungus"), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms (Figure **28.7.12**). Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.



Figure 28.7.12: A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (Figure 28.7.13). Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called cytoplasmic streaming, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.

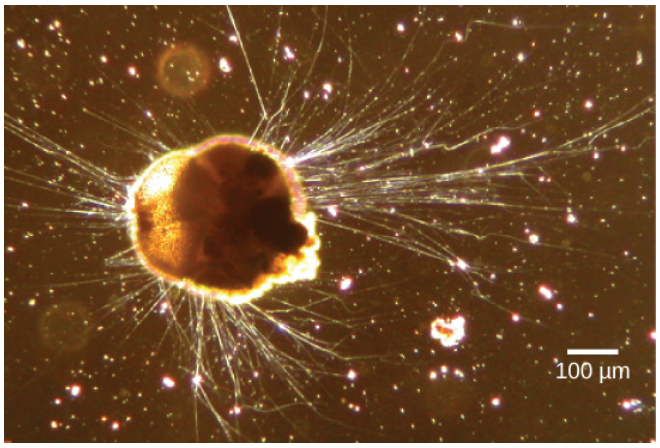


Figure 28.7.13: *Ammonia tepida*, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia. (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

Link to Learning



Take a look at this video to see cytoplasmic streaming in a green alga.

Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails (Figure 28.7.14). As a group, the forams exhibit porous shells, called tests that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.

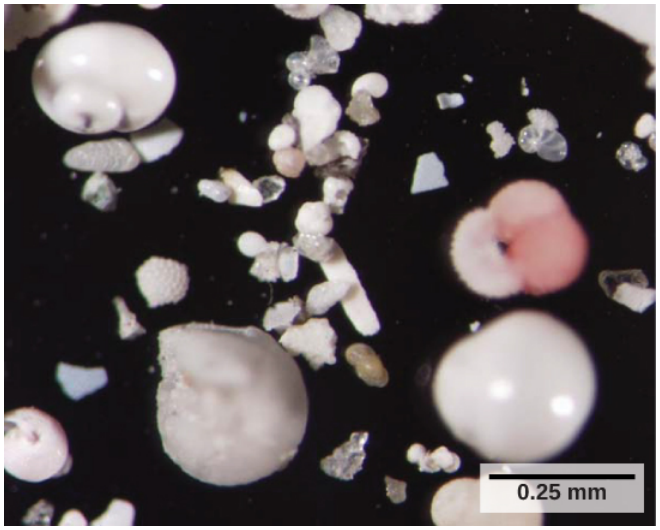


Figure 28.7.14: These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER)

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry (Figure 28.7.15). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

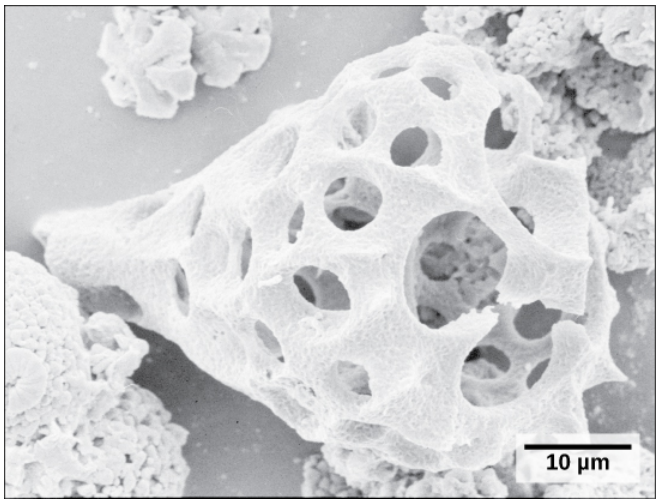


Figure 28.7.15: This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism (Figure 28.7.16). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



Figure **28.7.16**: *Volvox aureus* is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters (Figure **28.7.17**). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure **28.7.17**: *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Amoebozoa

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba (Figure **28.7.18**). The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.

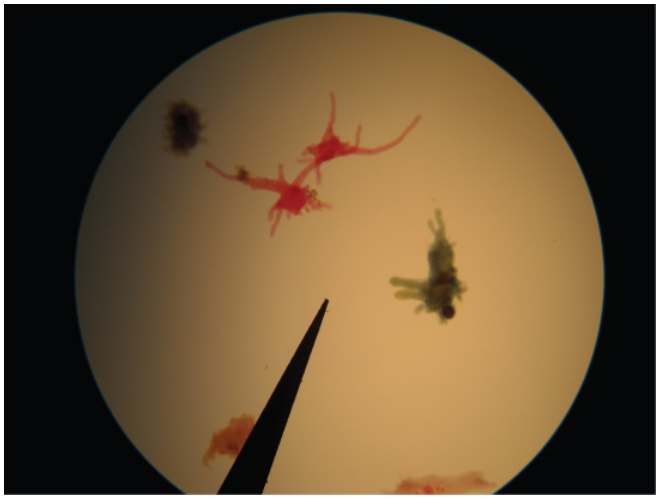


Figure **28.7.18**: Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage (Figure **28.7.19**). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

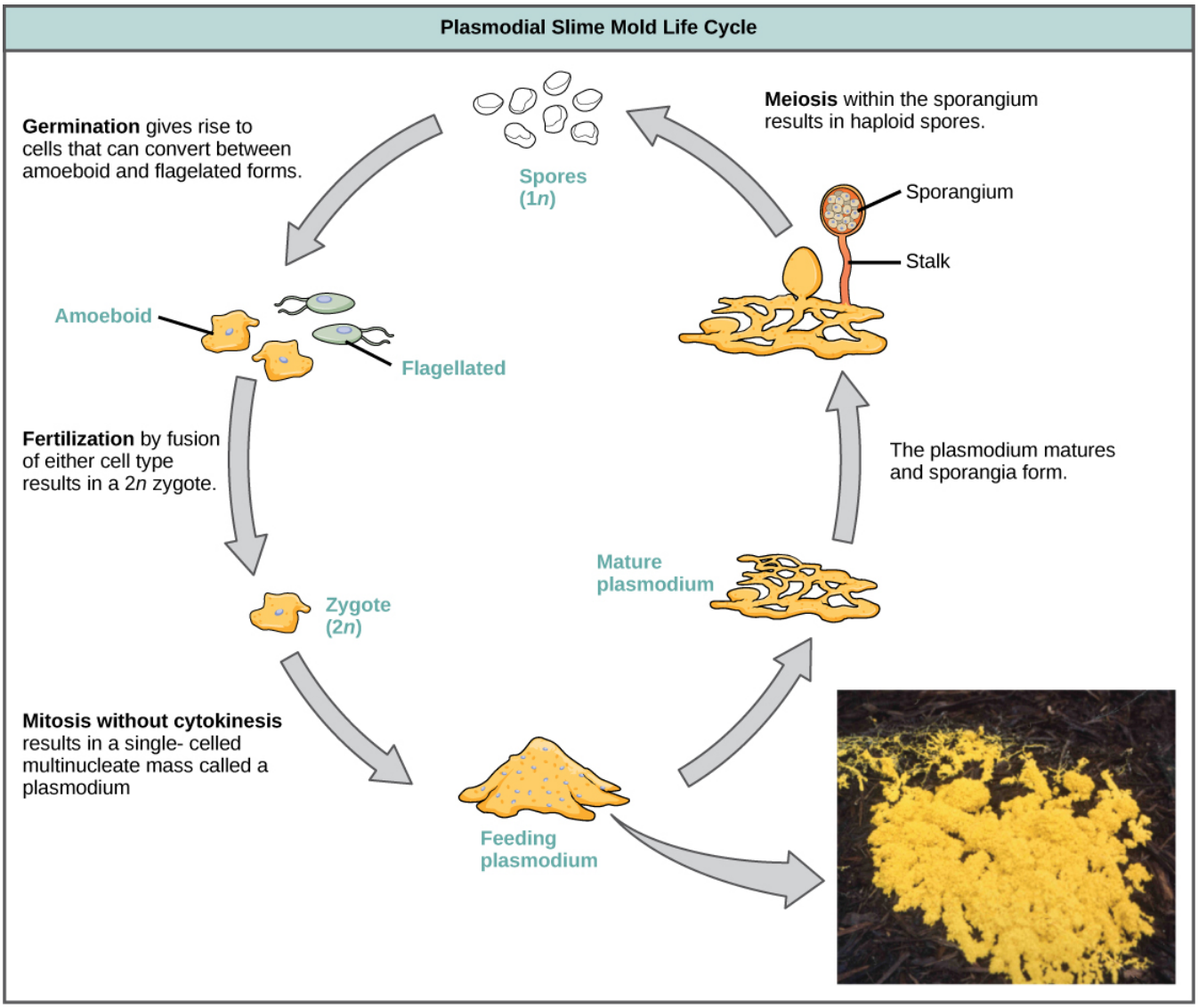


Figure **28.7.19**: The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant (Figure **28.7.20**). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

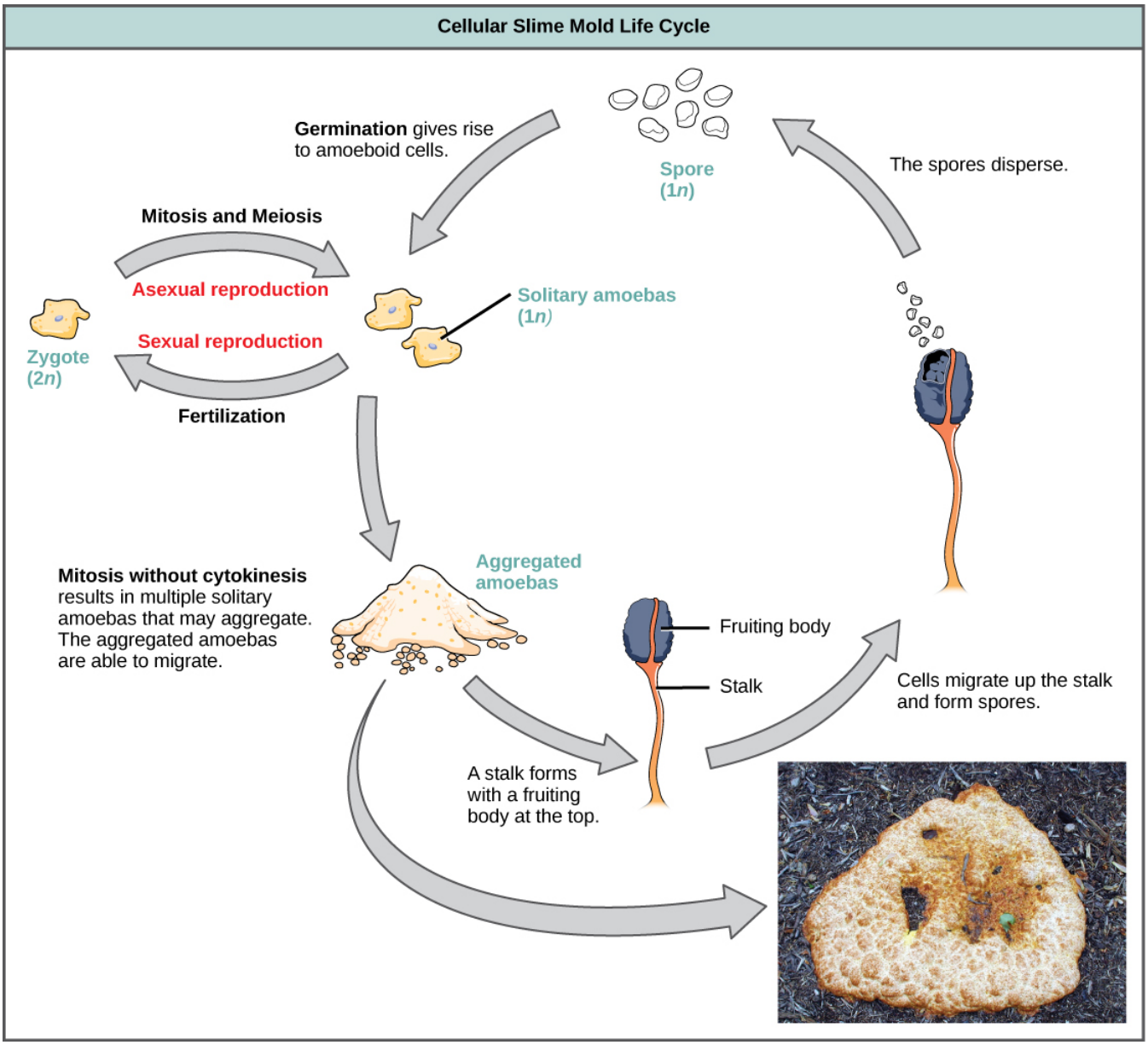


Figure **28.7.20**: Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

Link to Learning

https://bio.libretexts.org/@go/page/74274



View this site to see the formation of a fruiting body by a cellular slime mold.

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

The Mesomycetozoa form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood. These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology.

Summary

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Amoebozoa, and Opisthokonta. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor. At present, the monophyly of some of the supergroups are better supported by genetic data than others. Although tremendous variation exists within the supergroups, commonalities at the morphological, physiological, and ecological levels can be identified.

Art Connections

Figure **28.7.8**: Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronuclei.
D. Each parent produces four daughter cells.

Answer

C

Figure **28.7.11**: Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.

B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

Answer

C

Glossary

biological carbon pump
process by which inorganic carbon is fixed by photosynthetic species that then die and fall to the sea floor where they cannot be reached by saprobes and their carbon dioxide consumption cannot be returned to the atmosphere

bioluminescence
generation and emission of light by an organism, as in dinoflagellates

contractile vacuole
vesicle that fills with water (as it enters the cell by osmosis) and then contracts to squeeze water from the cell; an osmoregulatory vesicle

cytoplasmic streaming
movement of cytoplasm into an extended pseudopod such that the entire cell is transported to the site of the pseudopod

hydrogenosome
organelle carried by parabasalids (Excavata) that functions anaerobically and outputs hydrogen gas as a byproduct; likely evolved from mitochondria

kinetoplast
mass of DNA carried within the single, oversized mitochondrion, characteristic of kinetoplastids (phylum: Euglenozoa)

mitosome
nonfunctional organelle carried in the cells of diplomonads (Excavata) that likely evolved from a mitochondrion

plankton
diverse group of mostly microscopic organisms that drift in marine and freshwater systems and serve as a food source for larger aquatic organisms

raphe
slit in the silica shell of diatoms through which the protist secretes a stream of mucopolysaccharides for locomotion and attachment to substrates

test
porous shell of a foram that is built from various organic materials and typically hardened with calcium carbonate

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28.8: Characteristics of Opisthokonta

Skills to Develop

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called **convergent evolution**, is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six "supergroups" that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor (Figure 28.8.1). The supergroups are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

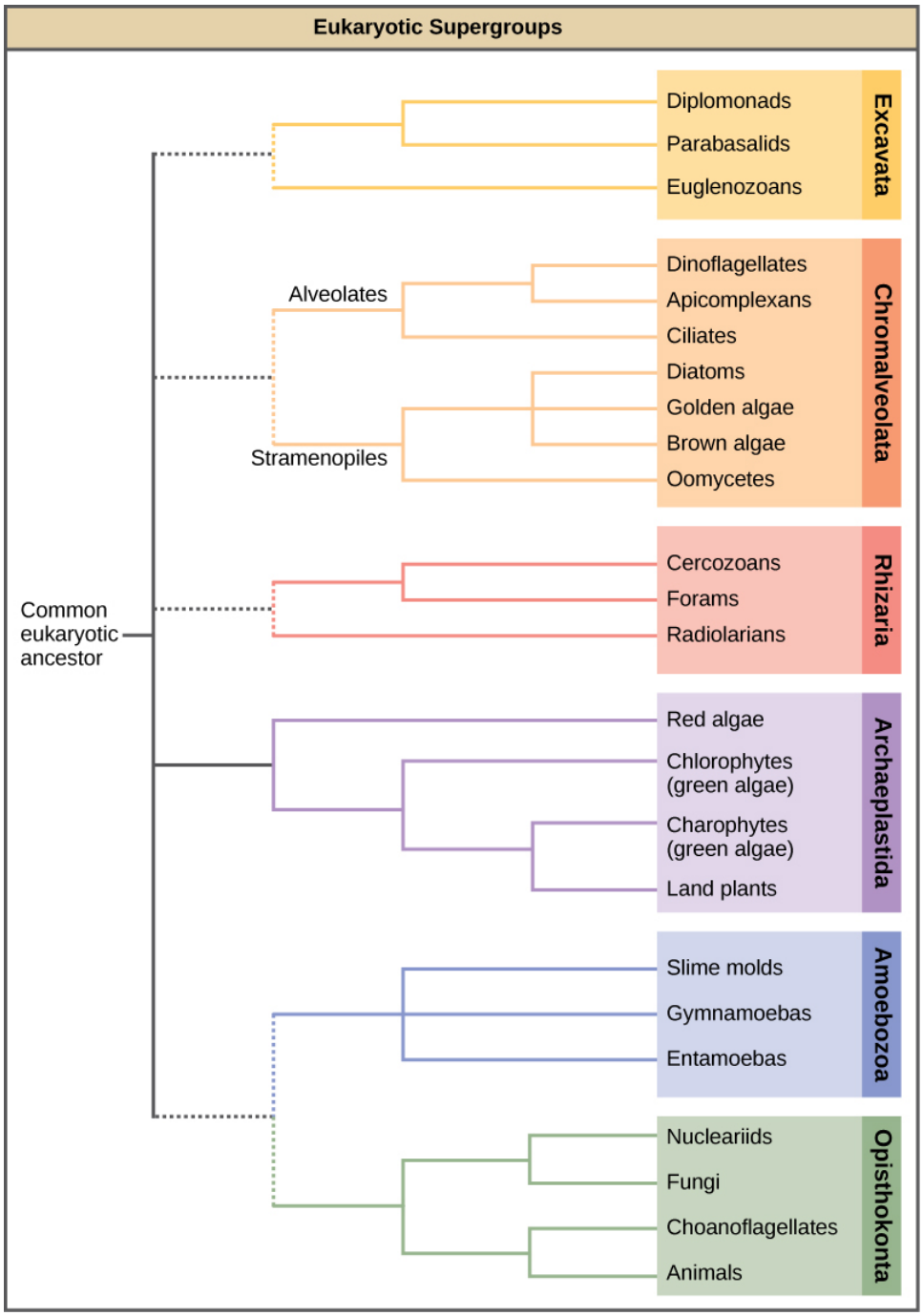


Figure **28.8.1**: This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia* (Figure **28.8.2**). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called mitosomes, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.



Figure **28.8.2**: The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell)

Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called hydrogenosomes because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichamoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the kinetoplast, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human

or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.

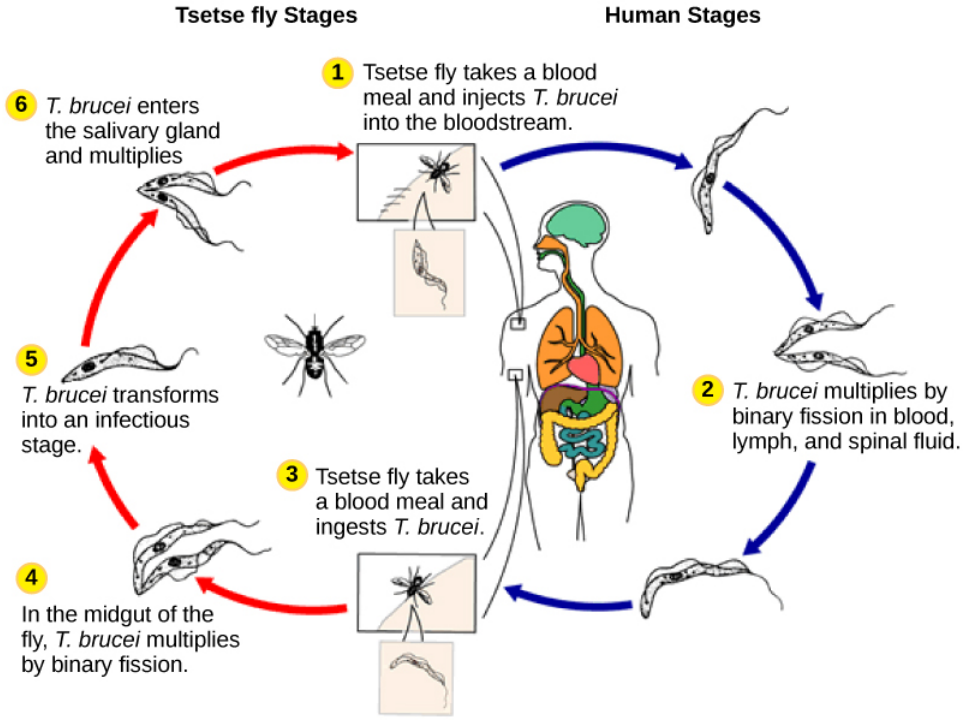


Figure **28.8.3**: *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Trypanosoma brucei



Watch this video to see *T. brucei* swimming. https://youtu.be/EnsydwITLYk

Chromalveolata

Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether.

Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexians, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate (Figure **28.8.4**). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of plankton, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.

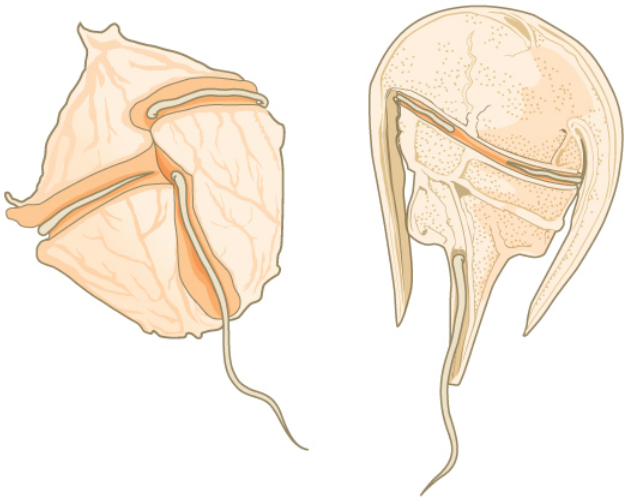


Figure **28.8.4**: The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

Some dinoflagellates generate light, called bioluminescence, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color (Figure **28.8.5**). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



Figure 28.8.5: Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: "catalano82"/Flickr)

The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex (Figure 28.8.6). The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

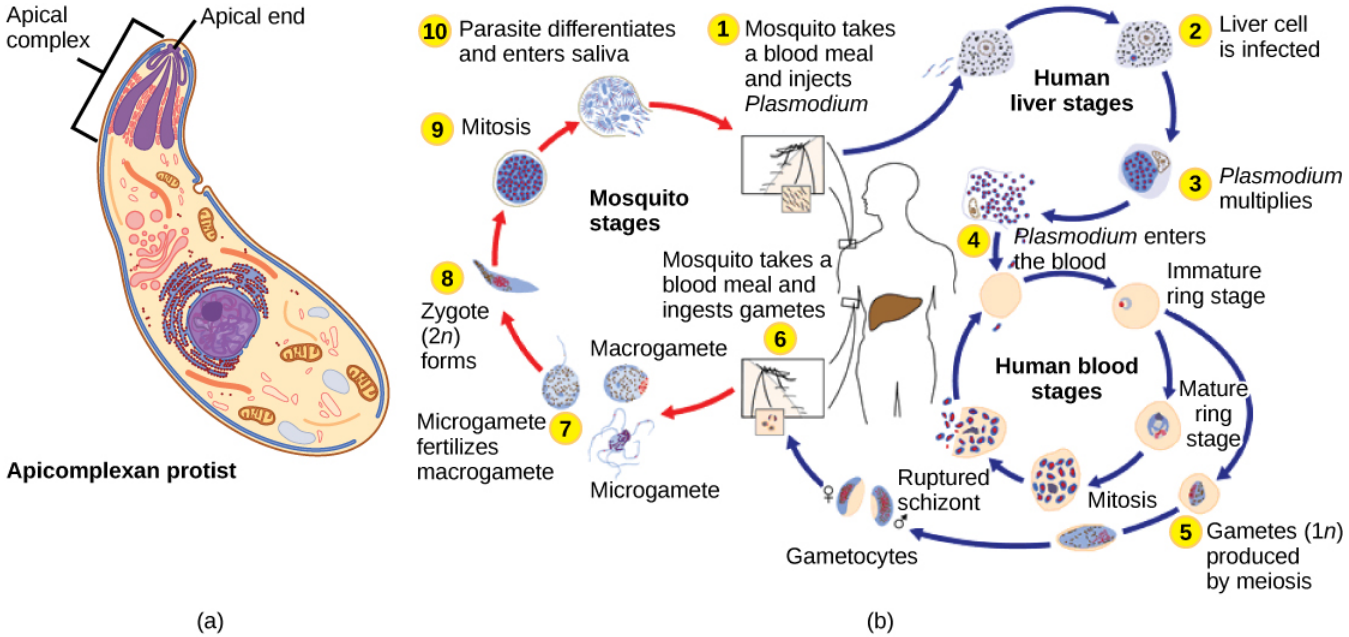


Figure 28.8.6: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria (Figure 28.8.7). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses contractile vacuoles, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.

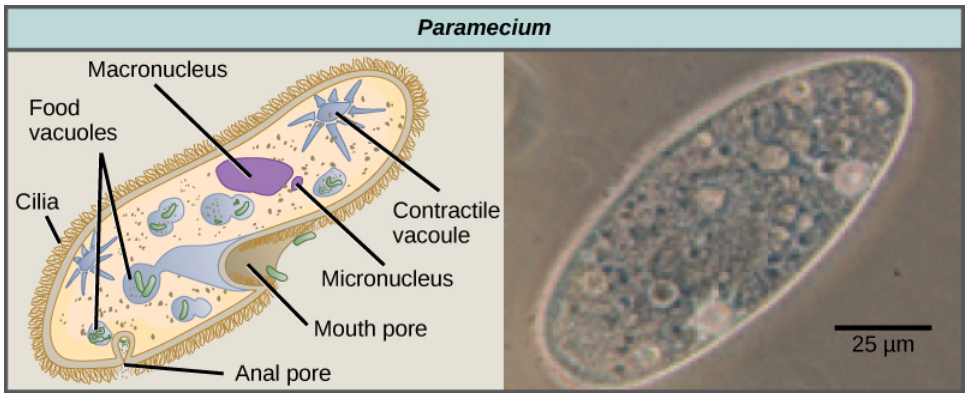
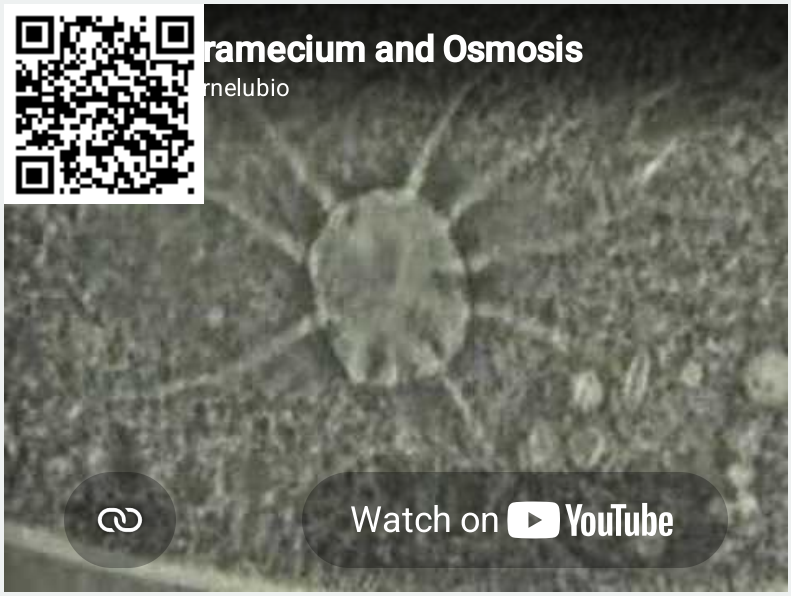


Figure 28.8.7: *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt Russell)

Link to Learning



Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge (Figure 28.8.8). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

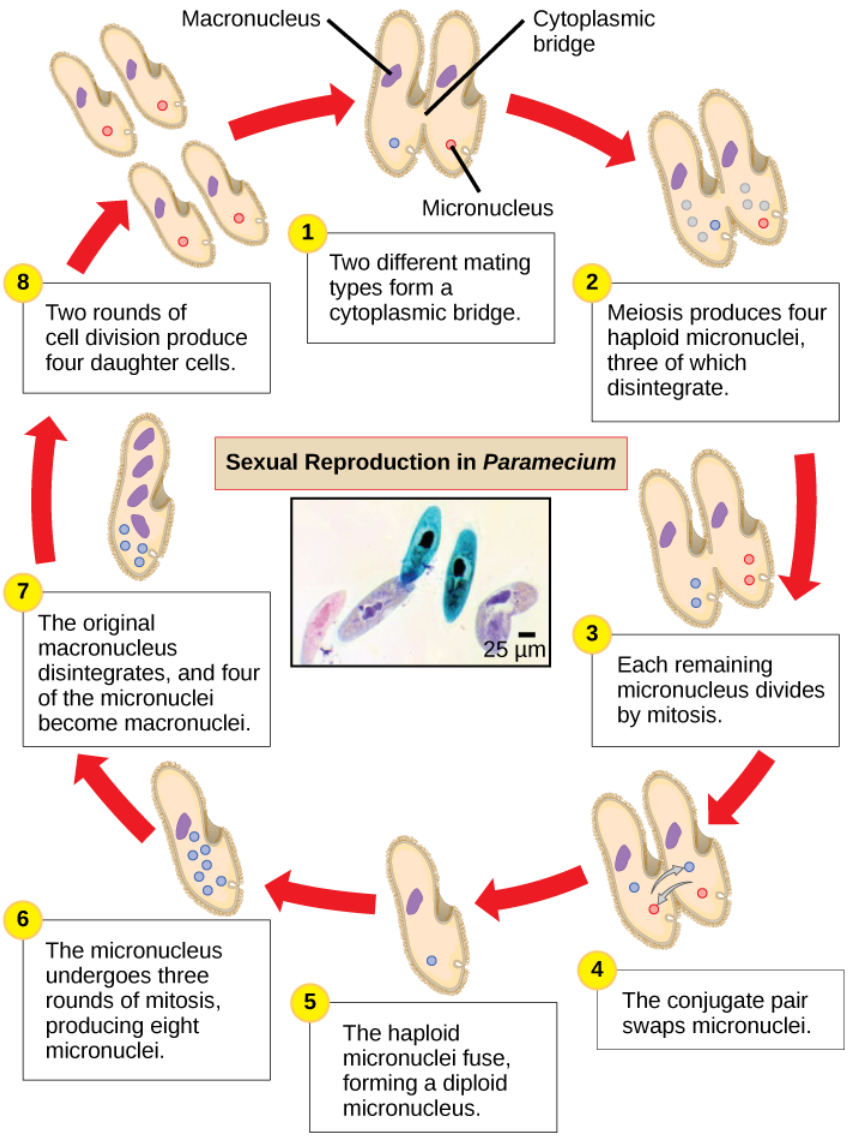


Figure 28.8.8: The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work by Ian Sutton; scale-bar data from Matt Russell)

Exercise

Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronucleii.
D. Each parent produces four daughter cells.

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or "hairy," flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections (Figure 28.8.9). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

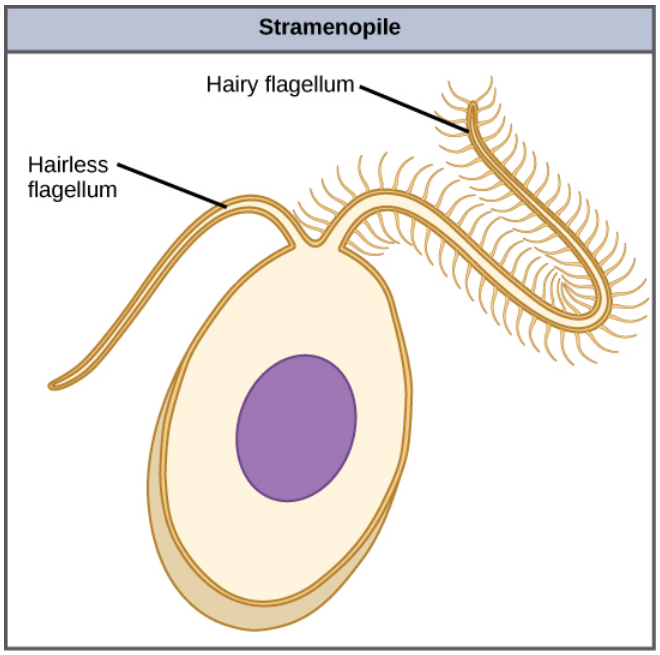


Figure **28.8.9**: This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles (Figure **28.8.10**). These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell, called a raphe. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

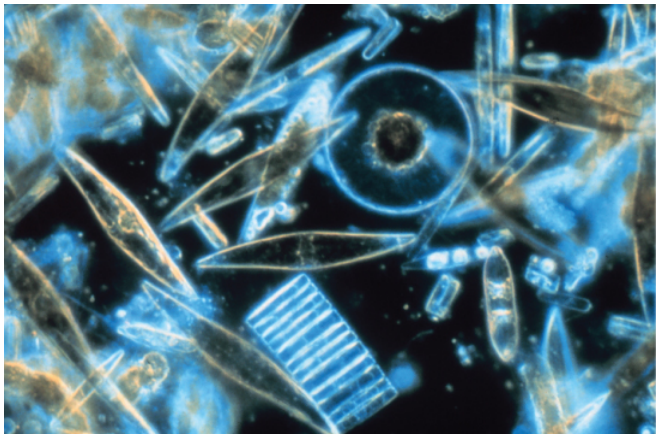


Figure **28.8.10**: Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the biological carbon pump, because carbon is “pumped” to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form (Figure **28.8.11**). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

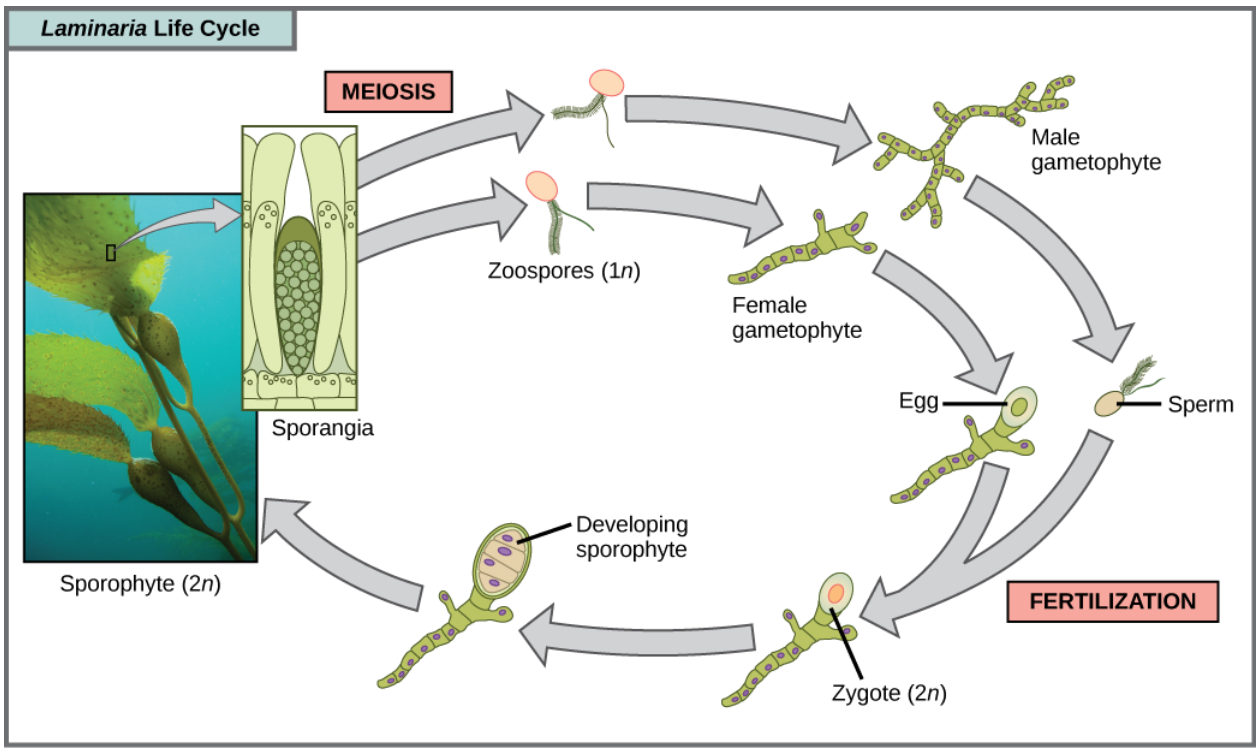


Figure **28.8.11**: Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit "laminaria photograph": modification of work by Claire Fackler, CINMS, NOAA Photo Library)

Exercise

Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.
B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

The water molds, oomycetes ("egg fungus"), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms (Figure **28.8.12**). Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.



Figure 28.8.12: A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (Figure 28.8.13). Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called cytoplasmic streaming, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.

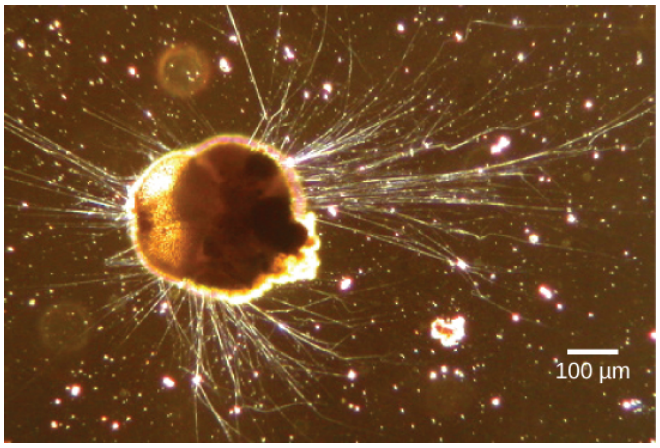


Figure 28.8.13: *Ammonia tepida*, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia. (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

Link to Learning



Take a look at this video to see cytoplasmic streaming in a green alga.

Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails (Figure 28.8.14). As a group, the forams exhibit porous shells, called tests that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.

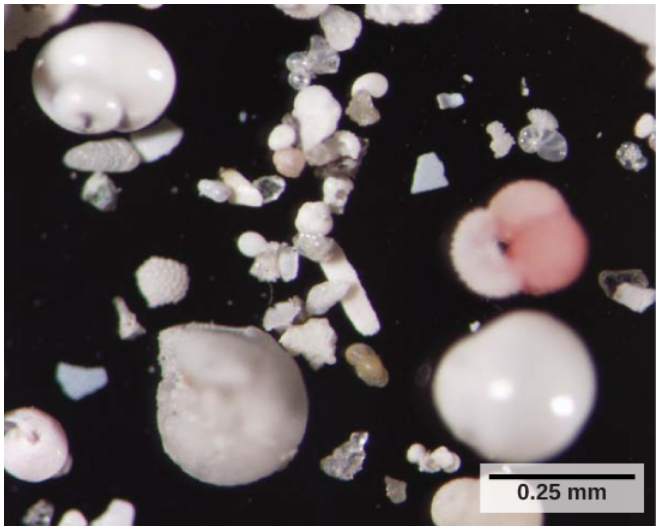


Figure 28.8.14: These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER)

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry (Figure 28.8.15). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

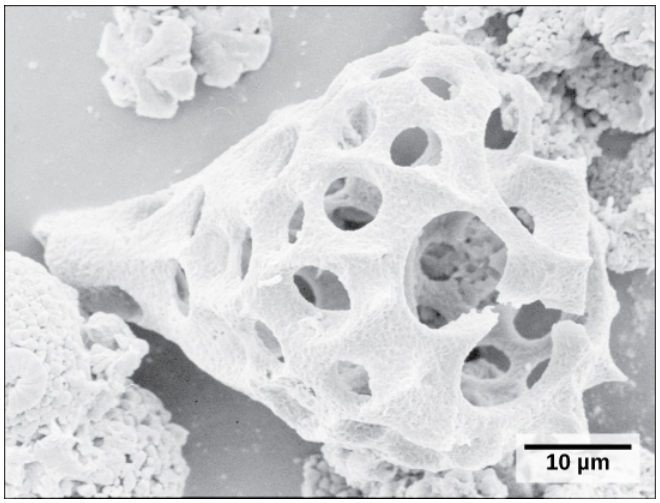


Figure 28.8.15: This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism (Figure 28.8.16). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



Figure **28.8.16**: *Volvox aureus* is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters (Figure **28.8.17**). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure **28.8.17**: *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Amoebozoa

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba (Figure **28.8.18**). The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.

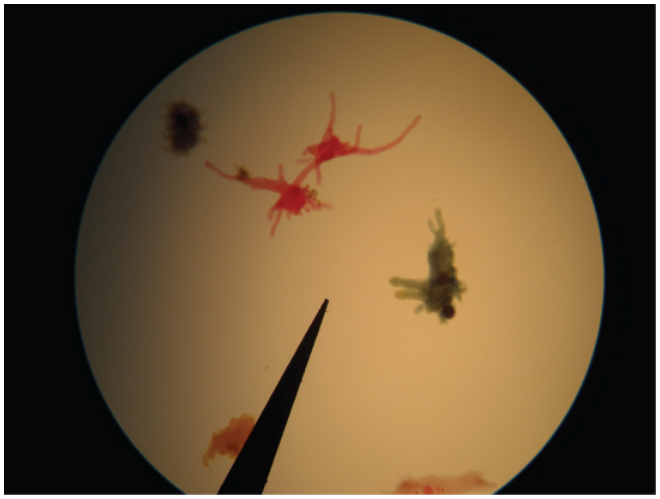


Figure **28.8.18**: Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage (Figure **28.8.19**). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

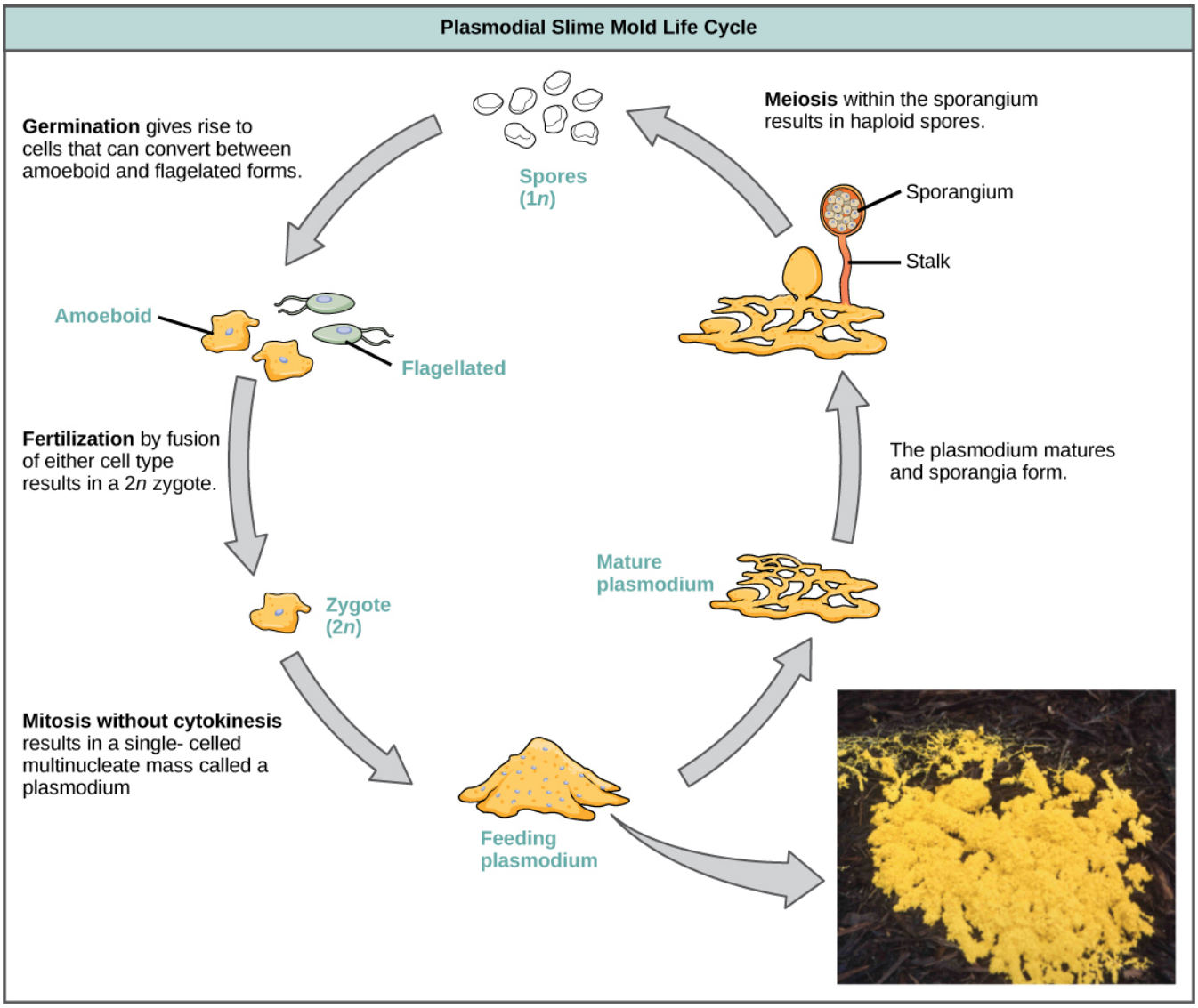


Figure 28.8.19: The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant (Figure 28.8.20). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

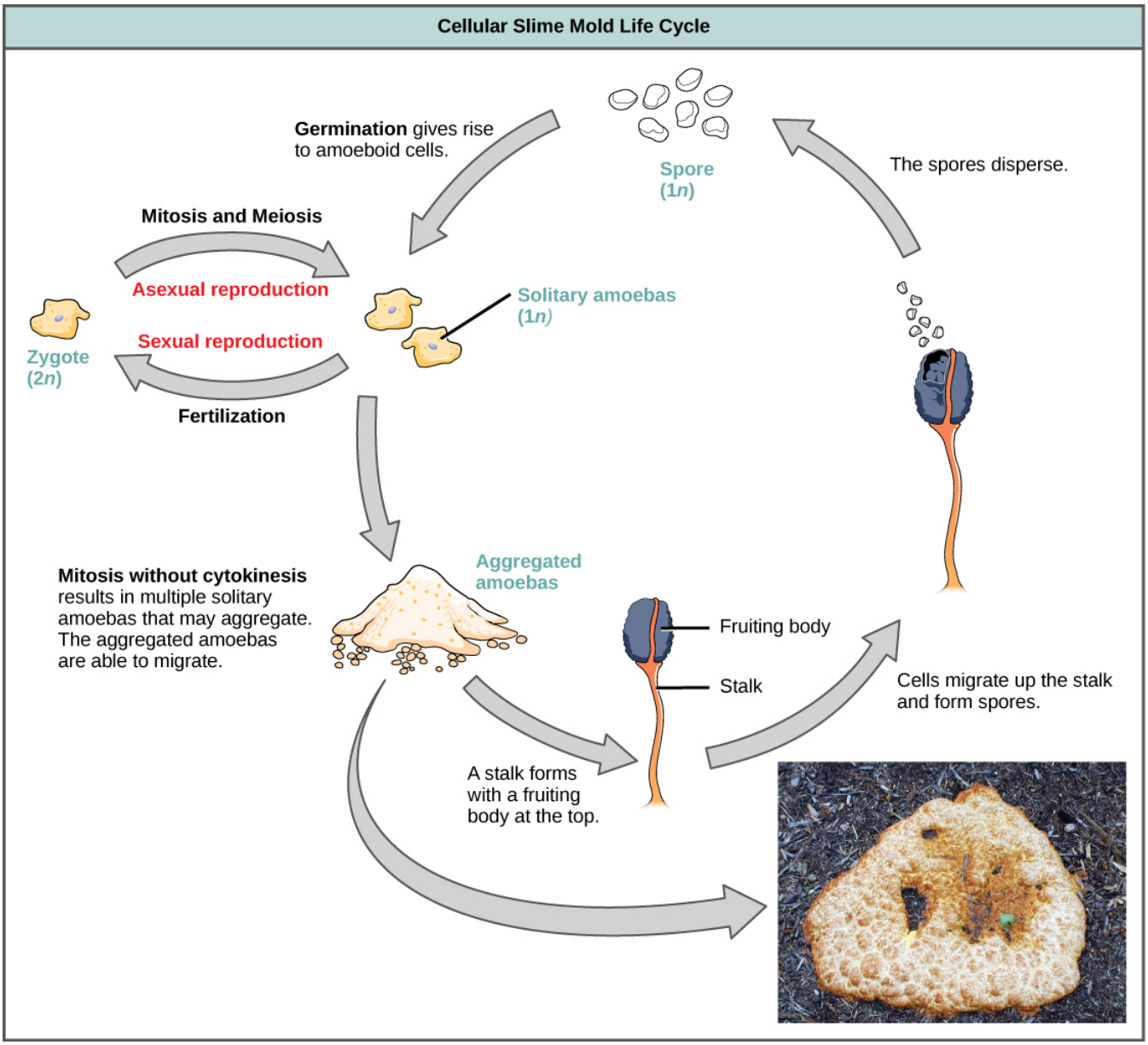


Figure 28.8.20: Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

Link to Learning



View this site to see the formation of a fruiting body by a cellular slime mold.

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

The Mesomycetozoa form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood. These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology.

Summary

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Amoebozoa, and Opisthokonta. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor. At present, the monophyly of some of the supergroups are better supported by genetic data than others. Although tremendous variation exists within the supergroups, commonalities at the morphological, physiological, and ecological levels can be identified.

Art Connections

Figure **28.8.8**: Which of the following statements about *Paramecium* sexual reproduction is false?

A. The macronuclei are derived from micronuclei.
B. Both mitosis and meiosis occur during sexual reproduction.
C. The conjugate pair swaps macronuclei.
D. Each parent produces four daughter cells.

Answer

C

Figure **28.8.11**: Which of the following statements about the *Laminaria* life cycle is false?

A. 1*n* zoospores form in the sporangia.

B. The sporophyte is the 2*n* plant.
C. The gametophyte is diploid.
D. Both the gametophyte and sporophyte stages are multicellular.

Answer

C

Glossary

biological carbon pump
process by which inorganic carbon is fixed by photosynthetic species that then die and fall to the sea floor where they cannot be reached by saprobes and their carbon dioxide consumption cannot be returned to the atmosphere

bioluminescence
generation and emission of light by an organism, as in dinoflagellates

contractile vacuole
vesicle that fills with water (as it enters the cell by osmosis) and then contracts to squeeze water from the cell; an osmoregulatory vesicle

cytoplasmic streaming
movement of cytoplasm into an extended pseudopod such that the entire cell is transported to the site of the pseudopod

hydrogenosome
organelle carried by parabasalids (Excavata) that functions anaerobically and outputs hydrogen gas as a byproduct; likely evolved from mitochondria

kinetoplast
mass of DNA carried within the single, oversized mitochondrion, characteristic of kinetoplastids (phylum: Euglenozoa)

mitosome
nonfunctional organelle carried in the cells of diplomonads (Excavata) that likely evolved from a mitochondrion

plankton
diverse group of mostly microscopic organisms that drift in marine and freshwater systems and serve as a food source for larger aquatic organisms

raphe
slit in the silica shell of diatoms through which the protist secretes a stream of mucopolysaccharides for locomotion and attachment to substrates

test
porous shell of a foram that is built from various organic materials and typically hardened with calcium carbonate

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CHAPTER OVERVIEW

29: Seedless Plants

29.1: Origin of Land Plants

29.1.1: Plant Adaptations to Life on Land

29.2: Bryophytes Have a Dominant Gametophyte Generation

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29.5.1: Ferns and Other Seedless Vascular Plants

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29.1: Origin of Land Plants

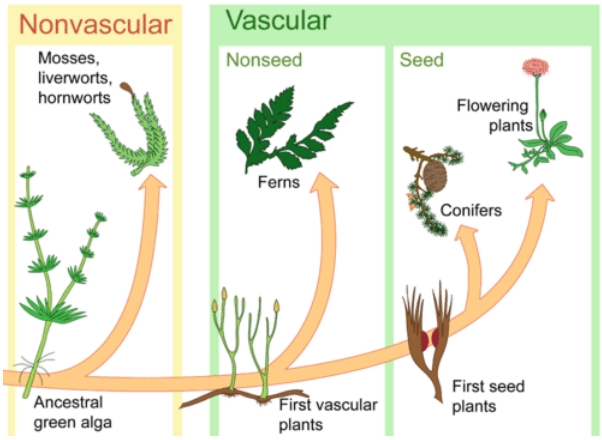


Which moved onto land first, plants or animals?

This fossilized fern may be millions of years old. Over 200 million years ago, the first evidence of ferns related to several modern families appeared. The "great fern radiation" occurred in the late-Cretaceous, which ended 65 million years ago, when many modern families of ferns first appeared. And if animals were the first on land, would many have starved?

Evolution of Plants

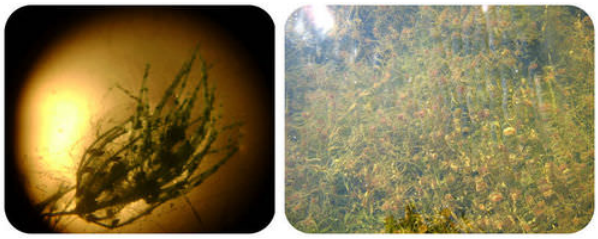
As shown in **Figure** below, plants are thought to have evolved from an aquatic green alga protist. Later, they evolved important adaptations for land, including vascular tissues, seeds, and flowers. Each of these major adaptations made plants better suited for life on dry land and much more successful.



From a simple, green alga ancestor that lived in the water, plants eventually evolved several major adaptations for life on land.

The Earliest Plants

The earliest plants were probably similar to the **stonewort**, an aquatic algae pictured in**Figure** below. Unlike most modern plants, stoneworts have stalks rather than stiff stems, and they have hair-like structures called **rhizoids** instead of roots. On the other hand, stoneworts have distinct male and female reproductive structures, which is a plant characteristic. For fertilization to occur, sperm need at least a thin film of moisture to swim to eggs. In all these ways, the first plants may have resembled stoneworts.



Modern stoneworts may be similar to the earliest plants. Shown is a field of modern stoneworts (right), and an example from the Charophyta, a division of green algae that includes the closest relatives of the earliest plants (left).

Life on Land

By the time the earliest plants evolved, animals were already the dominant organisms in the ocean. Plants were also constrained to the upper layer of water that received enough sunlight for photosynthesis. Therefore, plants never became dominant marine organisms. But when plants moved onto land, everything was wide open. Why was the land devoid of other life? Without plants growing on land, there was nothing for other organisms to feed on. Land could not be colonized by other organisms until land plants became established.

Plants may have colonized the land as early as 700 million years ago. The oldest fossils of land plants date back about 470 million years. The first land plants probably resembled modern plants called **liverworts**, like the one shown in **Figure** below.



The first land plants may have been similar to liverworts like this one.

Colonization of the land was a huge step in plant evolution. Until then, virtually all life had evolved in the ocean. Dry land was a very different kind of place. The biggest problem was the dryness. Simply absorbing enough water to stay alive was a huge challenge. It kept early plants small and low to the ground. Water was also needed for sexual reproduction, so sperm could swim to eggs. In addition, temperatures on land were extreme and always changing. Sunlight was also strong and dangerous. It put land organisms at high risk of mutations.

Vascular Plants Evolve

Plants evolved a number of adaptations that helped them cope with these problems on dry land. One of the earliest and most important was the evolution of vascular tissues. **Vascular tissues** form a plant's "plumbing system." They carry water and minerals from soil to leaves for photosynthesis. They also carry food (sugar dissolved in water) from photosynthetic cellsto other cells in the plant for growth or storage. The evolution of vascular tissues revolutionized the plant kingdom. The tissues allowed plants to grow large and endure periods of drought in harsh land environments. Early vascular plants probably resembled the fern shown in **Figure** below.



Early vascular plants may have looked like this modern fern.

In addition to vascular tissues, these early plants evolved other adaptations to life on land, including lignin, leaves, roots, and a change in their life cycle.

- **Lignin** is a tough carbohydrate molecule that is hydrophobic ("water fearing"). It adds support to vascular tissues in stems. It also waterproofs the tissues so they don't leak, which makes them more efficient at transporting fluids. Because most other organisms cannot break down lignin, it helps protect plants from herbivores and parasites.
- Leaves are rich in chloroplasts that function as solar collectors and food factories. The first leaves were very small, but leaves became larger over time.
- **Roots** are vascular organs that can penetrate soil and even rock. They absorb water andminerals from soil and carry them to leaves. They also anchor a plant in the soil. Roots evolved from rhizoids, which nonvascular plants had used for absorption.
- Land plants evolved a dominant diploid sporophyte generation. This was adaptive because diploid individuals are less likely to suffer harmful effects of mutations. They have two copies of each gene, so if a mutation occurs in one gene, they have a backup copy. This is extremely important on land, where there's a lot of solar radiation.

With all these advantages, it's easy to see why vascular plants spread quickly and widely on land. Many nonvascular plants went extinct as vascular plants became more numerous. Vascular plants are now the dominant land plants on Earth.





Summary

- The earliest plants are thought to have evolved in the ocean from a green alga ancestor.
- Plants were among the earliest organisms to leave the water and colonize land.
- The evolution of vascular tissues allowed plants to grow larger and thrive on land.

Review

1. What were the first plants to evolve?
2. What are vascular tissues of a plant? What is their function?
3. Explain why life on land was difficult for early plants.
4. Why did plants need to become established on land before animals could colonize the land?

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29.1.1: Plant Adaptations to Life on Land

Learning Objectives

- Discuss how lack of water in the terrestrial environment led to significant adaptations in plants

Plant Adaptations to Life on Land

As organisms adapted to life on land, they had to contend with several challenges in the terrestrial environment. The cell ‘s interior is mostly water: in this medium, small molecules dissolve and diffuse and the majority of the chemical reactions of metabolism take place. Desiccation, or drying out, is a constant danger for organisms exposed to air. Even when parts of a plant are close to a source of water, the aerial structures are prone to desiccation. Water also provides buoyancy to organisms. On land, plants need to develop structural support in a medium that does not give the same lift as water. The organism is also subject to bombardment by mutagenic radiation because air does not filter out the ultraviolet rays of sunlight. Additionally, the male gametes must reach the female gametes using new strategies because swimming is no longer possible. As such, both gametes and zygotes must be protected from desiccation. Successful land plants have developed strategies to face all of these challenges. Not all adaptations appeared at once; some species never moved very far from the aquatic environment, although others went on to conquer the driest environments on Earth.

Despite these survival challenges, life on land does offer several advantages. First, sunlight is abundant. Water acts as a filter, altering the spectral quality of light absorbed by the photosynthetic pigment chlorophyll. Second, carbon dioxide is more readily available in air than water since it diffuses faster in air. Third, land plants evolved before land animals; therefore, until dry land was also colonized by animals, no predators threatened plant life. This situation changed as animals emerged from the water and fed on the abundant sources of nutrients in the established flora. In turn, plants developed strategies to deter predation: from spines and thorns to toxic chemicals.

Early land plants, like the early land animals, did not live far from an abundant source of water and developed survival strategies to combat dryness. One of these strategies is called desiccation tolerance. Many mosses can dry out to a brown and brittle mat, but as soon as rain or a flood makes water available, mosses will absorb it and are restored to their healthy green appearance. Another strategy is to colonize environments where droughts are uncommon. Ferns, which are considered an early lineage of plants, thrive in damp and cool places such as the understory of temperate forests. Later, plants moved away from moist or aquatic environments and developed resistance to desiccation, rather than tolerance. These plants, like cacti, minimize the loss of water to such an extent they can survive in extremely dry environments.

The most successful adaptation solution was the development of new structures that gave plants the advantage when colonizing new and dry environments. Four major adaptations are found in all terrestrial plants: the alternation of generations, a sporangium in which the spores are formed, a gametangium that produces haploid cells, and apical meristem tissue in roots and shoots. The evolution of a waxy cuticle and a cell wall with lignin also contributed to the success of land plants. These adaptations are noticeably lacking in the closely-related green algae, which gives reason for the debate over their placement in the plant kingdom.

Alternation of Generations

Alternation of generations describes a life cycle in which an organism has both haploid and diploid multicellular stages (n represents the number of copies of chromosomes). Haplontic refers to a lifecycle in which there is a dominant haploid stage (1n), while diplontic refers to a lifecycle in which the diploid (2n) is the dominant life stage. Humans are diplontic. Most plants exhibit alternation of generations, which is described as haplodiplodontic. The haploid multicellular form, known as a gametophyte, is followed in the development sequence by a multicellular diploid organism: the sporophyte. The gametophyte gives rise to the gametes (reproductive cells) by mitosis. This can be the most obvious phase of the life cycle of the plant, as in the mosses. In fact, the sporophyte stage is barely noticeable in lower plants (the collective term for the plant groups of mosses, liverworts, and lichens). Alternatively, the gametophyte stage can occur in a microscopic structure, such as a pollen grain, in the higher plants (a common collective term for the vascular plants). Towering trees are the diplontic phase in the life cycles of plants such as sequoias and pines.

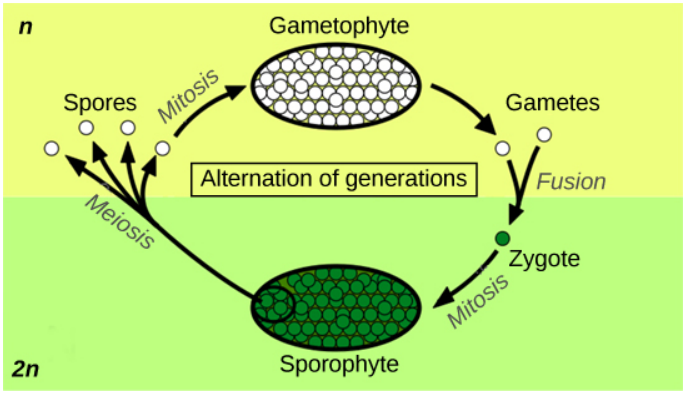


Figure **29.1.1.1**: Alternation of generations of plants: Plants exhibit an alternation of generations between a 1n gametophyte and 2n sporophyte.

Protection of the embryo is a major requirement for land plants. The vulnerable embryo must be sheltered from desiccation and other environmental hazards. In both seedless and seed plants, the female gametophyte provides protection and nutrients to the embryo as it develops into the new generation of sporophyte. This distinguishing feature of land plants gave the group its alternate name of embryophytes.

Key Points

- While some plants remain dependent on a moist and humid environment, many have adapted to a more arid climate by developing tolerance or resistance to drought conditions.
- Alternation of generations describes a life cycle in which an organism has both haploid (1n) and diploid (2n) multicellular stages, although in different species the haploid or diploid stage can be dominant.
- The life on land presents significant challenges for plants, including the potential for desiccation, mutagenic radiation from the sun, and a lack of buoyancy from the water.

Key Terms

- **desiccation tolerance**: the ability of an organism to withstand or endure extreme dryness, or drought-like condition
- **alternation of generation**: the life cycle of plants with a multicellular sporophyte, which is diploid, that alternates with a multicellular gametophyte, which is haploid

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29.2: Bryophytes Have a Dominant Gametophyte Generation

Learning Objectives

- Describe the characteristics of bryophytes

Bryophytes

Bryophytes are the group of seedles plants that are the closest-extant relative of early terrestrial plants. The first bryophytes (liverworts) probably appeared in the Ordovician period, about 450 million years ago. However, because they lack of lignin and other resistant structures, bryophyte fossil formation is improbable and the fossil record is poor. Some spores protected by sporopollenin have survived and are attributed to early bryophytes. By the Silurian period, however, vascular plants had spread through the continents. This compelling fact is used as evidence that non-vascular plants must have preceded the Silurian period.

More than 25,000 species of bryophytes thrive in mostly-damp habitats, although some live in deserts. They constitute the major flora of inhospitable environments like the tundra where their small size and tolerance to desiccation offer distinct advantages. They generally lack lignin and do not have actual tracheids (xylem cells specialized for water conduction). Rather, water and nutrients circulate inside specialized conducting cells. Although the term non-tracheophyte is more accurate, bryophytes are commonly called non-vascular plants.

In a bryophyte, all the conspicuous vegetative organs, including the photosynthetic leaf-like structures, the thallus, stem, and the rhizoid that anchors the plant to its substrate, belong to the haploid organism, or gametophyte. The sporophyte is barely noticeable. Thus, the gametophyte is the dominant and most familiar form; the sporophyte appears for only a short period. The gametes formed by bryophytes swim with a flagellum. The sporangium, the multicellular sexual reproductive structure, is present in bryophytes and absent in the majority of algae. The sporophyte embryo also remains attached to the parent plant, which protects and nourishes it. This is a characteristic of land plants. The bryophytes are divided into three phyla: the liverworts (Hepaticophyta), the hornworts (Anthocerotophyta), and the mosses (true Bryophyta).



Figure **29.2.1**: Moss: Mosses (true bryophyta) are one of the three kinds of bryophytes (along with liverworts and hornworts). This image shows a moss growing on a dry stone wall.

Key Points

- Bryophytes are the closest-living relative of early terrestrial plants; liverworts were the first Bryophytes, probably appearing during the Ordovician period.
- Bryophytes fossil formation is improbable since they do not possess lignin.
- Bryophytes thrive in mostly-damp habitats; however, some species can live in deserts while others can inhabit hostile environments such as the tundra.
- Bryophytes are nonvascular because they do not have tracheids; instead, water and nutrients circulate inside specialized conducting cells.

- In a bryophyte, all the vegetative organs belong to the gametophyte, which is the dominant and most familiar form; the sporophyte appears for only a short period.
- The sporophyte is dependent on the gametophyte and remains permanently attached to it in order to gain nutrition and protection.

Key Terms

- **bryophyte**: seedless, nonvascular plants that are the closest extant relative of early terrestrial plants
- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts
- **sporangium**: a case, capsule, or container in which spores are produced by an organism

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29.2.1: Bryophytes

Learning Objectives

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29.2.2: Liverworts and Hornworts

Learning Objectives

- Describe the distinguishing traits of hornworts and liverworts

Liverworts and Hornworts

Liverworts

Liverworts (Hepaticophyta) are viewed as the plants most closely related to the ancestor that moved to land. Liverworts have colonized every terrestrial habitat on earth and diversified to more than 7000 existing species. Liverwort gametophytes (the dominant stage of the life cycle) form lobate green structures. The shape of these leaves are similar to the lobes of the liver; hence, providing the origin of the name given to the phylum. Openings that allow the movement of gases may be observed in liverworts. However, these are not stomata because they do not actively open and close. The plant takes up water over its entire surface and has no cuticle to prevent desiccation.



Figure **29.2.2.1**: Liverworts: A liverwort, *Lunularia cruciata*, displays its lobate, flat thallus. The organism in the photograph is in the dominant gametophyte stage.

The liverwort's life cycle begins with the release of haploid spores from the sporangium that developed on the sporophyte. Spores disseminated by wind or water germinate into flattened thalli gametophytes attached to the substrate by thin, single-celled filaments. Male and female gametangia develop on separate, individual plants. Once released, male gametes swim with the aid of their flagella to the female gametangium (the archegonium), and fertilization ensues. The zygote grows into a small sporophyte still attached to the parent gametophyte and develops spore-producing cells and elaters. The spore-producing cells undergo meiosis to form spores, which disperse (with the help of elaters), giving rise to new gametophytes. Thus, the life cycle of liverworts follows the pattern of alternation of generations.

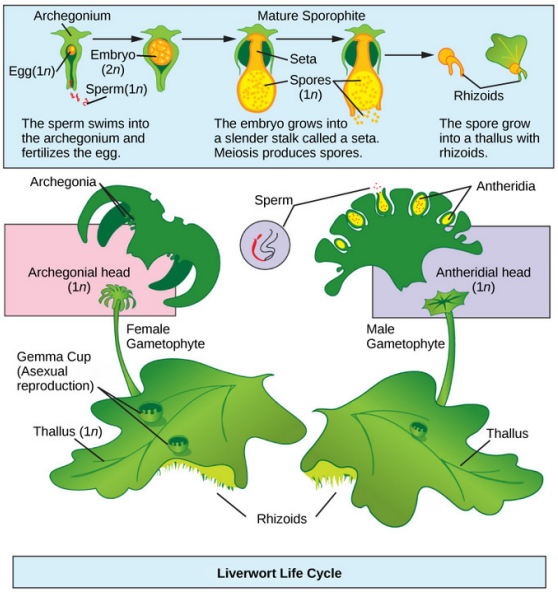


Figure **29.2.2.1**: Liverwort Life Cycle: The life cycle of a typical liverwort follows the pattern of alternation of generations. Spores are released from sporophytes and form the gametophyte. Male gametes fertilize female gametes to form a zygote, which grows into a sporophyte. This sporophyte disperses spores with the help of elaters; the process begins again.

Liverwort plants can also reproduce asexually by the breaking of branches or the spreading of leaf fragments called gemmae. In this latter type of reproduction, the gemmae (small, intact, complete pieces of plant that are produced in a cup on the surface of the thallus) are splashed out of the cup by raindrops. The gemmae then land nearby and develop into gametophytes.

Hornworts

The hornworts (Anthocerotophyta) belong to the broad bryophyte group that have colonized a variety of habitats on land, although they are never far from a source of moisture. The short, blue-green gametophyte is the dominant phase of the lifecycle of a hornwort. The narrow, pipe-like sporophyte is the defining characteristic of the group. The sporophytes emerge from the parent gametophyte and continue to grow throughout the life of the plant. Stomata appear in the hornworts and are abundant on the sporophyte. Photosynthetic cells in the thallus contain a single chloroplast. Meristem cells at the base of the plant keep dividing and adding to its height. Many hornworts establish symbiotic relationships with cyanobacteria that fix nitrogen from the environment.



Figure **29.2.2.1**: Hornworts: Unlike liverworts, hornworts grow a tall and slender sporophyte.

The life cycle of hornworts also follows the general pattern of alternation of generations and has a similar life cycle to liverworts. The gametophytes grow as flat thalli on the soil with embedded gametangia. Flagellated sperm swim to the archegonia and fertilize eggs. However, unlike liverworts, the zygote develops into a long and slender sporophyte that eventually splits open, releasing spores. Additionally, thin cells called pseudoelaters surround the spores and help propel them further in the environment. Unlike the elaters observed in liverworts, the hornwort pseudoelaters are single-celled structures. The haploid spores germinate and produce the next generation of gametophytes. Like liverworts, some hornworts may also produce asexually through fragmentation.

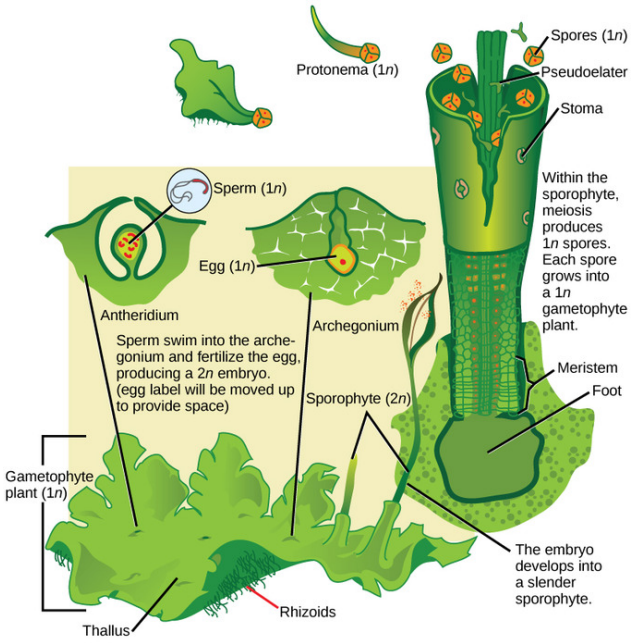


Figure **29.2.2.1**: Life Cycle of Hornworts: The life cycle of hornworts is similar to that of liverworts. Both follow the pattern of alternation of generations. However, liverworts develop a small sporophyte, whereas hornworts develop a long, slender sporophyte. Liverworts also disperse their spores with the help of elaters, while hornworts utilize pseudoelaters to aid in spore dispersal.

Key Points

- The leaves of liverworts are lobate green structures similar to the lobes of the liver, while hornworts have narrow, pipe-like structures.
- The gametophyte stage is the dominant stage in both liverworts and hornworts; however, liverwort sporophytes do not contain stomata, while hornwort sporophytes do.
- The life cycle of liverworts and hornworts follows alternation of generations: spores germinate into gametophytes, the zygote develops into a sporophyte that releases spores, and then spores produce new gametophytes.
- Liverworts develop short, small sporophytes, whereas hornworts develop long, slender sporophytes.
- To aid in spore dispersal, liverworts utilize elaters, whereas hornworts utilize pseudoelaters.
- Liverworts and hornworts can reproduce asexually through the fragmentation of leaves into gemmae that disperse and develop into gametophytes.

Key Terms

- **alternation of generation**: the life cycle of plants with a multicellular sporophyte, which is diploid, that alternates with a multicellular gametophyte, which is haploid
- **pseudoelater**: single-celled structure that aids in spore dispersal
- **gemmae**: small, intact, complete pieces of plant that are produced in a cup on the surface of the thallus and develop into gametophytes through asexual reproduction

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29.2.3: Mosses

Learning Objectives

- Describe the distinguishing traits of mosses

Mosses

More than 10,000 species of mosses have been cataloged. Their habitats vary from the tundra, where they are the main vegetation, to the understory of tropical forests. In the tundra, the mosses' shallow rhizoids allow them to fasten to a substrate without penetrating the frozen soil. Mosses slow down erosion, store moisture and soil nutrients, and provide shelter for small animals as well as food for larger herbivores, such as the musk ox. Mosses are very sensitive to air pollution and are used to monitor air quality. They are also sensitive to copper salts. Such salts are a common ingredient of compounds marketed to eliminate mosses from lawns.

Mosses form diminutive gametophytes, which are the dominant phase of the life cycle. Green, flat structures resembling true leaves, but lacking vascular tissue are attached in a spiral to a central stalk or seta. The plants absorb water and nutrients directly through these leaf-like structures. The seta (plural, setae) contains tubular cells that transfer nutrients from the base of the sporophyte (the foot) to the sporangium. Some mosses have small branches. Some primitive traits of green algae, such as flagellated sperm, are still present in mosses that are dependent on water for reproduction. Other features of mosses are adaptations to dry land. For example, stomata are present on the stems of the sporophyte and a primitive vascular system runs up the sporophyte's stalk. Additionally, mosses are anchored to the substrate, whether it is soil, rock, or roof tiles, by multicellular rhizoids. These structures are precursors of roots. They originate from the base of the gametophyte, but are not the major route for the absorption of water and minerals. The lack of a true root system explains why it is so easy to rip moss mats from a tree trunk.



Figure **29.2.3.1**: Setae: This photograph shows the long slender stems, called setae, connected to capsules of the moss Thamnobryum alopecurum.

The moss life cycle follows the pattern of alternation of generations. The most familiar structure is the haploid gametophyte, which germinates from a haploid spore and forms first a protonema: usually, a tangle of single-celled filaments that hug the ground. Cells akin to an apical meristem actively divide and give rise to a gametophore, consisting of a photosynthetic stem and foliage-like structures. Rhizoids form at the base of the gametophore. Gametangia of both sexes develop on separate gametophores. The male organ (the antheridium) produces many sperm, whereas the archegonium (the female organ) forms a single egg. At fertilization, the sperm swims down the neck to the venter and unites with the egg inside the archegonium. The zygote, protected by the archegonium, divides and grows into a sporophyte, still attached by its foot to the gametophyte.

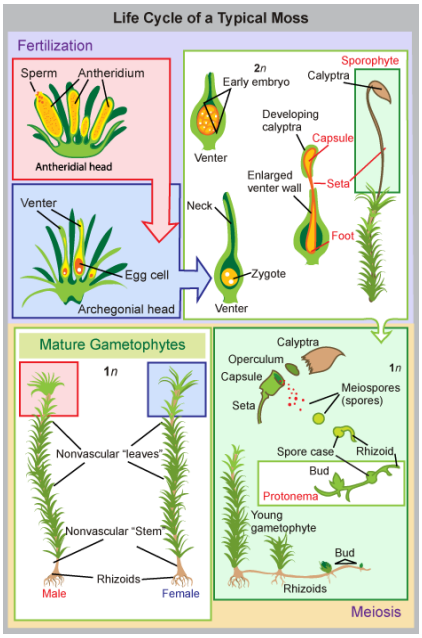


Figure **29.2.3.1**: Life cycle of mosses: The alternation of generations cycle begins when the gametophyte germinates from a haploid spore and forms a protonema. Apical meristem-like cells divide and give rise to the gametophores. The archegonium (female organ) and antheridium (male organ) develop on separate gametophores. After fertilization, the zygote divides and grows into a sporophyte, which stays attached to the gametophyte. Spores released from the sporophyte germinate and produce gametophytes; the process begins again.

A structure called a peristome increases the spread of spores after the tip of the capsule falls off at dispersal. The concentric tissue around the mouth of the capsule is made of triangular, close-fitting units, a little like “teeth”; these open and close depending on moisture levels, periodically releasing spores.

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Key Points

- Mosses slow down erosion, store moisture and soil nutrients, and provide shelter for small animals and food for larger herbivores.
- Mosses have green, flat structures that resemble true leaves, which absorb water and nutrients; some mosses have small branches.
- Mosses have traits that are adaptations to dry land, such as stomata present on the stems of the sporophyte.
- Mosses are anchored to the substrate by rhizoids, which originate from the base of the gametophyte.
- The moss life cycle follows the pattern of alternation of generations where gametophytes form male and female gametophores, which fertilize to form the sporophyte; spores are released from the sporophyte to produce new gametophytes.
- The concentric tissue around the mouth of the capsule is made of triangular, close-fitting units that open and close to release spores, and the peristome increases the spread of spores after the tip of the capsule falls off at dispersal.

Key Terms

- **peristome**: one or two rings of tooth-like appendages surrounding the opening of the capsule of many mosses that aid in spreading spores
- **rhizoid**: a rootlike structure that acts as support and anchors the plant to its substrate
- **seta**: the stalk of a moss sporangium, or occasionally in a liverwort

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29.2.4: Sporophytes and Gametophytes in Seedless Plants

Learning Objectives

- Describe the role of the sporophyte and gametophyte in plant reproduction

Sporangia in Seedless Plants

The sporophyte of seedless plants is diploid and results from syngamy (fusion) of two gametes. The sporophyte bears the sporangia (singular, sporangium): organs that first appeared in the land plants. The term “sporangia” literally means “spore in a vessel”: it is a reproductive sac that contains spores. Inside the multicellular sporangia, the diploid sporocytes, or mother cells, produce haploid spores by meiosis, where the 2n chromosome number is reduced to 1n (note that many plant sporophytes are polyploid: for example, durum wheat is tetraploid, bread wheat is hexaploid, and some ferns are 1000-ploid). The spores are later released by the sporangia and disperse in the environment.



Figure **29.2.4.1**: Sporangia: Spore-producing sacs called sporangia grow at the ends of long, thin stalks in this photo of the moss Esporangios bryum.

Two different spore-forming methods are used in land plants, resulting in the separation of sexes at different points in the lifecycle. Seedless, non- vascular plants produce only one kind of spore and are called homosporous. The gametophyte phase (1n) is dominant in these plants. After germinating from a spore, the resulting gametophyte produces both male and female gametangia, usually on the same individual. In contrast, heterosporous plants produce two morphologically different types of spores. The male spores are called microspores, because of their smaller size, and develop into the male gametophyte; the comparatively larger megaspores develop into the female gametophyte. Heterospory is observed in a few seedless vascular plants and in all seed plants.

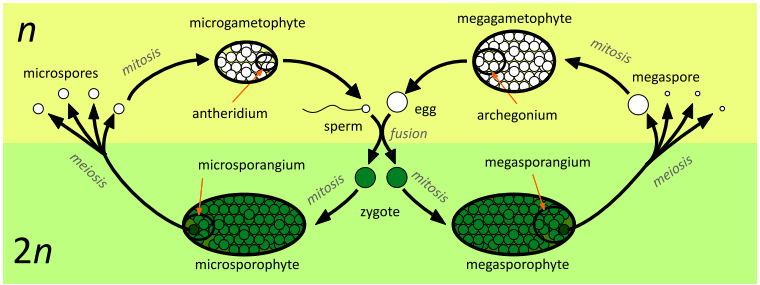


Figure **29.2.4.1**: Lifecycle of heterosporous plants: Heterosporous plants produce two morphologically different types of spores: microspores, which develop into the male gametophyte, and megaspores, which develop into the female gametophyte.

When the haploid spore germinates in a hospitable environment, it generates a multicellular gametophyte by mitosis. The gametophyte supports the zygote formed from the fusion of gametes and the resulting young sporophyte (vegetative form). The cycle then begins anew.

The spores of seedless plants are surrounded by thick cell walls containing a tough polymer known as sporopollenin. This complex substance is characterized by long chains of organic molecules related to fatty acids and carotenoids: hence the yellow color of most pollen. Sporopollenin is unusually resistant to chemical and biological degradation. In seed plants, which use pollen to transfer the male sperm to the female egg, the toughness of sporopollenin explains the existence of well-preserved pollen fossils. Sporopollenin was once thought to be an innovation of land plants; however, the green algae, Coleochaetes, also forms spores that contain sporopollenin.

Gametangia in Seedless Plants

Gametangia (singular, gametangium) are organs observed on multicellular haploid gametophytes. In the gametangia, precursor cells give rise to gametes by mitosis. The male gametangium (antheridium) releases sperm. Many seedless plants produce sperm equipped with flagella that enable them to swim in a moist environment to the archegonia: the female gametangium. The embryo develops inside the archegonium as the sporophyte. Gametangia are prominent in seedless plants, but are replaced by pollen grains in seed-producing plants.

Key Points

- The diploid stage of a plant (2n), the sporophyte, bears a sporangium, an organ that produces spores during meiosis.
- Homosporous plants produce one type of spore which develops into a gametophyte (1n) with both male and female organs.
- Heterosporous plants produce separate male and female gametophytes, which produce sperm and eggs, respectively.
- In seedless plants, male gametangia (antheridium) release sperm, which can then swim to and fertilize an egg at the female gametangia (archegonia); this mode of reproduction is replaced by pollen production in seed plants.

Key Terms

- **gametophyte**: a plant (or the haploid phase in its life cycle) that produces gametes by mitosis in order to produce a zygote
- **gametangium**: an organ or cell in which gametes are produced that is found in many multicellular protists, algae, fungi, and the gametophytes of plants
- **sporopollenin**: a combination of biopolymers observed in the tough outer layer of the spore and pollen wall
- **syngamy**: the fusion of two gametes to form a zygote
- **sporophyte**: a plant (or the diploid phase in its life cycle) that produces spores by meiosis in order to produce gametophytes

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SECTION OVERVIEW

29.3: Tracheophytes Have a Dominant Sporophyte Generation

29.3.1: Seedless Vascular Plants

29.3.2: Vascular Tissue- Xylem and Phloem

29.3.3: The Evolution of Roots in Seedless Plants

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29.3.1: Seedless Vascular Plants

Learning Objectives

- Evaluate the evolution of seedless vascular plants

Seedless Vascular Plants

The vascular plants, or tracheophytes, are the dominant and most conspicuous group of land plants. They contain tissue that transports water and other substances throughout the plant. More than 260,000 species of tracheophytes represent more than 90 percent of the earth's vegetation. By the late Devonian period, plants had evolved vascular tissue, well-defined leaves, and root systems. With these advantages, plants increased in height and size and were able to spread to all habitats.

Seedless vascular plants are plants that contain vascular tissue, but do not produce flowers or seeds. In seedless vascular plants, such as ferns and horsetails, the plants reproduce using haploid, unicellular spores instead of seeds. The spores are very lightweight (unlike many seeds), which allows for their easy dispersion in the wind and for the plants to spread to new habitats. Although seedless vascular plants have evolved to spread to all types of habitats, they still depend on water during fertilization, as the sperm must swim on a layer of moisture to reach the egg. This step in reproduction explains why ferns and their relatives are more abundant in damp environments, including marshes and rainforests. The life cycle of seedless vascular plants is an alternation of generations, where the diploid sporophyte alternates with the haploid gametophyte phase. The diploid sporophyte is the dominant phase of the life cycle, while the gametophyte is an inconspicuous, but still-independent, organism. Throughout plant evolution, there is a clear reversal of roles in the dominant phase of the life cycle.

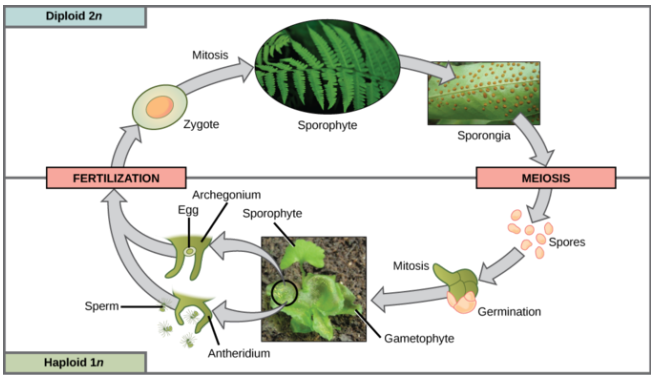


Figure **29.3.1.1**: Life cycle of a fern: This life cycle of a fern shows alternation of generations with a dominant sporophyte stage.

Key Points

- The life cycle of seedless vascular plants alternates between a diploid sporophyte and a haploid gametophyte phase.
- Seedless vascular plants reproduce through unicellular, haploid spores instead of seeds; the lightweight spores allow for easy dispersion in the wind.
- Seedless vascular plants require water for sperm motility during reproduction and, thus, are often found in moist environments.

Key Terms

- **gametophyte**: a plant (or the haploid phase in its life cycle) that produces gametes by mitosis in order to produce a zygote
- **sporophyte**: a plant (or the diploid phase in its life cycle) that produces spores by meiosis in order to produce gametophytes
- **tracheophyte**: any plant possessing vascular tissue (xylem and phloem), including ferns, conifers, and flowering plants

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29.3.2: Vascular Tissue- Xylem and Phloem

Learning Objectives

- Describe the functions of plant vascular tissue

Vascular Tissue: Xylem and Phloem

The first fossils that show the presence of vascular tissue date to the Silurian period, about 430 million years ago. The simplest arrangement of conductive cells shows a pattern of xylem at the center surrounded by phloem. Together, xylem and phloem tissues form the vascular system of plants.

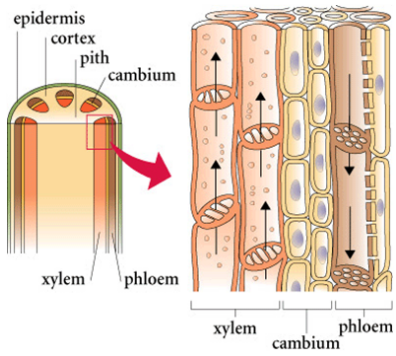


Figure 29.3.2.1: Xylem and phloem: Xylem and phloem tissue make up the transport cells of stems. The direction of water and sugar transportation through each tissue is shown by the arrows.

Xylem is the tissue responsible for supporting the plant as well as for the storage and long-distance transport of water and nutrients, including the transfer of water-soluble growth factors from the organs of synthesis to the target organs. The tissue consists of vessel elements, conducting cells, known as tracheids, and supportive filler tissue, called parenchyma. These cells are joined end-to-end to form long tubes. Vessels and tracheids are dead at maturity. Tracheids have thick secondary cell walls and are tapered at the ends. It is the thick walls of the tracheids that provide support for the plant and allow it to achieve impressive heights. Tall plants have a selective advantage by being able to reach unfiltered sunlight and disperse their spores or seeds further away, thus expanding their range. By growing higher than other plants, tall trees cast their shadow on shorter plants and limit competition for water and precious nutrients in the soil. The tracheids do not have end openings like the vessels do, but their ends overlap with each other, with pairs of pits present. The pit pairs allow water to pass horizontally from cell to cell.

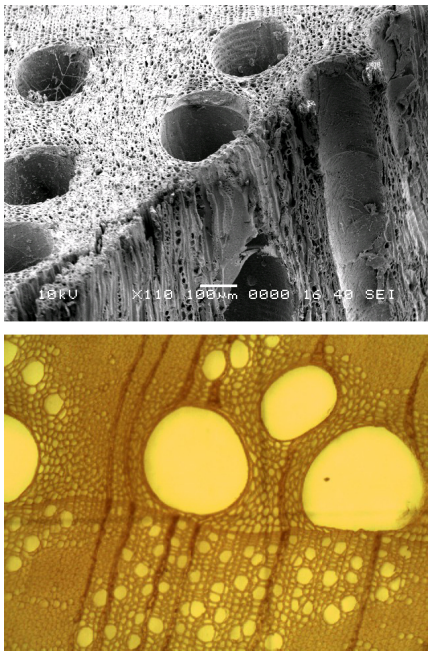


Figure **29.3.2.1**: Tracheids and vessel elements: Tracheids (top) and vessel elements (bottom) are the water conducting cells of xylem tissue.

Phloem tissue is responsible for translocation, which is the transport of soluble organic substances, for example, sugar. The substances travel along sieve elements, but other types of cells are also present: the companion cells, parenchyma cells, and fibers. The end walls, unlike vessel members in xylem, do not have large openings. The end walls, however, are full of small pores where cytoplasm extends from cell to cell. These porous connections are called sieve plates. Despite the fact that their cytoplasm is actively involved in the conduction of food materials, sieve-tube members do not have nuclei at maturity. The activity of the sieve tubes is controlled by companion cells through plasmadesmata.

Key Points

- Xylem transports and stores water and water-soluble nutrients in vascular plants.
- Phloem is responsible for transporting sugars, proteins, and other organic molecules in plants.
- Vascular plants are able to grow higher than other plants due to the rigidity of xylem cells, which support the plant.

Key Terms

- **xylem**: a vascular tissue in land plants primarily responsible for the distribution of water and minerals taken up by the roots; also the primary component of wood
- **phloem**: a vascular tissue in land plants primarily responsible for the distribution of sugars and nutrients manufactured in the shoot
- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts

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29.3.3: The Evolution of Roots in Seedless Plants

Learning Objectives

- Explain how roots provide support for plants

Roots: Support for the Plant

Roots are not well preserved in the fossil record. Nevertheless, it seems that roots appeared later in evolution than vascular tissue. The development of an extensive network of roots represented a significant new feature of vascular plants. Roots provided seed plants with three major functions: anchoring the plant to the soil, absorbing water and minerals and transporting them upwards, and storing the products of photosynthesis. Importantly, roots are modified to absorb moisture and exchange gases. In addition, while most roots are underground, some plants have adventitious roots, which emerge above the ground from the shoot.

Types of Root Systems

There are mainly two types of root systems. Dicots (flowering plants with two embryonic seed leaves) have a tap root system while monocots (flowering plants with one embryonic seed leaf) have a fibrous root system. A tap root system has a main root that grows down vertically from which many smaller lateral roots arise. Dandelions are a good example; their tap roots usually break off when trying to pull these weeds; they can regrow another shoot from the remaining root.



Figure **29.3.3.1**: Root types: (a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots.

A tap root system penetrates deep into the soil. In contrast, a fibrous root system is located closer to the soil surface, forming a dense network of roots that also helps prevent soil erosion (lawn grasses are a good example, as are wheat, rice, and corn). In addition, some plants actually have a combination of tap root and fibrous roots. Plants that grow in dry areas often have deep root systems, whereas plants growing in areas with abundant water tend to have shallower root systems.

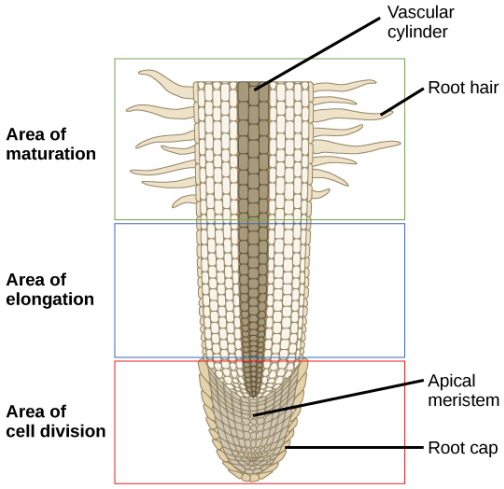


Figure 29.3.3.1: Zones on a root tip: A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem.

Root growth begins with seed germination. When the plant embryo emerges from the seed, the radicle of the embryo forms the root system. The tip of the root is protected by the root cap, a structure exclusive to roots and unlike any other plant structure. The root cap is continuously replaced because it gets damaged easily as the root pushes through soil. The root tip can be divided into three zones: a zone of cell division, a zone of elongation, and a zone of maturation and differentiation. The zone of cell division is closest to the root tip; it is made up of the actively-dividing cells of the root meristem. The zone of elongation is where the newly-formed cells increase in length, thereby lengthening the root. Beginning at the first root hair is the zone of cell maturation where the root cells begin to differentiate into special cell types. All three zones are in the first centimeter or so of the root tip.



Figure 29.3.3.1: Modified roots: Many vegetables are modified roots, such as radishes and carrots, which store energy in the form of starches and sugars.

The vascular tissue in the root is arranged in the inner portion of the root, which is called the vascular cylinder. A layer of cells, known as the endodermis, separates the vascular tissue from the ground tissue in the outer portion of the root. The endodermis is exclusive to roots, serving as a checkpoint for materials entering the root's vascular system. A waxy substance called suberin is present on the walls of the endodermal cells. This waxy region, known as the Casparian strip, forces water and solutes to cross the plasma membranes of endodermal cells instead of slipping between the cells. This ensures that only materials required by the root pass through the endodermis, while toxic substances and pathogens are generally excluded. The outermost cell layer of the root's vascular tissue is the pericycle, an area that can give rise to lateral roots. In dicot roots, the xylem and phloem of the stele are arranged alternately in an X shape, whereas in monocot roots, the vascular tissue is arranged in a ring around the pith.

Root Modifications

Root structures may be modified for specific purposes. For example, some roots are bulbous and store starch. Aerial roots and prop roots are two forms of aboveground roots that provide additional support to anchor the plant. Tap roots, such as carrots, turnips, and beets, are examples of roots that are modified for food storage.

Key Points

- There are two main types of root systems: tap root systems consist of one main root that grows down vertically with smaller lateral roots growing off of the main root, while fibrous root systems form a dense network of roots near the soil surface.
- Roots can be modified to store food or starches and to provide additional support for plants; many vegetables, such as carrots, are modified roots.
- A zone of cell division, a zone of elongation, and a zone of maturation and differentiation make up a root tip, where the root cells divide, grow, and differentiate into specialized cells.
- The vascular system of roots is surrounded by an epidermis, which regulates materials that enter the root's vascular system.

Key Terms

- **endodermis**: in a plant stem or root, a cylinder of cells that separates the outer cortex from the central core and controls the flow of water and minerals within the plant
- **suberin**: a waxy material found in bark that can repel water
- **pericycle**: in a plant root, the cylinder of plant tissue between the endodermis and phloem

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SECTION OVERVIEW

29.4: Lycophytes Diverged from the Main Lineage of Vascular Plants

29.4.1: Ferns and Other Seedless Vascular Plants

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29.4.1: Ferns and Other Seedless Vascular Plants

Learning Objectives

- Identify types of seedless vascular plants

Ferns and Other Seedless Vascular Plants

Water is required for fertilization of seedless vascular plants; most favor a moist environment. Modern-day seedless tracheophytes include lycophytes and monilophytes.

Phylum Lycopodiophyta: Club Mosses

The club mosses, or phylum Lycopodiophyta, are the earliest group of seedless vascular plants. They dominated the landscape of the Carboniferous, growing into tall trees and forming large swamp forests. Today's club mosses are diminutive, evergreen plants consisting of a stem (which may be branched) and microphylls (leaves with a single unbranched vein). The phylum Lycopodiophyta consists of close to 1,200 species, including the quillworts (Isoetales), the club mosses (Lycopodiales), and spike mosses (Selaginellales), none of which are true mosses or bryophytes.

Lycophytes follow the pattern of alternation of generations seen in the bryophytes, except that the sporophyte is the major stage of the life cycle. The gametophytes do not depend on the sporophyte for nutrients. Some gametophytes develop underground and form mycorrhizal associations with fungi. In club mosses, the sporophyte gives rise to sporophylls arranged in strobili, cone-like structures that give the class its name. Lycophytes can be homosporous or heterosporous.



Figure **29.4.1.1**: Strobili of club mosses: In some club mosses such as *Lycopodium clavatum*, sporangia are arranged in clusters called strobili.

Phylum Monilophyta: Class Equisetopsida (Horsetails)

Horsetails, whisk ferns, and ferns belong to the phylum Monilophyta, with horsetails placed in the Class Equisetopsida. The single extant genus *Equisetum* is the survivor of a large group of plants, which produced large trees, shrubs, and vines in the swamp forests in the Carboniferous. The plants are usually found in damp environments and marshes.

The stem of a horsetail is characterized by the presence of joints or nodes, hence the old name Arthrophyta (arthro- = "joint"; -phyta = "plant"). Leaves and branches come out as whorls from the evenly-spaced joints. The needle-shaped leaves do not contribute greatly to photosynthesis, the majority of which takes place in the green stem.



Figure 29.4.1.1: Leaves of a horsetail: The whorls of green structures at the joints are actually stems. The leaves are barely noticeable as brown rings just above each joint. Horsetails were once used as scrubbing brushes and so were called scouring rushes.

Silica collects in the epidermal cells, contributing to the stiffness of horsetail plants. Underground stems known as rhizomes anchor the plants to the ground. Modern-day horsetails are homosporous and produce bisexual gametophytes.

Phylum Monilophyta: Class Psilotopsida (Whisk Ferns)

While most ferns form large leaves and branching roots, the whisk ferns, Class Psilotopsida, lack both roots and leaves, which were probably lost by reduction. Photosynthesis takes place in their green stems; small yellow knobs form at the tip of the branch stem and contain the sporangia. Whisk ferns were considered an early pterophytes. However, recent comparative DNA analysis suggests that this group may have lost both leaves and roots through evolution and is more closely related to ferns.

Phylum Monilophyta: Class Polypodiopsida (Ferns)

With their large fronds, ferns are the most-readily recognizable seedless vascular plants. More than 20,000 species of ferns live in environments ranging from tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist, shaded places. Ferns made their appearance in the fossil record during the Devonian period and expanded during the Carboniferous.

The dominant stage of the life cycle of a fern is the sporophyte, which typically consists of large compound leaves called fronds. Fronds fulfill a double role; they are photosynthetic organs that also carry reproductive structure. The stem may be buried underground as a rhizome from which adventitious roots grow to absorb water and nutrients from the soil, or they may grow above ground as a trunk in tree ferns. Adventitious organs are those that grow in unusual places, such as roots growing from the side of a stem. Most ferns produce the same type of spores and are, therefore, homosporous. The diploid sporophyte is the most conspicuous stage of the life cycle. On the underside of its mature fronds, sori (singular, sorus) form as small clusters where sporangia develop. Sporangia in a sorus produce spores by meiosis and release them into the air. Those that land on a suitable substrate germinate and form a heart-shaped gametophyte, which is attached to the ground by thin filamentous rhizoids. The inconspicuous gametophyte harbors both sex gametangia. Flagellated sperm are released and swim on a wet surface to where the egg is fertilized. The newly-formed zygote grows into a sporophyte that emerges from the gametophyte, growing by mitosis into the next generation sporophyte.



Figure **29.4.1.1**: Sori on a fern frond: Sori appear as small bumps on the underside of a fern frond.

Key Points

- Club mosses, which are the earliest form of seedless vascular plants, are lycophytes that contain a stem and microphylls.
- Horsetails are often found in marshes and are characterized by jointed hollow stems with whorled leaves.
- Photosynthesis occurs in the stems of whisk ferns, which lack roots and leaves.
- Most ferns have branching roots and form large compound leaves, or fronds, that perform photosynthesis and carry the reproductive organs of the plant.

Key Terms

- **sorus**: a cluster of sporangia associated with a fern leaf
- **lycophyte**: a tracheophyte subdivision of the Kingdom Plantae; the oldest extant (living) vascular plant division at around 410 million years old
- **sporangia**: enclosures in which spores are formed

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SECTION OVERVIEW

29.5: Pterophytes Are the Ferns and Their Relatives

29.5.1: Ferns and Other Seedless Vascular Plants

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29.5.1: Ferns and Other Seedless Vascular Plants

Learning Objectives

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Ferns and Other Seedless Vascular Plants

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CHAPTER OVERVIEW

30: Seed Plants

30.1: The Evolution of Seed Plants

30.2: Gymnosperms - Plants with "Naked Seeds"

30.2.1: Characteristics of Gymnosperms

30.2.2: Life Cycle of a Conifer

30.2.3: Diversity of Gymnosperms

30.3: Angiosperms - The Flowering Plants

30.3.1: Angiosperm Flowers

30.3.2: The Life Cycle of an Angiosperm

30.3.3: Diversity of Angiosperms

30.4: Seeds

30.4.1: The Evolution of Seed Plants and Adaptations for Land

30.5: Fruit

30.5.1: Angsiosperm Fruit

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30.1: The Evolution of Seed Plants



Why are they called sunflowers?

When the plant is in the bud stage, the flower tends to track the movement of the sun across the horizon, hence the name sunflower. Flowering plants were the last group of plants to evolve. The flower contains both the male and female reproductive structures, and these plants have become tremendously successful. But these plants could not have evolved without the prior evolution of the seed. So what exactly is a seed?

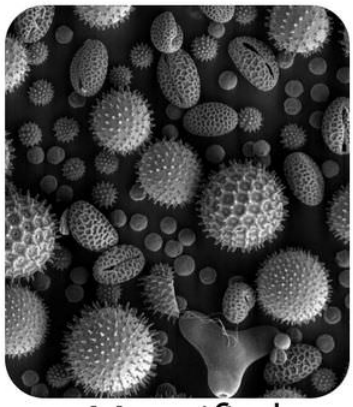
Seed Plants Emerge

For reproduction, early vascular plants still needed moisture. Sperm had to swim from male to female reproductive organs for fertilization. Spores also needed some water to grow and often to disperse as well. Of course, dryness and other harsh conditions made it very difficult for tiny new offspring plants to survive. With the evolution of **seeds** in vascular plants, all that changed. Seed plants evolved a number of adaptations that made it possible to reproduce without water. As a result, seed plants were wildly successful. They exploded into virtually all of Earth's habitats.

Why are seeds so adaptive on land? A seed contains an embryo and a food supply enclosed within a tough coating. An embryo is a zygote that has already started to develop and grow. Early growth and development of a plant embryo in a seed is called **germination**. The seed protects and nourishes the embryo and gives it a huge head start in the "race" of life. Many seeds can wait to germinate until conditions are favorable for growth. This increases the offspring's chance of surviving even more.

Other reproductive adaptations that evolved in seed plants include ovules, pollen, pollen tubes, and pollination by animals.

- An **ovule** is a female reproductive structure in seed plants that contains a tiny female gametophyte. The gametophyte produces an egg cell. After the egg is fertilized by sperm, the ovule develops into a seed.
- A grain of **pollen** is a tiny male gametophyte enclosed in a tough capsule (see **Figure** below). It carries sperm to an ovule while preventing it from drying out. Pollen grains can't swim, but they are very light, so the wind can carry them. Therefore, they can travel through air instead of water.
- Wind-blown pollen might land anywhere and be wasted. Another adaptation solved this problem. Plants evolved traits that attract specific animal **pollinators**. Like the bee in **Figure** below, a pollinator picks up pollen on its body and carries it directly to another plant of the same species. This greatly increases the chance that fertilization will occur.
- Pollen also evolved the ability to grow a tube, called a **pollen tube**, through which sperm could be transferred directly from the pollen grain to the egg. This allowed sperm to reach an egg without swimming through a film of water. It finally freed up plants from depending on moisture to reproduce.



Magnified Pollen Grain



Bee Peppered with Yellow Pollen Grains

Individual grains of pollen may have prickly surfaces that help them stick to pollinators such as bees. What other animals pollinate plants?

Seed Plants Diverge

The first seed plants formed seeds in cones. **Cones** are made up of overlapping scales, which are modified leaves (see **Figure** below). Male cones contain pollen, and female cones contain eggs. Seeds also develop in female cones. Modern seed plants that produce seeds in cones are called **gymnosperms**.





Gymnosperms produce seeds in cones (left). Each scale has a seed attached (right).

Later, seed plants called **angiosperms** evolved. They produce **flowers**, which consist of both male and female reproductive structures. The female reproductive structure in a flower includes an organ called an **ovary**. Eggs form in ovules inside ovaries, which also enclose and protect developing seeds after fertilization occurs. In many species of flowering plants, ovaries develop into **fruits**, which attract animals that disperse the seeds.

Summary

- The evolution of seeds and pollen allowed plants to reproduce on land without moisture.
- Flowering plants evolved flowers with ovaries that formed fruits. They have been the most successful plants of all.

Review

1. What is a seed?
2. Describe cones.
3. Compare and contrast gymnosperms and angiosperms, and give an example of each.
4. Which major plant adaptation—vascular tissues or seeds—do you think was more important in the evolution of plants? Choose one of the two adaptations, and write a logical argument to support your choice.

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SECTION OVERVIEW

30.2: Gymnosperms - Plants with "Naked Seeds"

30.2.1: Characteristics of Gymnosperms

30.2.2: Life Cycle of a Conifer

30.2.3: Diversity of Gymnosperms

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30.2.1: Characteristics of Gymnosperms

Learning Objectives

- Discuss the type of seeds produced by gymnosperms

Characteristics of Gymnosperms

Gymnosperms are seed plants adapted to life on land; thus, they are autotrophic, photosynthetic organisms that tend to conserve water. They have a vascular system (used for the transportation of water and nutrients) that includes roots, xylem, and phloem. The name gymnosperm means “naked seed,” which is the major distinguishing factor between gymnosperms and angiosperms, the two distinct subgroups of seed plants. This term comes from the fact that the ovules and seeds of gymnosperms develop on the scales of cones rather than in enclosed chambers called ovaries.

Gymnosperms are older than angiosperms on the evolutionary scale. They are found far earlier in the fossil record than angiosperms. As will be discussed in subsequent sections, the various environmental adaptations gymnosperms have represent a step on the path to the most successful (diversity-wise) clade (monophyletic branch).



Figure **30.2.1.1**: Female cone of Tamarack pine: The female cone of *Pinus tontorta*, the Tamarack Pine, showing the rough scales. This is the cone that produces ovules.

Gymnosperm Reproduction and Seeds

Gymnosperms are sporophytes (a plant with two copies of its genetic material, capable of producing spores). Their sporangia (receptacle in which sexual spores are formed) are found on sporophylls, plated scale-like structures that together make up cones. The female gametophyte develops from the haploid (meaning one set of genetic material) spores that are contained within the sporangia. Like all seed plants, gymnosperms are heterosporous: both sexes of gametophytes develop from different types of spores produced by separate cones. One type of cone is the small pollen cone, which produces microspores that subsequently develop into pollen grains. The other type of cones, the larger “ovulate” cones, make megaspores that develop into female gametophytes called ovules. Incredibly, this whole sexual process can take three years: from the production of the two sexes of gametophytes, to bringing the gametophytes together in the process of pollination, and finally to forming mature seeds from fertilized ovules. After this process is completed, the individual sporophylls separate (the cone breaks apart) and float in the wind to a habitable place. This is concluded with germination and the formation of a seedling. Conifers have sperm that do not have flagella, but instead are conveyed to the egg via a pollen tube. It is important to note that the seeds of gymnosperms are not enclosed in their final state upon the cone.



Figure **30.2.1.2**: Male cone of Tamarack pine: The male cone of *Pinus tontorta*, the Tamarack pine, showing the close proximity of the scales. This is the cone that produces pollen.

Key Points

- Gymnosperms produce both male and female cones, each making the gametes needed for fertilization; this makes them heterosporous.
- Megaspores made in cones develop into the female gametophytes inside the ovules of gymnosperms, while pollen grains develop from cones that produce microspores.
- Conifer sperm do not have flagella but rather move by way of a pollen tube once in contact with the ovule.

Key Terms

- **ovule**: the structure in a plant that develops into a seed after fertilization; the megasporangium of a seed plant with its enclosing integuments
- **sporophyll**: the equivalent to a leaf in ferns and mosses that bears the sporangia
- **heterosporous**: producing both male and female gametophytes

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30.2.2: Life Cycle of a Conifer

Learning Objectives

- Describe the life cycle of a gymnosperm

Life Cycle of a Conifer

Pine trees are conifers (cone bearing) and carry both male and female sporophylls on the same mature sporophyte. Therefore, they are monoecious plants. Like all gymnosperms, pines are heterosporous, generating two different types of spores: male microspores and female megaspores. In the male cones (staminate cones), the microsporocytes give rise to pollen grains by meiosis. In the spring, large amounts of yellow pollen are released and carried by the wind. Some gametophytes will land on a female cone. Pollination is defined as the initiation of pollen tube growth. The pollen tube develops slowly as the generative cell in the pollen grain divides into two haploid sperm cells by mitosis. At fertilization, one of the sperm cells will finally unite its haploid nucleus with the haploid nucleus of an egg cell.

Female cones (ovulate cones) contain two ovules per scale. One megaspore mother cell (megasporocyte) undergoes meiosis in each ovule. Three of the four cells break down leaving only a single surviving cell which will develop into a female multicellular gametophyte. It encloses archegonia (an archegonium is a reproductive organ that contains a single large egg). Upon fertilization, the diploid egg will give rise to the embryo, which is enclosed in a seed coat of tissue from the parent plant. Fertilization and seed development is a long process in pine trees: it may take up to two years after pollination. The seed that is formed contains three generations of tissues: the seed coat that originates from the sporophyte tissue, the gametophyte that will provide nutrients, and the embryo itself.

In the life cycle of a conifer, the sporophyte (2n) phase is the longest phase. The gametophytes (1n), microspores and megaspores, are reduced in size. This phase may take more than one year between pollination and fertilization while the pollen tube grows towards the megasporocyte (2n), which undergoes meiosis into megaspores. The megaspores will mature into eggs (1n).

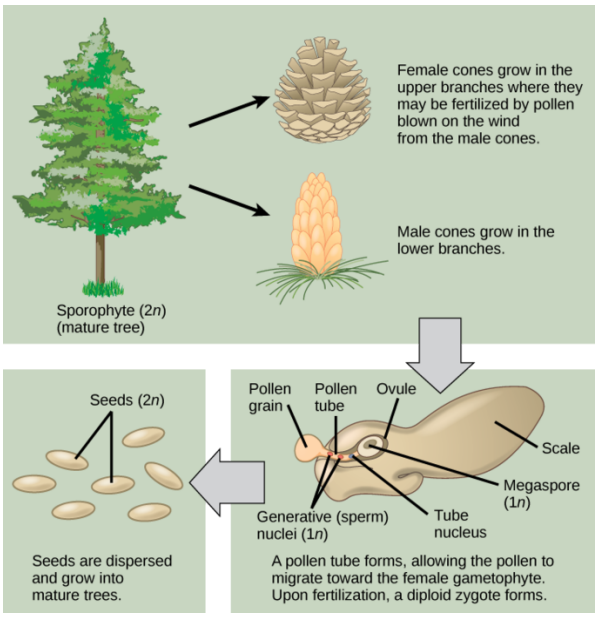


Figure **30.2.2.1**: Life cycle of a conifer: This image shows the life cycle of a conifer. Pollen from male cones moves up into upper branches where it fertilizes female cones.

Key Points

- Male cones give rise to microspores, which produce pollen grains, while female cones give rise to megaspores, which produce ovules.
- The pollen tube develops from the pollen grain to initiate fertilization; the pollen grain divides into two sperm cells by mitosis; one of the sperm cells unites with the egg cell during fertilization.

- Once the ovule is fertilized, a diploid sporophyte is produced, which gives rise to the embryo enclosed in a seed coat of tissue from the parent plant.
- Fertilization and seed development can take years; the seed that is formed is made up of three tissues: the seed coat, the gametophyte, and the embryo.

Key Terms

- **megaspore**: the larger spore of a heterosporous plant, typically producing a female gametophyte
- **microspore**: a small spore, as contrasted to the larger megaspore, which develops into male gametophytes
- **monoecious**: having the male (stamen) and female (carpel) reproductive organs on the same plant rather than on separate plants

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30.2.3: Diversity of Gymnosperms

Learning Objectives

- Give examples showing the diversity of gymnosperms

Diversity of Gymnosperms

Modern gymnosperms are classified into four phyla. The first three (the Coniferophyta, Cycadophyta, and Gingkophyta) are similar in their production of secondary cambium (cells that generate the vascular system of the trunk or stem and are partially specialized for water transportation) and their pattern of seed development. However, these three phyla are not closely related phylogenetically to each other. The fourth phylum (the Gnetophyta) are considered the closest group to angiosperms because they produce true xylem tissue.

Coniferophytes

Conifers are the dominant phylum of gymnosperms, with the most variety of species. They are typically tall trees that usually bear scale-like or needle-like leaves. Water evaporation from leaves is reduced by their thin shape and the thick cuticle. Snow slides easily off needle-shaped leaves, keeping the load light and decreasing breaking of branches. Adaptations to cold and dry weather explain the predominance of conifers at high altitudes and in cold climates. Conifers include familiar evergreen trees such as pines, spruces, firs, cedars, sequoias, and yews. A few species are deciduous, losing their leaves in fall. The European larch and the tamarack are examples of deciduous conifers. Many coniferous trees are harvested for paper pulp and timber. The wood of conifers is more primitive than the wood of angiosperms; it contains tracheids, but no vessel elements, and is, therefore, referred to as “soft wood.”



Figure **30.2.3.1**: Diversity of conifers: Conifers are the dominant form of vegetation in cold or arid environments and at high altitudes. Shown here are the (a) evergreen spruce Picea sp., (b) juniper Juniperus sp., (c) sequoia Sequoia Semervirens, which is a deciduous gymnosperm, and (d) the tamarack Larix larcinia. Notice the yellow leaves of the tamarack.

Cycads

Cycads thrive in mild climates. They are often mistaken for palms because of the shape of their large, compound leaves. Cycads bear large cones and may be pollinated by beetles rather than wind, which is unusual for a gymnosperm (). They dominated the landscape during the age of dinosaurs in the Mesozoic, but only a hundred or so species persisted to modern times. Cycads face possible extinction; several species are protected through international conventions. Because of their attractive shape, they are often used as ornamental plants in gardens in the tropics and subtropics.



Figure **30.2.3.2**: Cycad leaves: This *Encephalartos ferox* cycad has large cones and broad, fern-like leaves.

Gingkophytes

The single surviving species of the gingkophytes group is the *Gingko biloba*. Its fan-shaped leaves, unique among seed plants because they feature a dichotomous venation pattern, turn yellow in autumn and fall from the tree. For centuries, *G. biloba* was cultivated by Chinese Buddhist monks in monasteries, which ensured its preservation. It is planted in public spaces because it is unusually resistant to pollution. Male and female organs are produced on separate plants. Typically, gardeners plant only male trees because the seeds produced by the female plant have an off-putting smell of rancid butter.



Gingko biloba

Gingko biloba is the only surviving species of the phylum Gingkophyta. This plate from the 1870 book Flora Japonica, Sectio Prima (Tafelband) depicts the leaves and fruit of Gingko biloba, as drawn by Philipp Franz von Siebold and Joseph Gerhard Zuccarini.

Gnetophytes

Gnetophytes are the closest relative to modern angiosperms and include three dissimilar genera of plants: *Ephedra*, *Gnetum*, and *Welwitschia*. Like angiosperms, they have broad leaves. In tropical and subtropical zones, gnetophytes are vines or small shrubs. *Ephedra* occurs in dry areas of the West Coast of the United States and Mexico. *Ephedra's* small, scale-like leaves are the source of the compound ephedrine, which is used in medicine as a potent decongestant. Because ephedrine is similar to amphetamines, both in chemical structure and neurological effects, its use is restricted to prescription drugs. Like angiosperms, but unlike other gymnosperms, all gnetophytes possess vessel elements in their xylem.



(a) *Ephedra* (b) *Gnetum* (c) *Welwitschia*

Figure **30.2.3.3**: Gnetophytes: (a) *Ephedra viridis*, known by the common name Mormon tea, grows on the West Coast of the United States and Mexico. (b) *Gnetum gnemon* grows in Malaysia. (c) The large *Welwitschia mirabilis* can be found in the Namibian desert.

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Key Points

- Gymnosperms consist of four main phyla: the Coniferophyta, Cycadophyta, Gingkophyta and Gnetophyta.
- Conifers are the dominant plant of the gymnosperms, having needle-like leaves and living in areas where the weather is cold and dry.
- Cycads live in warm climates, have large, compound leaves, and are unusual in that they are pollinated by beetles rather than wind.
- *Gingko biloba* is the only remaining species of the Gingkophyta and is usually resistant to pollution.
- Gnetophytes are the gymnosperms believed to be most closely related to the angiosperms because of the presence of vessel elements within their stems.

Key Terms

- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts
- **angiosperm**: a plant whose ovules are enclosed in an ovary
- **conifer**: a plant belonging to the conifers; a cone-bearing seed plant with vascular tissue, usually a tree

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SECTION OVERVIEW

30.3: Angiosperms - The Flowering Plants

30.3.1: Angiosperm Flowers

30.3.2: The Life Cycle of an Angiosperm

30.3.3: Diversity of Angiosperms

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30.3.1: Angiosperm Flowers

Learning Objectives

- Describe the main parts of a flower and their purposes

Flowers

Flowers are modified leaves, or sporophylls, organized around a central stalk. Although they vary greatly in appearance, all flowers contain the same structures: sepals, petals, carpels, and stamens. The peduncle attaches the flower to the plant. A whorl of sepals (collectively called the calyx) is located at the base of the peduncle and encloses the unopened floral bud. Sepals are usually photosynthetic organs, although there are some exceptions. For example, the corolla in lilies and tulips consists of three sepals and three petals that look virtually identical. Petals, collectively the corolla, are located inside the whorl of sepals and often display vivid colors to attract pollinators. Flowers pollinated by wind are usually small, feathery, and visually inconspicuous. Sepals and petals together form the perianth. The sexual organs (carpels and stamens) are located at the center of the flower.

Styles, stigmas, and ovules constitute the female organ: the gynoecium or carpel. Flower structure is very diverse. Carpels may be singular, multiple, or fused. Multiple fused carpels comprise a pistil. The megaspores and the female gametophytes are produced and protected by the thick tissues of the carpel. A long, thin structure called a style leads from the sticky stigma, where pollen is deposited, to the ovary, enclosed in the carpel. The ovary houses one or more ovules, each of which will develop into a seed upon fertilization. The male reproductive organs, the stamens (collectively called the androecium), surround the central carpel. Stamens are composed of a thin stalk called a filament and a sac-like structure called the anther. The filament supports the anther, where the microspores are produced by meiosis and develop into pollen grains.

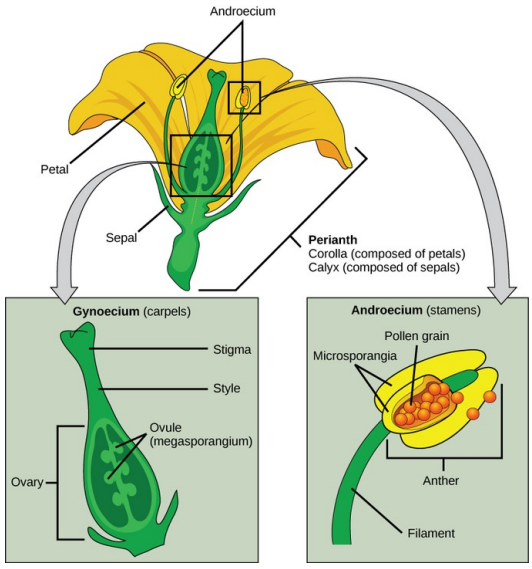


Figure **30.3.1.1**: Structure of flowers: This image depicts the structure of a flower. Perfect flowers produce both male and female floral organs. The flower shown has only one carpel, but some flowers have a cluster of carpels. Together, all the carpels make up the gynoecium.

Key Points

- Sepals, petals, carpels, and stamens are structures found in all flowers.
- To attract pollinators, petals usually exhibit vibrant colors; however, plants that depend on wind pollination contain flowers that are small and light.
- Carpels protect the female gametophytes and megaspores.
- The stigma is the structure where pollen is deposited and is connected to the ovary through the style.
- The anther, which comprises the stamen, is the site of microspore production and their development into pollen.

Key Terms

- **sepal**: a part of an angiosperm, and one of the component parts of the calyx; collectively the sepals are called the calyx (plural calyces), the outermost whorl of parts that form a flower
- **corolla**: an outermost-but-one whorl of a flower, composed of petals, when it is not the same in appearance as the outermost whorl (the calyx); it usually comprises the petal, which may be fused
- **stamen**: in flowering plants, the structure in a flower that produces pollen, typically consisting of an anther and a filament
- **carpel**: one of the individual female reproductive organs in a flower composed of an ovary, a style, and a stigma; also known as the gynoecium

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30.3.2: The Life Cycle of an Angiosperm

Learning Objectives

- Explain the life cycle of an angiosperm, including cross-pollination and the ways in which it takes place

The Life Cycle of an Angiosperm

The adult, or sporophyte, phase is the main phase of an angiosperm's life cycle. As with gymnosperms, angiosperms are heterosporous. Therefore, they generate microspores, which will produce pollen grains as the male gametophytes, and megaspores, which will form an ovule that contains female gametophytes. Inside the anthers' microsporangia, male gametophytes divide by meiosis to generate haploid microspores, which, in turn, undergo mitosis and give rise to pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm and a second cell that will become the pollen tube cell.

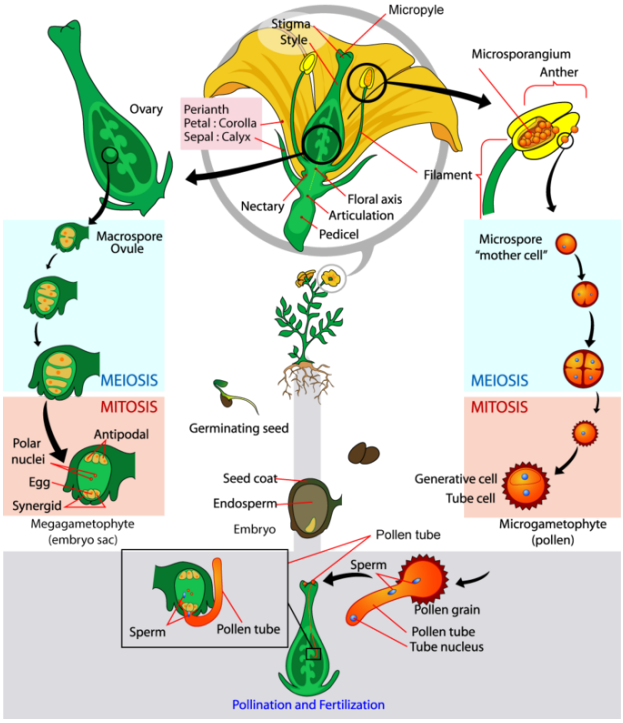


Figure **30.3.2.1**: Life cycle of angiosperms: The life cycle of an angiosperm is shown. Anthers and carpels are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms.

The ovule, sheltered within the ovary of the carpel, contains the megasporangium protected by two layers of integuments and the ovary wall. Within each megasporangium, a megasporocyte undergoes meiosis, generating four megaspores: three small and one large. Only the large megaspore survives; it produces the female gametophyte referred to as the embryo sac. The megaspore divides three times to form an eight-cell stage. Four of these cells migrate to each pole of the embryo sac; two come to the equator and will eventually fuse to form a 2n polar nucleus. The three cells away from the egg form antipodals while the two cells closest to the egg become the synergids.

The mature embryo sac contains one egg cell, two synergids ("helper" cells), three antipodal cells, and two polar nuclei in a central cell. When a pollen grain reaches the stigma, a pollen tube extends from the grain, grows down the style, and enters through the micropyle, an opening in the integuments of the ovule. The two sperm cells are deposited in the embryo sac.

A double fertilization event then occurs. One sperm and the egg combine, forming a diploid zygote, the future embryo. The other sperm fuses with the 2n polar nuclei, forming a triploid cell that will develop into the endosperm, which is tissue that serves as a food reserve. The zygote develops into an embryo with a radicle, or small root, and one (monocot) or two (dicot) leaf-like organs called cotyledons. This difference in the number of embryonic leaves is the basis for the two major groups of angiosperms: the monocots and the eudicots. Seed food reserves are stored outside the embryo in the form of complex carbohydrates, lipids, or

proteins. The cotyledons serve as conduits to transmit the broken-down food reserves from their storage site inside the seed to the developing embryo. The seed consists of a toughened layer of integuments forming the coat, the endosperm with food reserves, and the well-protected embryo at the center.



Figure **30.3.2.1**: The fruit of the Aesculus or Horse Chestnut tree: These seeds are enclosed a protective outer covering called the seed coat, usually with some stored food. After fertilization and some growth in the angiosperm, the ripened ovule is produced. The formation of the seed completes the process of reproduction in seed plants (started with the development of flowers and pollination), with the embryo developed from the zygote and the seed coat from the integuments of the ovule.

Some species of angiosperms are hermaphroditic (stamens and pistils are contained on a single flower), some species are monoecious (stamens and pistils occur on separate flowers, but the same plant), and some are dioecious (staminate and pistillate flowers occur on separate plants). Both anatomical and environmental barriers promote cross-pollination mediated by a physical agent (wind or water) or an animal, such as an insect or bird. Cross-pollination increases genetic diversity in a species.

Key Points

- Microspores develop into pollen grains, which are the male gametophytes, while megaspores form an ovule that contains the female gametophytes.
- In the ovule, the megasporocyte undergoes meiosis, generating four megaspores; three small and one large; only the large megaspore survives and produces the female gametophyte (embryo sac).
- When the pollen grain reaches the stigma, it extends its pollen tube to enter the ovule and deposits two sperm cells in the embryo sac.
- The two available sperm cells allow for double fertilization to occur, which results in a diploid zygote (the future embryo) and a triploid cell (the future endosperm), which acts as a food store.
- Some species are hermaphroditic (stamens and pistils are contained on a single flower), some species are monoecious (stamens and pistils occur on separate flowers, but the same plant), and some are dioecious (staminate and pistillate flowers occur on separate plants).

Key Terms

- **cotyledon**: the leaf of the embryo of a seed-bearing plant; after germination it becomes the first leaves of the seedling
- **heterosporous**: producing both male and female gametophytes
- **synergid**: either of two nucleated cells at the top of the embryo sac that aid in the production of the embryo; helper cells

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30.3.3: Diversity of Angiosperms

Learning Objectives

- Explain how angiosperm diversity is classified

Diversity of Angiosperms

Angiosperms are classified in a single phylum: the Anthophyta. Modern angiosperms appear to be a monophyletic group, which means that they originated from a single ancestor. Flowering plants are divided into two major groups according to the structure of the cotyledons and pollen grains, among others. Monocots include grasses and lilies while eudicots or dicots form a polyphyletic group. However, many species exhibit characteristics that belong to either group; as such, the classification of a plant as a monocot or a eudicot is not always clearly evident. Basal angiosperms are a group of plants that are believed to have branched off before the separation into monocots and eudicots because they exhibit traits from both groups. They are categorized separately in many classification schemes. The Magnoliidae (magnolia trees, laurels, and water lilies) and the Piperaceae (peppers) belong to the basal angiosperm group.

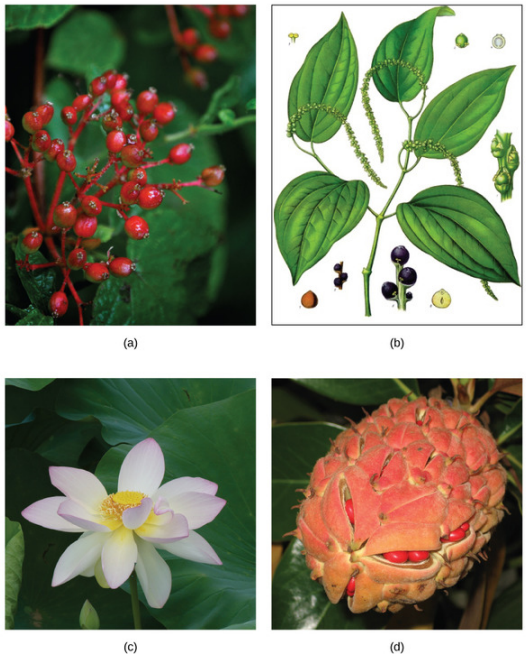


Figure **30.3.3.1**: Examples of basal angiosperms: The (a) common spicebush belongs to the Laurales, the same family as cinnamon and bay laurel. The fruit of (b) the *Piper nigrum* plant is black pepper, the main product that was traded along spice routes. Notice the small, unobtrusive, clustered flowers. (c) Lotus flowers, *Nelumbo nucifera*, have been cultivated since ancient times for their ornamental value; the root of the lotus flower is eaten as a vegetable. The red seeds of (d) a magnolia tree, characteristic of the final stage, are just starting to appear.

Basal Angiosperms

Examples of basal angiosperms include the Magnoliidae, Laurales, Nymphaeales, and the Piperales. Members in these groups all share traits from both monocot and dicot groups. The Magnoliidae are represented by the magnolias: tall trees bearing large, fragrant flowers that have many parts and are considered archaic. Laurel trees produce fragrant leaves and small, inconspicuous flowers. The Laurales grow mostly in warmer climates and are small trees and shrubs. Familiar plants in this group include the bay laurel, cinnamon, spice bush, and avocado tree. The Nymphaeales are comprised of the water lilies, lotus, and similar plants; all species thrive in freshwater biomes and have leaves that float on the water surface or grow underwater. Water lilies are particularly prized by gardeners and have graced ponds and pools for thousands of years. The Piperales are a group of herbs, shrubs, and small trees that grow in the tropical climates. They have small flowers without petals that are tightly arranged in long spikes. Many

species are the source of prized fragrance or spices; for example, the berries of *Piper nigrum* are the familiar black peppercorns that are used to flavor many dishes.

Monocots

Plants in the monocot group are primarily identified as such by the presence of a single cotyledon in the seedling. Other anatomical features shared by monocots include veins that run parallel to the length of the leaves and flower parts that are arranged in a three- or six-fold symmetry. True woody tissue is rarely found in monocots. In palm trees, vascular and parenchyma tissues produced by the primary and secondary thickening of meristems form the trunk. The pollen from the first angiosperms was monosulcate, containing a single furrow or pore through the outer layer. This feature is still seen in the modern monocots. Vascular tissue of the stem is not arranged in any particular pattern. The root system is mostly adventitious and unusually positioned, with no major tap root. The monocots include familiar plants such as the true lilies (which are the origin of their alternate name: Liliopsida), orchids, grasses, and palms. Many important crops are monocots, such as rice and other cereals, corn, sugar cane, and tropical fruits like bananas and pineapples.



Figure **30.3.3.1**: Monocots and Dicots: major crops of the world: The world's major crops are flowering plants. (a) Rice, (b) wheat, and (c) bananas are monocots, while (d) cabbage, (e) beans, and (f) peaches are dicots.

Eudicots

Eudicots, or true dicots, are characterized by the presence of two cotyledons in the developing shoot. Veins form a network in leaves, while flower parts come in four, five, or many whorls. Vascular tissue forms a ring in the stem whereas in monocots, vascular tissue is scattered in the stem. Eudicots can be herbaceous (like grasses), or produce woody tissues. Most eudicots produce pollen that is trisulcate or triporate, with three furrows or pores. The root system is usually anchored by one main root developed from the embryonic radicle. Eudicots comprise two-thirds of all flowering plants.

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Key Points

- Angiosperm are flowering plants that are classified based on characteristics that include (but are not limited to) cotyledon structure, pollen grains, as well as flower and vascular tissue arrangement.
- Basal angiosperms, classified separately, contain features found in both monocots and dicots, as they are believed to have originated before the separation of these two main groups.
- Monocots contain a single cotyledon and have veins that run parallel to the length of their leaves; their flowers are arranged in three to six-fold symmetry.
- Dicots have flowers arranged in whorls, two cotyledons, and a vein arrangement that forms networks within their leaves.
- Monocots do not contain any true woody tissue while dicots can be herbacious or woody and have vascular tissue that forms a ring in the stem.

Key Terms

- **dicot**: a plant whose seedlings have two cotyledons; a dicotyledon
- **angiosperm**: a plant whose ovules are enclosed in an ovary
- **monocot**: one of two major groups of flowering plants (or angiosperms) that are traditionally recognized; seedlings typically have one cotyledon (seed-leaf)
- **cotyledon**: the leaf of the embryo of a seed-bearing plant; after germination it becomes the first leaves of the seedling
- **basal angiosperm**: the first flowering plants to diverge from the ancestral angiosperm, including a single species of shrub from New Caledonia, water lilies and some other aquatic plants, and woody aromatic plants

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30.4: Seeds

Angiosperms are the flowering plants (today the most abundant and diverse plants on earth). Most are terrestrial and all lack locomotion. This poses several problems. Gametes are delicate single cells. For two plants to cross fertilize, there must be a mechanism for the two gametes to reach each other safely. Moreover, there must also be a mechanism to disperse their offspring far enough away from the parent so that they do not have to compete with the parent for light, water, and soil minerals. The functions of the **flower** solve both of these problems.

The Flower and Its Pollination

In angiosperms, meiosis in the sporophyte generation produces two kinds of spores: (1) **microspores** which develop in the **microsporangium** and will germinate and develop into the male gametophyte generation and (2) **megaspores** that develop in the **megasporangium** will develop into the female gametophyte generation. Both types of sporangia are formed in flowers. In most angiosperms, the flowers are **perfect**: each has both microsporangia and megasporangia, although some angiosperms are **imperfect**, having either microsporangia or megasporangia but not both.

- **Monoecious** plants have both types of imperfect flower on the same plant.
- **Dioecious** plants have imperfect flowers on separate plants; that is, some plants are male, some female. Examples include willows, poplars, and the date palm. Most dioecious plants use an X-Y system of of sex determination like that in mammals. However, a few species use an X-to-autosome ratio system like that of *Drosophila*, and a very few use a ZW system like that of birds and lepidoptera.

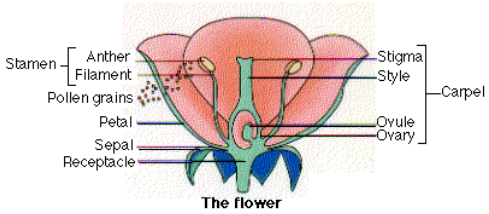


Figure 16.3.4.1 Flower

Flowers develop from flower buds. Each bud contains 4 concentric whorls of tissue. From the outer to the inner, these develop into

- a whorl of **sepals** (collectively called the **calyx**)
- a whorl of **petals** (collectively called the **corolla**)
- **stamens** in which the microsporangia form
- **carpels** in which the megasporangia form.

Stamens

Each stamen consists of a lobed **anther**, containing the microsporangia and supported by a thin **filament.** Meiosis of the diploid microspore mother cells in the anther produces four haploid **microspores**. Each of these develops into a **pollen grain** consisting of **a larger vegetative cell** (also called the tube cell) inside of which is a a smaller **germ cell** (also called the generative cell). At some point, depending on the species, the germ cell divides by mitosis to produce 2 **sperm cells**.

Carpels

Carpels consist of a **stigma**, usually mounted at the tip of a **style** with an **ovary** at the base. Often the entire whorl of carpels is fused into a single **pistil**. The megasporangia, called **ovules**, develop within the ovary. Meiosis of the megaspore mother cell in each ovule produces 4 haploid cells, a large **megaspore** and 3 small cells that disintegrate.

Development of the megaspore

The nucleus of the megaspore undergoes three successive mitotic divisions. The 8 nuclei that result are distributed and partitioned off by cell walls to form the **embryo sac**. This is the **mature female gametophyte generation**. The **egg cell** will start the new sporophyte generation if it is fertilized. It is flanked by 2 synergid cells. In several (perhaps all) angiosperms, they secrete an

attractant that guides the pollen tube through the **micropyle** into the embryo sac. The large **central cell**, which in most angiosperms contains 2 **polar nuclei**, will after its fertilization develop into the **endosperm** of the seed. It also contains 3 antipodal cells.

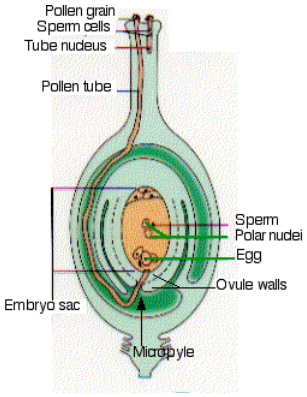


Figure 16.3.4.2 Embryo sac

Pollination

When a pollen grain reaches the stigma, it germinates into a **pollen tube**. If it hasn't done so already, the germ cell divides by mitosis forming 2 **sperm cells**. These, along with the tube nucleus (also known as the vegetative nucleus), migrate down the pollen tube as it grows through the style, the micropyle, and into the ovule chamber.

In Arabidopsis the pollen tube follows a gradient of increasing concentration of a small defensin-like protein secreted by the synergids. The pollen tube with its contents makes up the **mature male gametophyte generation**.

Double fertilization

The pollen tube enters the ovule through the micropyle and ruptures. One sperm cell fuses with the egg forming the diploid **zygote**. The other sperm cell fuses with the polar nuclei forming the **endosperm nucleus**. Most angiosperms have two polar nuclei so the endosperm is **triploid** (3n). The tube nucleus disintegrates.

Most angiosperms have mechanisms by which they avoid self-fertilization.

Seeds

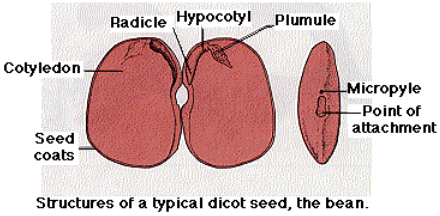


Figure 16.3.4.3 Bean seed

After double fertilization, **each ovule develops into a seed**, which consists of

- a **plumule**, made up of two embryonic leaves, which will become the first true leaves of the seedling, and a terminal (apical) bud. The terminal bud contains the meristem at which later growth of the stem takes place.
- One or two **cotyledons** which store food that will be used by the germinating seedling. Angiosperms that produce seeds with two cotyledons are called **dicots**. Examples include beans, squashes, Arabidopsis. Angiosperms whose seeds contain only a single cotyledon are **monocots**. Examples include corn and other grasses.
- The **hypocotyl** and **radicle**, which will grow into the part of the stem below the first node ("hypocotyl" = below the cotyledons) and primary root respectively. The development of each of the parts of the plant embryo depends on gradients of the plant hormone, auxin.
- In addition to the embryo plant (derived from the zygote), each seed is covered with protective seed coats derived from the walls of the ovule.

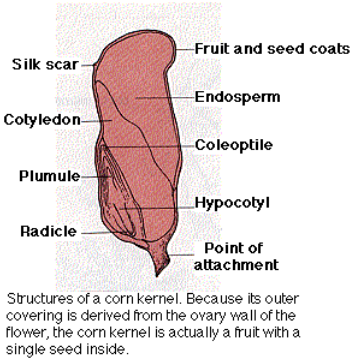


Figure 16.3.4.4 Corn kernel

The food in the cotyledons is derived from the endosperm which, in turn, received it from the parent sporophyte. In many angiosperms (e.g., beans), when the seeds are mature, the endosperm has been totally consumed and its food transferred to the cotyledons. In others (some dicots and all monocots), the endosperm persists in the mature seed.

The seed is thus a dormant embryo sporophyte with stored food and protective coats. Its two functions are

- dispersal of the species to new locations (aided in angiosperms by the **fruit**)
- survival of the species during unfavorable climatic periods (e.g., winter). "Annual" plants (e.g., beans, cereal grains, many weeds) can survive freezing only as seeds. When the parents die in the fall, the seeds remain alive — though dormant— over the winter. When conditions are once more favorable, **germination** occurs and a new generation of plants develops.

Fruits

Fruits are a development of the **ovary wall** and sometimes other flower parts as well. As seeds mature, they release the hormone auxin, which stimulates the wall of the ovary to develop into the fruit. In fact, commercial fruit growers may stimulate fruit development in unpollinated flowers by applying synthetic auxin to the flower.

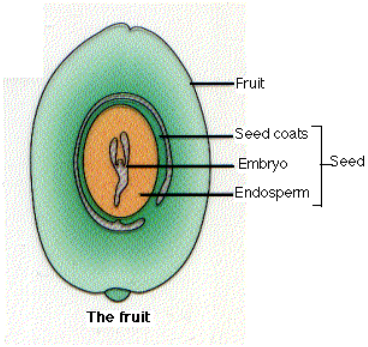


Figure 16.3.4.5 Fruit

Fruits promote the dispersal of their content of seeds in a variety of ways.

- Wind. The maple "key" and dandelion parachute are examples.
- Water. Many aquatic angiosperms and shore dwellers (e.g., the coconut palm) have floating fruits that are carried by water currents to new locations.
- Hitchhikers. The cocklebur and sticktights achieve dispersal of their seeds by sticking to the coat (or clothing) of a passing animal.
- Edible fruits. Nuts and berries entice animals to eat them. Buried and forgotten (nuts) or passing through their g.i. tract unharmed (berries), the seeds may end up some distance away from the parent plant.
- Mechanical. Some fruits, as they dry, open explosively expelling their seeds. The pods of many legumes (e.g., wisteria) do this.

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30.4.1: The Evolution of Seed Plants and Adaptations for Land

Learning Objectives

- Recognize the significance of seed plant evolution

Evolution of Seed Plants

The lush palms on tropical shorelines do not depend upon water for the dispersal of their pollen, fertilization, or the survival of the zygote, unlike mosses, liverworts, and ferns of the terrain. Seed plants, such as palms, have broken free from the need to rely on water for their reproductive needs. They play an integral role in all aspects of life on the planet, shaping the physical terrain, influencing the climate, and maintaining life as we know it. For millennia, human societies have depended upon seed plants for nutrition and medicinal compounds; and more recently, for industrial by-products, such as timber and paper, dyes, and textiles. Palms provide materials including rattans, oils, and dates. Wheat is grown to feed both human and animal populations. The fruit of the cotton boll flower is harvested as a boll, with its fibers transformed into clothing or pulp for paper. The showy opium poppy is valued both as an ornamental flower and as a source of potent opiate compounds.

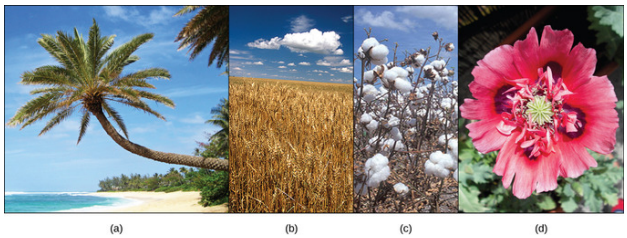


Figure **30.4.1.1**: Seed plants dominate the landscape: Seed plants dominate the landscape and play an integral role in human societies. (a) Palm trees grow along the shoreline; (b) wheat is a crop grown in most of the world; (c) the flower of the cotton plant produces fibers that are woven into fabric; (d) the potent alkaloids of the beautiful opium poppy have influenced human life both as a medicinal remedy and as a dangerously-addictive drug.

Seeds and Pollen as an Evolutionary Adaptation to Dry Land

Unlike bryophyte and fern spores (which are haploid cells dependent on moisture for rapid development of gametophytes), seeds contain a diploid embryo that will germinate into a sporophyte. Storage tissue to sustain growth and a protective coat give seeds their superior evolutionary advantage. Several layers of hardened tissue prevent desiccation, freeing reproduction from the need for a constant supply of water. Furthermore, seeds remain in a state of dormancy induced by desiccation and the hormone abscisic acid until conditions for growth become favorable. Whether blown by the wind, floating on water, or carried away by animals, seeds are scattered in an expanding geographic range, thus avoiding competition with the parent plant.

Pollen grains are male gametophytes carried by wind, water, or a pollinator. The whole structure is protected from desiccation and can reach the female organs without dependence on water. Male gametes reach female gametophyte and the egg cell gamete though a pollen tube: an extension of a cell within the pollen grain. The sperm of modern gymnosperms lack flagella, but in cycads and the Gingko, the sperm still possess flagella that allow them to swim down the pollen tube to the female gamete; however, they are enclosed in a pollen grain.

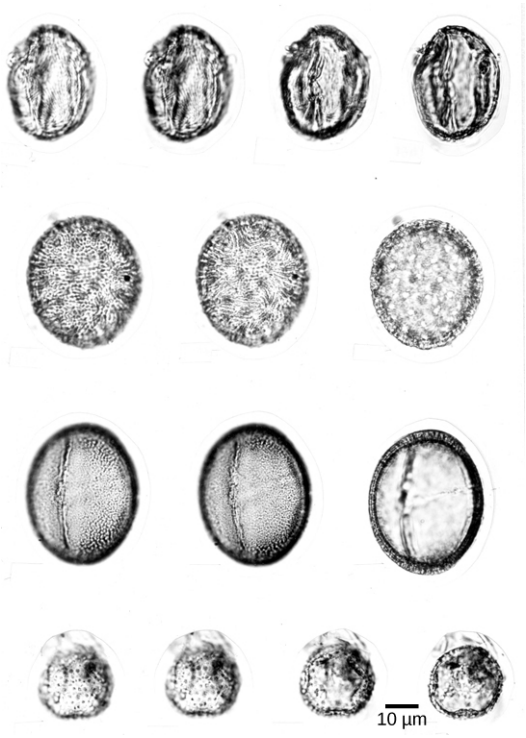


Figure **30.4.1.1**: Fossilized pollen grains: This fossilized pollen is from a Buckbean fen core found in Yellowstone National Park, Wyoming. The pollen is magnified 1,054 times.

Key Points

- Plants are used for food, textiles, medicines, building materials, and many other products that are important to humans.
- The evolution of seeds allowed plants to decrease their dependency upon water for reproduction.
- Seeds contain an embryo that can remain dormant until conditions are favorable when it grows into a diploid sporophyte.
- Seeds are transported by the wind, water, or by animals to encourage reproduction and reduce competition with the parent plant.

Key Terms

- **seed**: a fertilized ovule, containing an embryonic plant
- **sporophyte**: a plant (or the diploid phase in its life cycle) that produces spores by meiosis in order to produce gametophytes
- **pollen**: microspores produced in the anthers of flowering plants

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30.5: Fruit

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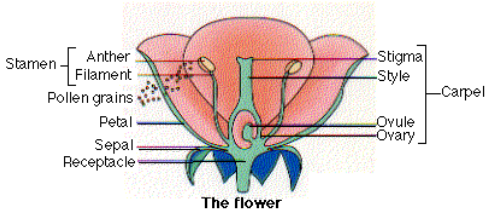


Figure 16.3.4.1 Flower

Flowers develop from flower buds. Each bud contains 4 concentric whorls of tissue. From the outer to the inner, these develop into

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- a whorl of **petals** (collectively called the **corolla**)
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Development of the megaspore

The nucleus of the megaspore undergoes three successive mitotic divisions. The 8 nuclei that result are distributed and partitioned off by cell walls to form the **embryo sac**. This is the **mature female gametophyte generation**. The **egg cell** will start the new sporophyte generation if it is fertilized. It is flanked by 2 synergid cells. In several (perhaps all) angiosperms, they secrete an

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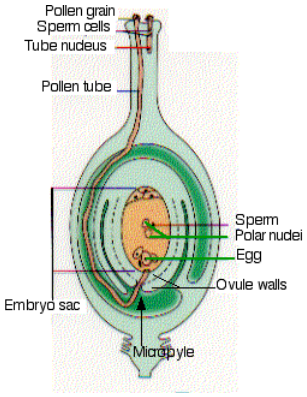


Figure 16.3.4.2 Embryo sac

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When a pollen grain reaches the stigma, it germinates into a **pollen tube**. If it hasn't done so already, the germ cell divides by mitosis forming 2 **sperm cells**. These, along with the tube nucleus (also known as the vegetative nucleus), migrate down the pollen tube as it grows through the style, the micropyle, and into the ovule chamber.

In Arabidopsis the pollen tube follows a gradient of increasing concentration of a small defensin-like protein secreted by the synergids. The pollen tube with its contents makes up the **mature male gametophyte generation**.

Double fertilization

The pollen tube enters the ovule through the micropyle and ruptures. One sperm cell fuses with the egg forming the diploid **zygote**. The other sperm cell fuses with the polar nuclei forming the **endosperm nucleus**. Most angiosperms have two polar nuclei so the endosperm is **triploid** (3n). The tube nucleus disintegrates.

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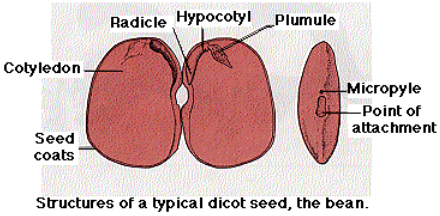


Figure 16.3.4.3 Bean seed

After double fertilization, **each ovule develops into a seed**, which consists of

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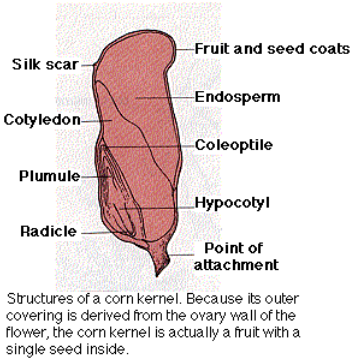


Figure 16.3.4.4 Corn kernel

The food in the cotyledons is derived from the endosperm which, in turn, received it from the parent sporophyte. In many angiosperms (e.g., beans), when the seeds are mature, the endosperm has been totally consumed and its food transferred to the cotyledons. In others (some dicots and all monocots), the endosperm persists in the mature seed.

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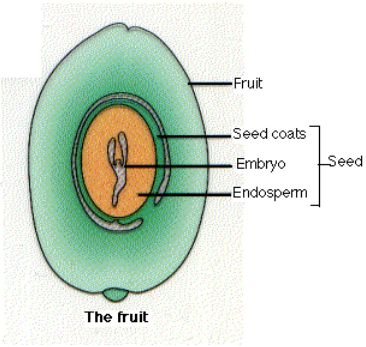


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- Mechanical. Some fruits, as they dry, open explosively expelling their seeds. The pods of many legumes (e.g., wisteria) do this.

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30.5.1: Angsiosperm Fruit

Learning Objectives

- Recall the evolutionary advantage of fruits

Fruit

In botany, a fertilized, fully-grown, and ripened ovary is a fruit. As the seed develops, the walls of the ovary in which it forms thicken and form the fruit, enlarging as the seeds grow. Many foods commonly-called vegetables are actually fruit. Eggplants, zucchini, string beans, and bell peppers are all technically fruit because they contain seeds and are derived from the thick ovary tissue. Acorns are nuts and winged, maple whirligigs (whose botanical name is samara) are also fruit. Botanists classify fruit into more than two dozen different categories, only a few of which are actually fleshy and sweet.

Mature fruit can be fleshy or dry. Fleshy fruit include the familiar berries, peaches, apples, grapes, and tomatoes. Rice, wheat, and nuts are examples of dry fruit. Another distinction is that not all fruits are derived from the ovary. For instance, strawberries are derived from the receptacle, while apples are derived from the pericarp, or hypanthium. Some fruits are derived from separate ovaries in a single flower, such as the raspberry. Other fruits, such as the pineapple, form from clusters of flowers. Additionally, some fruits, like watermelon and oranges, have rinds.

Regardless of how they are formed, fruits are an agent of seed dispersal. The variety of shapes and characteristics reflect the mode of dispersal, whether it be wind, water, or animals. Wind carries the light dry fruit of trees and dandelions. Water transports floating coconuts. Some fruits attract herbivores with color or perfume, or as food. Once eaten, tough, undigested seeds are dispersed through the herbivore's feces. Other fruits have burs and hooks to cling to fur and hitch rides on animals.



Figure **30.5.1.1**: Wind dispersal: The winged shape of *Alsomitra macrocarpa*'s seeds allow them to use wind for dispersal. They can, therefore, glide for great distances.



Figure **30.5.1.1**: Fruit dispersal: A fruit's distinctive shape and specialized characteristics will determine its dispersal mechanism.

Key Points

- Scientists classify fruit in many different categories that include descriptions, such as mature, fleshy, and dry; only a few are actually classified as being fleshy and sweet.
- Some fruit are developed from ovaries, while others develop from the pericarp, from clusters of flowers, or from separate ovaries in a single flower.
- Fruit are vital dispersal agents for plants; their unique shapes and features evolved to take advantage of specific dispersal modes.
- Dispersal methods of seeds within fruit include wind, water, herbivores, and animal fur.

Key Terms

- **fruit**: the seed-bearing part of a plant, often edible, colorful, and fragrant, produced from a floral ovary after fertilization
- **pericarp**: the outermost layer, or skin, of a ripe fruit or ovary
- **hypanthium**: the bowl-shaped part of a flower on which the sepals, petals, and stamens are borne

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CHAPTER OVERVIEW

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31.6: Ascomycota- The Sac (Ascus) Fungi

31.7: Glomeromycota- Asexual Plant Symbionts

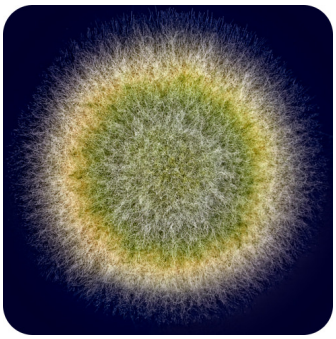
31.8: Zygomycota- Zygote-Producing Fungi

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31.1: Classification of Fungi



What type of fungus is this?

Obviously a mold. But what type of mold? There are thousands of known species of molds. How are they classified?

Classification of Fungi

For a long time, scientists considered fungi to be members of the plant kingdom because they have obvious similarities with plants. Both fungi and plants are immobile, have cell walls, and grow in soil. Some fungi, such as **lichens**, even look like plants (see **Figure** below).



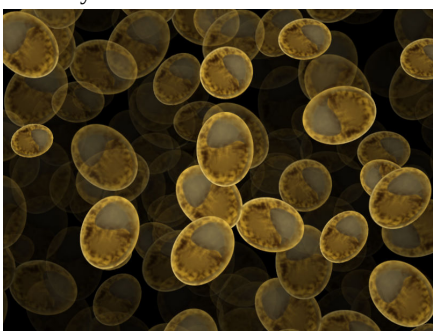
Moss (Plant) and Lichen Growing on Tree Bark. Both fungi and moss are growing on this tree. Can you tell them apart?

The Kingdom Fungi

Today, fungi are no longer classified as plants. We now know that they have unique physical, chemical, and genetic traits that set them apart from plants and other eukaryotes. For example, the cell walls of fungi are made of **chitin**, not cellulose. Also, fungi absorb nutrients from other organisms, whereas plants make their own food. These are just a few of the reasons fungi are now placed in their own kingdom.

Fungal Phyla

Classification of fungi below the level of the kingdom is controversial. There is no single, widely-accepted system of fungal classification. Most classifications include several phyla (the next major taxon below the kingdom). Three of the most common phyla are compared in**Table** below.

Phylum	Description	Example
Zygomycota	mainly terrestrial, live in soil and compost and on foods such as bread	black bread mold 
Basidiomycota	have many different shapes, considerable variation exists even within species	button mushrooms 
Ascomycota	found in all terrestrial ecosystems world-wide, even in Antarctica, often involved in symbiotic relationships	baker's yeast 



Summary

- Fungi used to be classified as plants. Now, they are known to have unique traits that set them apart from plants. For example, fungal cell walls contain chitin, not cellulose, and fungi absorb food rather than make their own.
- Below the level of the kingdom, classification of fungi is controversial.

Review

1. State why fungi were once classified as plants.
2. Explain the significance of the chitin cell wall of fungi.
3. Mushrooms belong to what phylum of fungi?

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31.2: Fungal Forms, Nutrition, and Reproduction



Figure 31.2.1: The (a) familiar mushroom is only one type of fungus. The brightly colored fruiting bodies of this (b) coral fungus are displayed. This (c) electron micrograph shows the spore-bearing structures of Aspergillus, a type of toxic fungi found mostly in soil and plants. (credit a: modification of work by Chris Wee; credit b: modification of work by Cory Zanker; credit c: modification of work by Janice Haney Carr, Robert Simmons, CDC; scale-bar data from Matt Russell)

The word *fungus* comes from the Latin word for mushroom. Indeed, the familiar mushrooms are fungi, but there are many other types of fungi as well (Figure 31.2.1). The kingdom Fungi includes an enormous variety of living organisms collectively referred to as Eumycota, or true fungi. While scientists have identified about 100,000 species of fungi, this is only a fraction of the over 1 million species likely present on Earth. Edible mushrooms, yeasts, black mold, and *Penicillium notatum* (the producer of the antibiotic penicillin) are all members of the kingdom Fungi, which belongs to the domain Eukarya. As eukaryotes, a typical fungal cell contains a true nucleus and many membrane-bound organelles.

Fungi were once considered plant-like organisms; however, DNA comparisons have shown that fungi are more closely related to animals than plants. Fungi are not capable of photosynthesis: They use complex organic compounds as sources of energy and carbon. Some fungal organisms multiply only asexually, whereas others undergo both asexual reproduction and sexual reproduction. Most fungi produce a large number of spores that are disseminated by the wind. Like bacteria, fungi play an essential role in ecosystems, because they are decomposers and participate in the cycling of nutrients by breaking down organic materials into simple molecules.

Fungi often interact with other organisms, forming mutually beneficial or mutualistic associations. Fungi also cause serious infections in plants and animals. For example, Dutch elm disease is a particularly devastating fungal infection that destroys many native species of elm (*Ulmus* spp.). The fungus infects the vascular system of the tree. It was accidentally introduced to North America in the 1900s and decimated elm trees across the continent. Dutch elm disease is caused by the fungus *Ophiostoma ulmi*. The elm bark beetle acts as a vector and transmits the disease from tree to tree. Many European and Asiatic elms are less susceptible than American elms.

In humans, fungal infections are generally considered challenging to treat because, unlike bacteria, they do not respond to traditional antibiotic therapy since they are also eukaryotes. These infections may prove deadly for individuals with a compromised immune system.

Fungi have many commercial applications. The food industry uses yeasts in baking, brewing, and wine making. Many industrial compounds are byproducts of fungal fermentation. Fungi are the source of many commercial enzymes and antibiotics.

Cell Structure and Function

Fungi are eukaryotes and as such have a complex cellular organization. As eukaryotes, fungal cells contain a membrane-bound nucleus. A few types of fungi have structures comparable to the plasmids (loops of DNA) seen in bacteria. Fungal cells also contain mitochondria and a complex system of internal membranes, including the endoplasmic reticulum and Golgi apparatus.

Fungal cells do not have chloroplasts. Although the photosynthetic pigment chlorophyll is absent, many fungi display bright colors, ranging from red to green to black. The poisonous *Amanita muscaria* (fly agaric) is recognizable by its bright red cap with white patches (Figure 31.2.2). Pigments in fungi are associated with the cell wall and play a protective role against ultraviolet radiation. Some pigments are toxic.



Figure 31.2.2: The poisonous Amanita muscaria is native to the temperate and boreal regions of North America. (credit: Christine Majul)

Like plant cells, fungal cells are surrounded by a thick cell wall; however, the rigid layers contain the complex polysaccharides chitin and glucan and not cellulose that is used by plants. Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The cell wall protects the cell from desiccation and predators. Fungi have plasma membranes similar to other eukaryotes, except that the structure is stabilized by ergosterol, a steroid molecule that functions like the cholesterol found in animal cell membranes. Most members of the kingdom Fungi are nonmotile. Flagella are produced only by the gametes in the primitive division Chytridiomycota.

Growth and Reproduction

The vegetative body of a fungus is called a thallus and can be unicellular or multicellular. Some fungi are dimorphic because they can go from being unicellular to multicellular depending on environmental conditions. Unicellular fungi are generally referred to as yeasts.*Saccharomyces cerevisiae* (baker's yeast) and *Candida* species (the agents of thrush, a common fungal infection) are examples of unicellular fungi.

Most fungi are multicellular organisms. They display two distinct morphological stages: vegetative and reproductive. The vegetative stage is characterized by a tangle of slender thread-like structures called hyphae (singular, hypha), whereas the reproductive stage can be more conspicuous. A mass of hyphae is called a mycelium (Figure 31.2.3). It can grow on a surface, in soil or decaying material, in a liquid, or even in or on living tissue. Although individual hypha must be observed under a microscope, the mycelium of a fungus can be very large with some species truly being "the fungus humongous." The giant *Armillaria ostoyae* (honey mushroom) is considered the largest organism on Earth, spreading across over 2,000 acres of underground soil in eastern Oregon; it is estimated to be at least 2,400 years old.

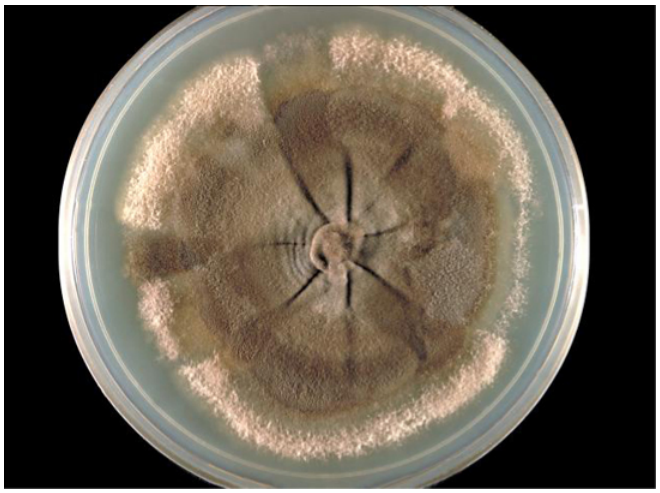


Figure 31.2.3: The mycelium of the fungus Neotestudina rosati can be pathogenic to humans. The fungus enters through a cut or scrape and develops into a mycetoma, a chronic subcutaneous infection. (credit: CDC)

Most fungal hyphae are divided into separate cells by end walls called septa (singular, septum). In most divisions (like plants, fungal phyla are called *divisions* by tradition) of fungi, tiny holes in the septa allow for the rapid flow of nutrients and small molecules from cell to cell along the hyphae. They are described as perforated septa. The hyphae in bread molds (which belong to the division Zygomycota) are not separated by septa. They are formed of large cells containing many nuclei, an arrangement described as coenocytic hyphae.

Fungi thrive in environments that are moist and slightly acidic, and can grow with or without light. They vary in their oxygen requirements. Most fungi are obligate aerobes, requiring oxygen to survive. Other species, such as the Chytridiomycota that reside in the rumen of cattle, are obligate anaerobes, meaning that they cannot grow and reproduce in an environment with oxygen. Yeasts are intermediate: They grow best in the presence of oxygen but can use fermentation in the absence of oxygen. The alcohol produced from yeast fermentation is used in wine and beer production, and the carbon dioxide they produce carbonates beer and sparkling wine, and makes bread rise.

Fungi can reproduce sexually or asexually. In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by either floating in the wind or hitching a ride on an animal. Fungal spores are smaller and lighter than plant seeds, but they are not usually released as high in the air. The giant puffball mushroom bursts open and releases trillions of spores: The huge number of spores released increases the likelihood of spores landing in an environment that will support growth (Figure 31.2.4).



Figure 31.2.4: The (a) giant puffball mushroom releases (b) a cloud of spores when it reaches maturity. (credit a: modification of work by Roger Griffith; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

How Fungi Obtain Nutrition

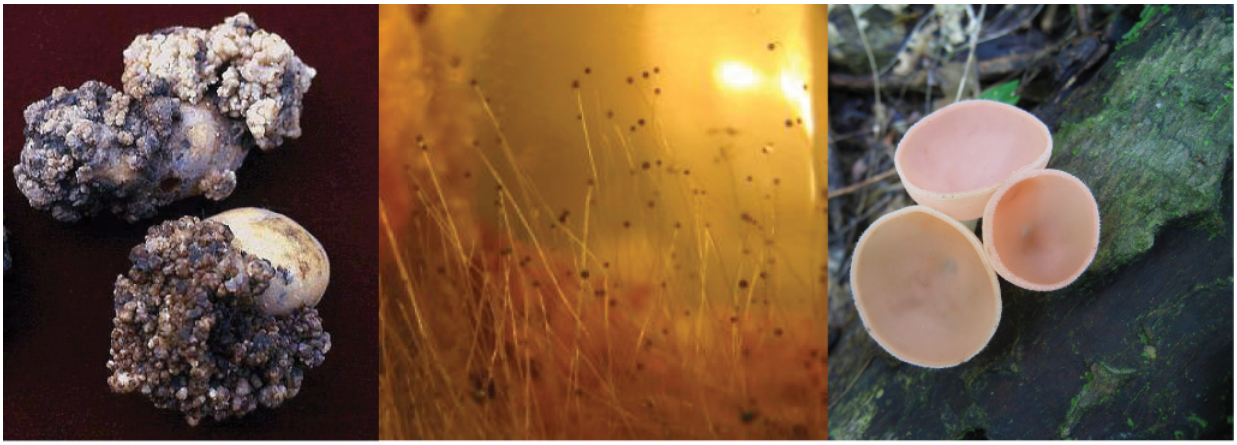
Like animals, fungi are heterotrophs: They use complex organic compounds as a source of carbon rather than fixing carbon dioxide from the atmosphere, as some bacteria and most plants do. In addition, fungi do not fix nitrogen from the atmosphere. Like animals, they must obtain it from their diet. However, unlike most animals that ingest food and then digest it internally in specialized organs, fungi perform these steps in the reverse order. Digestion precedes ingestion. First, exoenzymes, enzymes that catalyze reactions on compounds outside of the cell, are transported out of the hyphae where they break down nutrients in the environment. Then, the smaller molecules produced by the external digestion are absorbed through the large surface areas of the mycelium. As with animal cells, the fungal storage polysaccharide is glycogen rather than starch, as found in plants.

Fungi are mostly saprobes, organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter, mainly plant material. Fungal exoenzymes are able to break down insoluble polysaccharides, such as the cellulose and lignin of dead wood, into readily absorbable glucose molecules. Decomposers are important components of ecosystems, because they return nutrients locked in dead bodies to a form that is usable for other organisms. This role is discussed in more detail later. Because of their varied metabolic pathways, fungi fulfill an important ecological role and are being investigated as potential tools in bioremediation. For example, some species of fungi can be used to break down diesel oil and polycyclic aromatic hydrocarbons. Other species take up heavy metals such as cadmium and lead.

Fungal Diversity

The kingdom Fungi contains four major divisions that were established according to their mode of sexual reproduction. Polyphyletic, unrelated fungi that reproduce without a sexual cycle, are placed for convenience in a fifth division, and a sixth major fungal group that does not fit well with any of the previous five has recently been described. Not all mycologists agree with this scheme. Rapid advances in molecular biology and the sequencing of 18S rRNA (a component of ribosomes) continue to reveal new and different relationships between the various categories of fungi.

The traditional divisions of Fungi are the Chytridiomycota (chytrids), the Zygomycota(conjugated fungi), the Ascomycota (sac fungi), and the Basidiomycota (club fungi). An older classification scheme grouped fungi that strictly use asexual reproduction into Deuteromycota, a group that is no longer in use. The Glomeromycota belong to a newly described group (Figure **31.2.5**).



(a) (b) (c)



(d)

Figure 31.2.5: Divisions of fungi include (a) chytrids, (b) conjugated fungi, (c) sac fungi, and (d) club fungi. (credit a: modification of work by USDA APHIS PPQ; credit c: modification of work by "icelight"/Flickr; credit d: modification of work by Cory Zanker.)

Pathogenic Fungi

Many fungi have negative impacts on other species, including humans and the organisms they depend on for food. Fungi may be parasites, pathogens, and, in a very few cases, predators.

Plant Parasites and Pathogens

The production of enough good-quality crops is essential to our existence. Plant diseases have ruined crops, bringing widespread famine. Most plant pathogens are fungi that cause tissue decay and eventual death of the host (Figure 31.2.6). In addition to destroying plant tissue directly, some plant pathogens spoil crops by producing potent toxins. Fungi are also responsible for food spoilage and the rotting of stored crops. For example, the fungus *Claviceps purpurea* causes ergot, a disease of cereal crops (especially of rye). Although the fungus reduces the yield of cereals, the effects of the ergot's alkaloid toxins on humans and animals are of much greater significance: In animals, the disease is referred to as ergotism. The most common signs and symptoms are convulsions, hallucination, gangrene, and loss of milk in cattle. The active ingredient of ergot is lysergic acid, which is a precursor of the drug LSD. Smuts, rusts, and powdery or downy mildew are other examples of common fungal pathogens that affect crops.

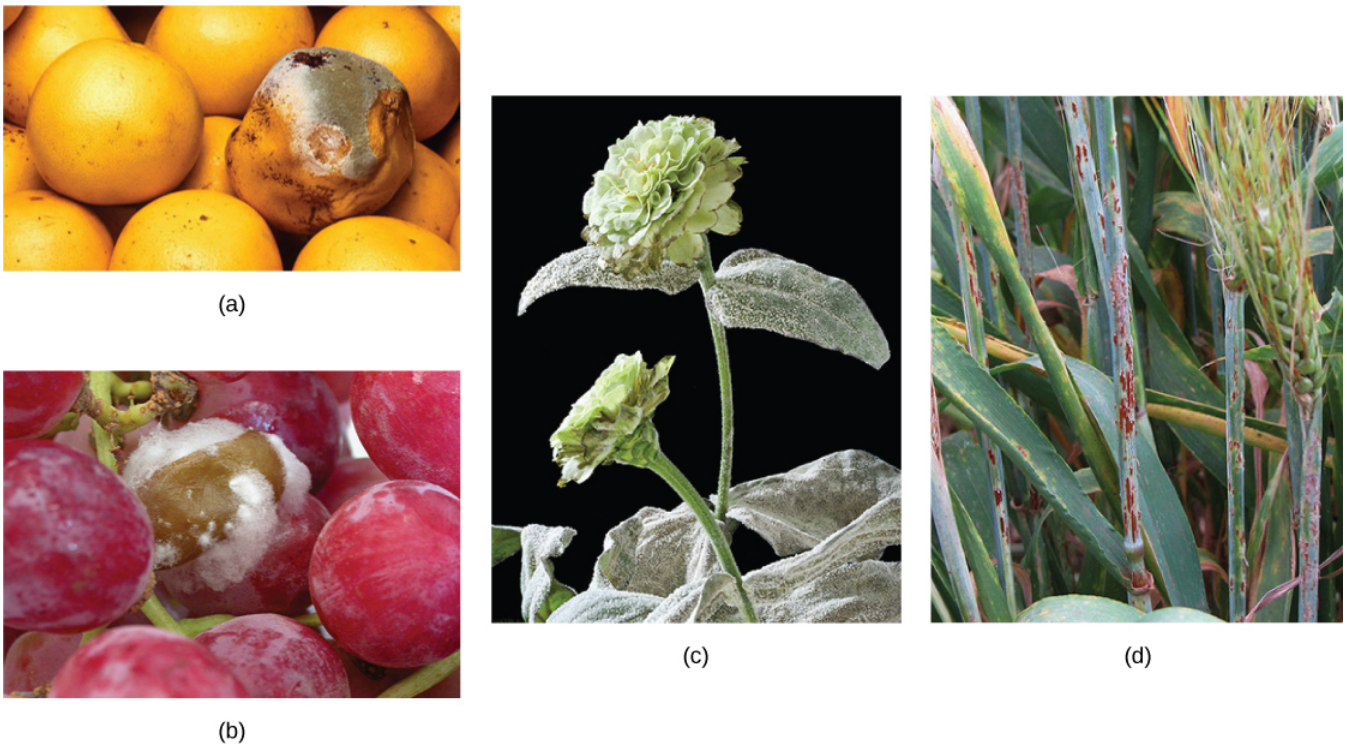


Figure 31.2.6: Some fungal pathogens include (a) green mold on grapefruit, (b) fungus on grapes, (c) powdery mildew on a zinnia, and (d) stem rust on a sheaf of barley. Notice the brownish color of the fungus in (b) Botrytis cinerea, also referred to as the "noble rot," which grows on grapes and other fruit. Controlled infection of grapes by Botrytis is used to produce strong and much-prized dessert wines. (credit a: modification of work by Scott Bauer, USDA ARS; credit b: modification of work by Stephen Ausmus, USDA ARS; credit c: modification of work by David Marshall, USDA ARS; credit d: modification of work by Joseph Smilanick, USDA ARS)

Aflatoxins are toxic and carcinogenic compounds released by fungi of the genus *Aspergillus*. Periodically, harvests of nuts and grains are tainted by aflatoxins, leading to massive recall of produce, sometimes ruining producers, and causing food shortages in developing countries.

Animal and Human Parasites and Pathogens

Fungi can affect animals, including humans, in several ways. Fungi attack animals directly by colonizing and destroying tissues. Humans and other animals can be poisoned by eating toxic mushrooms or foods contaminated by fungi. In addition, individuals who display hypersensitivity to molds and spores develop strong and dangerous allergic reactions. Fungal infections are generally very difficult to treat because, unlike bacteria, fungi are eukaryotes. Antibiotics only target prokaryotic cells, whereas compounds that kill fungi also adversely affect the eukaryotic animal host.

Many fungal infections (mycoses) are superficial and termed cutaneous (meaning "skin") mycoses. They are usually visible on the skin of the animal. Fungi that cause the superficial mycoses of the epidermis, hair, and nails rarely spread to the underlying tissue (Figure **31.2.7**). These fungi are often misnamed "dermatophytes" from the Greek *dermis* skin and *phyte* plant, but they are not plants. Dermatophytes are also called "ringworms" because of the red ring that they cause on skin (although the ring is caused by fungi, not a worm). These fungi secrete extracellular enzymes that break down keratin (a protein found in hair, skin, and nails), causing a number of conditions such as athlete's foot, jock itch, and other cutaneous fungal infections. These conditions are usually treated with over-the-counter topical creams and powders, and are easily cleared. More persistent, superficial mycoses may require prescription oral medications.

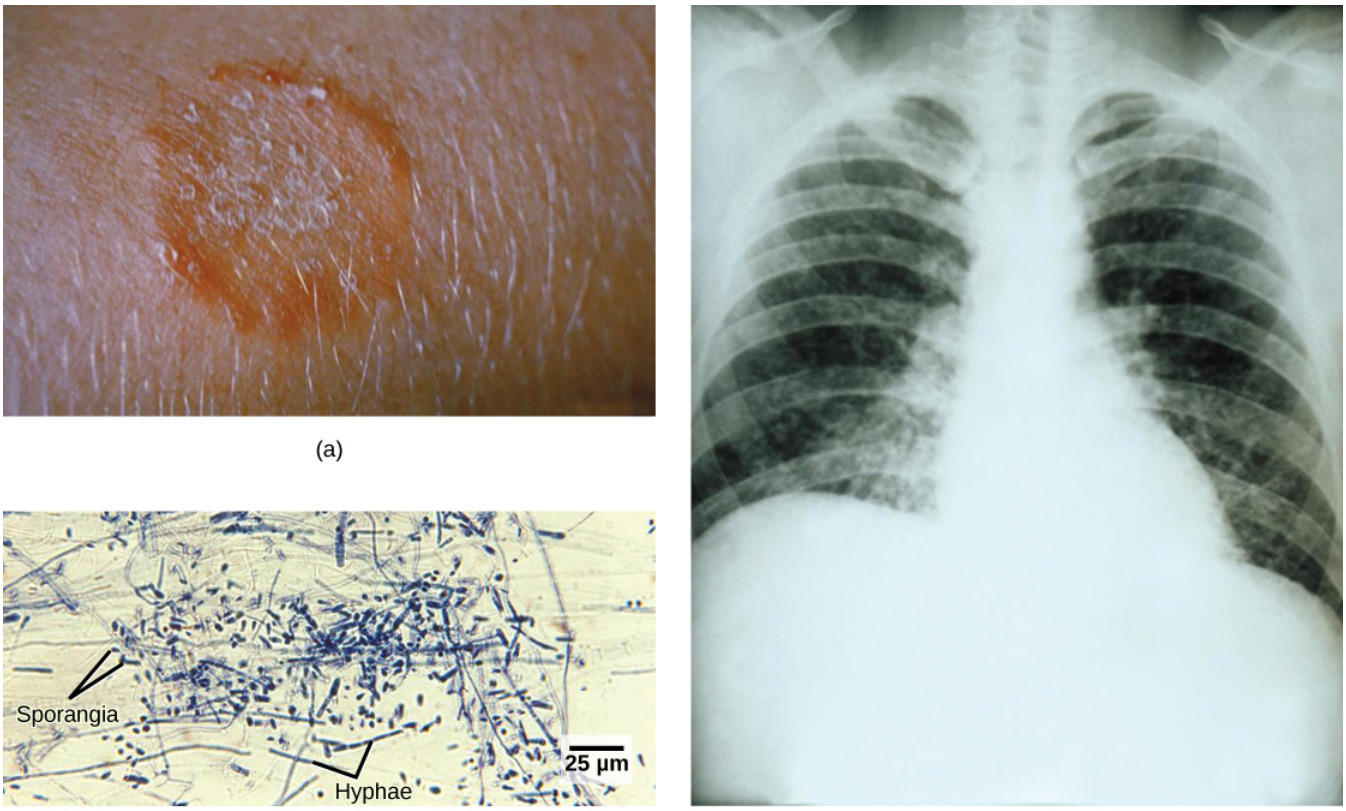


Figure 31.2.7: (a) Ringworm presents as a red ring on the skin. (b) Trichophyton violaceum is a fungus that causes superficial mycoses on the scalp. (c) Histoplasma capsulatum, seen in this X-ray as speckling of light areas in the lung, is a species of Ascomycota that infects airways and causes symptoms similar to the flu. (credit a, b: modification of work by Dr. Lucille K. Georg, CDC; credit c: modification of work by M Renz, CDC; scale-bar data from Matt Russell)

Systemic mycoses spread to internal organs, most commonly entering the body through the respiratory system. For example, coccidioidomycosis (valley fever) is commonly found in the southwestern United States, where the fungus resides in the dust. Once inhaled, the spores develop in the lungs and cause signs and symptoms similar to those of tuberculosis. Histoplasmosis (Figure 31.2.7c) is caused by the dimorphic fungus *Histoplasma capsulatum*; it causes pulmonary infections and, in rare cases, swelling of the membranes of the brain and spinal cord. Treatment of many fungal diseases requires the use of antifungal medications that have serious side effects.

Opportunistic mycoses are fungal infections that are either common in all environments or part of the normal biota. They affect mainly individuals who have a compromised immune system. Patients in the late stages of AIDS suffer from opportunistic mycoses, such as *Pneumocystis*, which can be life threatening. The yeast *Candida* spp., which is a common member of the natural biota, can grow unchecked if the pH, the immune defenses, or the normal population of bacteria is altered, causing yeast infections of the vagina or mouth (oral thrush).

Fungi may even take on a predatory lifestyle. In soil environments that are poor in nitrogen, some fungi resort to predation of nematodes (small roundworms). Species of *Arthrobotrys* fungi have a number of mechanisms to trap nematodes. For example, they have constricting rings within their network of hyphae. The rings swell when the nematode touches it and closes around the body of the nematode, thus trapping it. The fungus extends specialized hyphae that can penetrate the body of the worm and slowly digest the hapless prey.

Beneficial Fungi

Fungi play a crucial role in the balance of ecosystems. They colonize most habitats on Earth, preferring dark, moist conditions. They can thrive in seemingly hostile environments, such as the tundra, thanks to a most successful symbiosis with photosynthetic organisms, like lichens. Fungi are not obvious in the way that large animals or tall trees are. Yet, like bacteria, they are major

decomposers of nature. With their versatile metabolism, fungi break down organic matter that is insoluble and would not be recycled otherwise.

Importance to Ecosystems

Food webs would be incomplete without organisms that decompose organic matter and fungi are key participants in this process. Decomposition allows for cycling of nutrients such as carbon, nitrogen, and phosphorus back into the environment so they are available to living things, rather than being trapped in dead organisms. Fungi are particularly important because they have evolved enzymes to break down cellulose and lignin, components of plant cell walls that few other organisms are able to digest, releasing their carbon content.

Fungi are also involved in ecologically important coevolved symbioses, both mutually beneficial and pathogenic with organisms from the other kingdoms. Mycorrhiza, a term combining the Greek roots *myco* meaning fungus and *rhizo* meaning root, refers to the association between vascular plant roots and their symbiotic fungi. Somewhere between 80–90 percent of all plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus. Ectomycorrhizae ("outside" mycorrhiza) depend on fungi enveloping the roots in a sheath (called a mantle) and a net of hyphae that extends into the roots between cells. In a second type, the Glomeromycota fungi form arbuscular mycorrhiza. In these mycorrhiza, the fungi form arbuscles, a specialized highly branched hypha, which penetrate root cells and are the sites of the metabolic exchanges between the fungus and the host plant. Orchids rely on a third type of mycorrhiza. Orchids form small seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually Basidiomycota). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their lifecycle.

Lichens blanket many rocks and tree bark, displaying a range of colors and textures. Lichens are important pioneer organisms that colonize rock surfaces in otherwise lifeless environments such as are created by glacial recession. The lichen is able to leach nutrients from the rocks and break them down in the first step to creating soil. Lichens are also present in mature habitats on rock surfaces or the trunks of trees. They are an important food source for caribou. Lichens are not a single organism, but rather a fungus (usually an Ascomycota or Basidiomycota species) living in close contact with a photosynthetic organism (an alga or cyanobacterium). The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the green partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates and receives protection from the elements by the thallus of the fungal partner. Some cyanobacteria fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the symbiotic organism to the substrate.

Fungi have evolved mutualistic associations with numerous arthropods. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus. In a second example, leaf-cutting ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in gardens. Fungi are cultivated in these gardens, digesting the cellulose that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, they in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from the association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

Importance to Humans

Although we often think of fungi as organisms that cause diseases and rot food, fungi are important to human life on many levels. As we have seen, they influence the well-being of human populations on a large scale because they help nutrients cycle in ecosystems. They have other ecosystem roles as well. For example, as animal pathogens, fungi help to control the population of damaging pests. These fungi are very specific to the insects they attack and do not infect other animals or plants. The potential to use fungi as microbial insecticides is being investigated, with several species already on the market. For example, the fungus *Beauveria bassiana* is a pesticide that is currently being tested as a possible biological control for the recent spread of emerald ash borer. It has been released in Michigan, Illinois, Indiana, Ohio, West Virginia, and Maryland.

The mycorrhizal relationship between fungi and plant roots is essential for the productivity of farmland. Without the fungal partner in the root systems, 80–90% of trees and grasses would not survive. Mycorrhizal fungal inoculants are available as soil amendments from gardening supply stores and promoted by supporters of organic agriculture.

We also eat some types of fungi. Mushrooms figure prominently in the human diet. Morels, shiitake mushrooms, chanterelles, and truffles are considered delicacies (Figure **31.2.8**). The humble meadow mushroom, *Agaricus campestris*, appears in many dishes. Molds of the genus *Penicillium* ripen many cheeses. They originate in the natural environment such as the caves of Roquefort, France, where wheels of sheep milk cheese are stacked to capture the molds responsible for the blue veins and pungent taste of the cheese.



Figure 31.2.8: The morel mushroom is an ascomycete that is much appreciated for its delicate taste. (credit: Jason Hollinger)

Fermentation—of grains to produce beer, and of fruits to produce wine—is an ancient art that humans in most cultures have practiced for millennia. Wild yeasts are acquired from the environment and used to ferment sugars into CO_2 and ethyl alcohol under anaerobic conditions. It is now possible to purchase isolated strains of wild yeasts from different wine-making regions. Pasteur was instrumental in developing a reliable strain of brewer's yeast, *Saccharomyces cerevisiae*, for the French brewing industry in the late 1850s. It was one of the first examples of biotechnology patenting. Yeast is also used to make breads that rise. The carbon dioxide they produce is responsible for the bubbles produced in the dough that become the air pockets of the baked bread.

Many secondary metabolites of fungi are of great commercial importance. Antibiotics are naturally produced by fungi to kill or inhibit the growth of bacteria, and limit competition in the natural environment. Valuable drugs isolated from fungi include the immunosuppressant drug cyclosporine (which reduces the risk of rejection after organ transplant), the precursors of steroid hormones, and ergot alkaloids used to stop bleeding. In addition, as easily cultured eukaryotic organisms, some fungi are important model research organisms including the red bread mold *Neurospora crassa* and the yeast, *S. cerevisiae.*

Section Summary

Fungi are eukaryotic organisms that appeared on land over 450 million years ago. They are heterotrophs and contain neither photosynthetic pigments such as chlorophylls nor organelles such as chloroplasts. Because they feed on decaying and dead matter, they are saprobes. Fungi are important decomposers and release essential elements into the environment. External enzymes digest nutrients that are absorbed by the body of the fungus called a thallus. A thick cell wall made of chitin surrounds the cell. Fungi can be unicellular as yeasts or develop a network of filaments called a mycelium, often described as mold. Most species multiply by asexual and sexual reproductive cycles, and display an alternation of generations.

The divisions of fungi are the Chytridiomycota, Zygomycota, Ascomycota, Basidiomycota, and Glomeromycota.

Fungi establish parasitic relationships with plants and animals. Fungal diseases can decimate crops and spoil food during storage. Compounds produced by fungi can be toxic to humans and other animals. Mycoses are infections caused by fungi. Superficial mycoses affect the skin, whereas systemic mycoses spread through the body. Fungal infections are difficult to cure.

Fungi have colonized all environments on Earth but are most often found in cool, dark, moist places with a supply of decaying material. Fungi are important decomposers because they are saprobes. Many successful mutualistic relationships involve a fungus and another organism. They establish complex mycorrhizal associations with the roots of plants. Lichens are a symbiotic relationship between a fungus and a photosynthetic organism, usually an alga or cyanobacterium.

Fungi are important to everyday human life. Fungi are important decomposers in most ecosystems. Mycorrhizal fungi are essential for the growth of most plants. Fungi, as food, play a role in human nutrition in the form of mushrooms and as agents of fermentation in the production of bread, cheeses, alcoholic beverages, and numerous other food preparations. Secondary metabolites of fungi are used in medicine as antibiotics and anticoagulants. Fungi are used in research as model organisms for the study of eukaryotic genetics and metabolism.

Glossary

Ascomycota
(sac fungi) a division of fungi that store spores in a sac called ascus

basidiomycota
(club fungi) a division of fungi that produce club shaped structures, basidia, which contain spores

Chytridiomycota
(chytrids) a primitive division of fungi that live in water and produce gametes with flagella

Glomeromycota
a group of fungi that form symbiotic relationships with the roots of trees

hypha
a fungal filament composed of one or more cells

lichen
the close association of a fungus with a photosynthetic alga or bacterium that benefits both partners

mold
a tangle of visible mycelia with a fuzzy appearance

mycelium
a mass of fungal hyphae

mycorrhiza
a mutualistic association between fungi and vascular plant roots

mycosis

a fungal infection

septum
the cell wall division between hyphae

thallus
a vegetative body of a fungus

yeast
a general term used to describe unicellular fungi

Zygomycota
(conjugated fungi) the division of fungi that form a zygote contained in a zygospore

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SECTION OVERVIEW

31.3: Fungal Ecology

31.3.1: Fungi Habitat, Decomposition, and Recycling

31.3.2: Mutualistic Relationships with Fungi and Fungivores

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31.3.1: Fungi Habitat, Decomposition, and Recycling

Learning Objectives

- Explain the roles played by fungi in decomposition and recycling

Fungi & Their Roles as Decomposers and Recyclers

Fungi play a crucial role in the balance of ecosystems. They colonize most habitats on earth, preferring dark, moist conditions. They can thrive in seemingly-hostile environments, such as the tundra. However, most members of the Kingdom Fungi grow on the forest floor where the dark and damp environment is rich in decaying debris from plants and animals. In these environments, fungi play a major role as decomposers and recyclers, making it possible for members of the other kingdoms to be supplied with nutrients and to live.

The food web would be incomplete without organisms that decompose organic matter. Some elements, such as nitrogen and phosphorus, are required in large quantities by biological systems; yet, they are not abundant in the environment. The action of fungi releases these elements from decaying matter, making them available to other living organisms. Trace elements present in low amounts in many habitats are essential for growth, but would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.



Figure **31.3.1.1**: Fungi as decomposers: Fungi are an important part of ecosystem nutrient cycles. These bracket fungi growing on the side of a tree are the fruiting structures of a basidiomycete. They receive their nutrients through their hyphae, which invade and decay the tree trunk.

The ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. As seen earlier, digestion precedes ingestion. Fungi produce a variety of exoenzymes to digest nutrients. These enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Large molecules are broken down into small molecules, which are transported into the cell by a system of protein carriers embedded in the cell membrane. Because the movement of small molecules and enzymes is dependent on the presence of water, active growth depends on a relatively-high percentage of moisture in the environment.

As saprobes, fungi help maintain a sustainable ecosystem for the animals and plants that share the same habitat. In addition to replenishing the environment with nutrients, fungi interact directly with other organisms in beneficial, but sometimes damaging, ways.



Figure **31.3.1.1**: Fungi: beneficial & pathogenic: Shelf fungi, so called because they grow on trees in a stack, attack and digest the trunk or branches of a tree. While some shelf fungi are found only on dead trees, others can parasitize living trees, causing eventual death. They are considered serious tree pathogens.

Key Points

- Aiding the survival of species from other kingdoms through the supply of nutrients, fungi play a major role as decomposers and recyclers in the wide variety of habitats in which they exist.
- Fungi provide a vital role in releasing scarce, yet biologically-essential elements, such as nitrogen and phosphorus, from decaying matter.
- Their mode of nutrition, which involves digestion before ingestion, allows fungi to degrade many large and insoluble molecules that would otherwise remain trapped in a habitat.

Key Terms

- **decomposer**: any organism that feeds off decomposing organic material, especially bacterium or fungi
- **exoenzyme**: any enzyme, generated by a cell, that functions outside of that cell
- **saprobe**: an organism that lives off of dead or decaying organic material

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31.3.2: Mutualistic Relationships with Fungi and Fungivores

Learning Objectives

- Describe mutualistic relationships with fungi

Mutualistic Relationships

Symbiosis is the ecological interaction between two organisms that live together. However, the definition does not describe the quality of the interaction. When both members of the association benefit, the symbiotic relationship is called mutualistic. Fungi form mutualistic associations with many types of organisms, including cyanobacteria, plants, and animals.

Fungi & Plant Mutualism

Mycorrhiza, which comes from the Greek words “myco” meaning fungus and “rhizo” meaning root, refers to the association between vascular plant roots and their symbiotic fungi. About 90 percent of all plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant, thereby increasing a plant’s nutrient uptake. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

Mycorrhizae display many characteristics of primitive fungi: they produce simple spores, show little diversification, do not have a sexual reproductive cycle, and cannot live outside of a mycorrhizal association. There are a number of types of mycorrhizae. Ectomycorrhizae (“outside” mycorrhiza) depend on fungi enveloping the roots in a sheath (called a mantle) and a Hartig net of hyphae that extends into the roots between cells. The fungal partner can belong to the Ascomycota, Basidiomycota, or Zygomycota. In a second type, the Glomeromycete fungi form vesicular–arbuscular interactions with arbuscular mycorrhiza (sometimes called endomycorrhizae). In these mycorrhiza, the fungi form arbuscules that penetrate root cells and are the site of the metabolic exchanges between the fungus and the host plant. The arbuscules (from the Latin for “little trees”) have a shrub-like appearance. Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that form small seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their lifecycle.

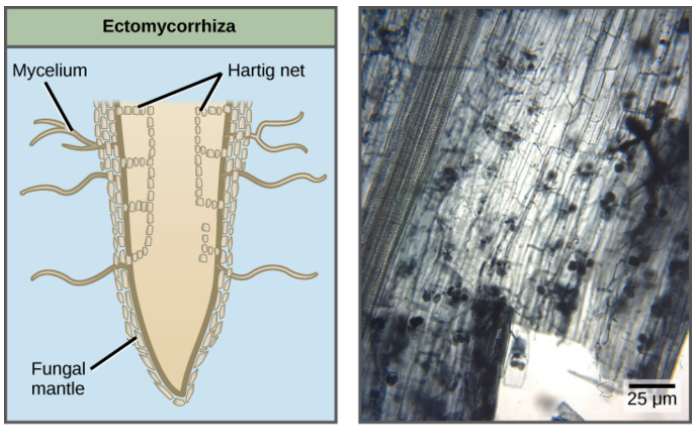


Figure **31.3.2.1**: Mycorrhizal fungi: (a) Ectomycorrhiza and (b) arbuscular mycorrhiza have different mechanisms for interacting with the roots of plants.

Lichens

Lichens display a range of colors and textures. They can survive in the most unusual and hostile habitats. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought: they become completely desiccated and then rapidly become active once water is available again. Lichens fulfill many

ecological roles, including acting as indicator species, which allow scientists to track the health of a habitat because of their sensitivity to air pollution.

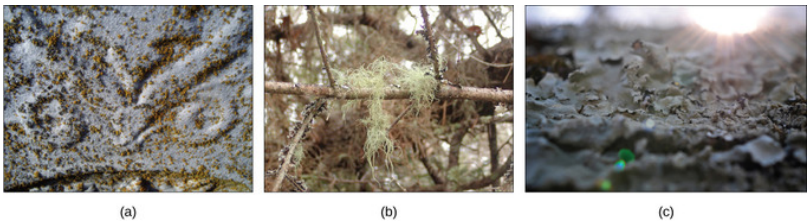


Figure **31.3.2.1**: Lichen: fungi and cyanobateria: Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like.

Lichens are not a single organism, but, rather, an example of a mutualism in which a fungus (usually a member of the Ascomycota or Basidiomycota phyla) lives in close contact with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship. The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. Some cyanobacteria fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the symbiotic organism to the substrate.

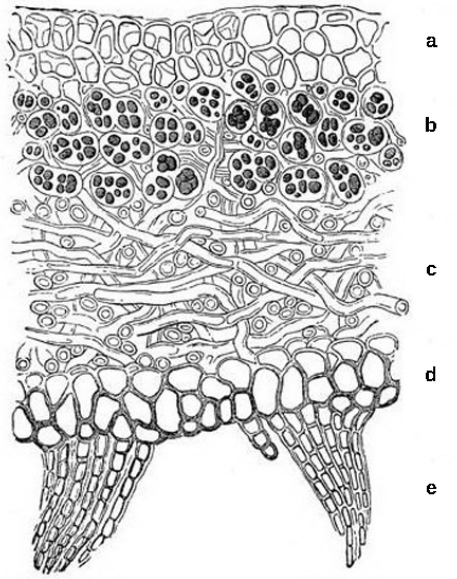


Figure **31.3.2.1**: Thallus of lichen: This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) rhizines to anchor the thallus to the substrate.

The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units for reproduction. Lichens produce soredia, clusters of algal cells surrounded by mycelia. Soredia are dispersed by wind and water and form new lichens.

Fungi & Animal Mutualism

Fungi have evolved mutualisms with numerous insects. Arthropods (jointed, legged invertebrates, such as insects) depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus. In a second example, leaf-cutting ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in gardens. Fungi are cultivated in these disk gardens, digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also

patrol their garden, preying on competing fungi. Both ants and fungi benefit from the association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

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Key Points

- Mutualistic relationships are those where both members of an association benefit; Fungi form these types of relationships with various other Kingdoms of life.
- Mycorrhiza, formed from an association between plant roots and primitive fungi, help increase a plant's nutrient uptake; in return, the plant supplies the fungi with photosynthesis products for their metabolic use.
- In lichen, fungi live in close proximity with photosynthetic cyanobateria; the algae provide fungi with carbon and energy while the fungi supplies minerals and protection to the algae.
- Mutualistic relationships between fungi and animals involves numerous insects; Arthropods depend on fungi for protection, while fungi receive nutrients in return and ensure a way to disseminate the spores into new environments.

Key Terms

- **mycorrhiza**: a symbiotic association between a fungus and the roots of a vascular plant
- **lichen**: any of many symbiotic organisms, being associations of fungi and algae; often found as white or yellow patches on old walls, etc.
- **thallus**: vegetative body of a fungus

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31.4: Fungal Parasites and Pathogens



Would you eat these mushrooms?

I would not recommend it. But certain red mushrooms, *Ganoderma Lucidum*, have been found to be good for you. Red Mushrooms comprise a family of more than 200 mushroom species, which are good for our health. Of these, 6 species have a particularly high therapeutic effect.

Fungi and Human Disease

Fungi cause human illness in three different ways: poisonings, parasitic infections, and allergic reactions. *Science on the SPOT: Fungus Fair* explores some of these dangerous but also tasty and weirdly wonderful fungi.

Fungal Poisoning

Many fungi protect themselves from parasites and predators by producing toxic chemicals. If people eat toxic fungi, they may experience digestive problems, hallucinations, organ failure, and even death. Most cases of mushroom poisoning are due to mistaken identity. That's because many toxic mushrooms look very similar to safe, edible mushrooms. An example is shown in **Figure** below.



Poisonous or Edible? The destroying angel mushroom on the left causes liver and kidney failure. The puffball mushroom on the right is tasty and harmless. Do you think you could tell these two species of mushrooms apart?

Fungal Parasites

Some fungi cause disease when they become human parasites. Two examples are fungi in the genera *Candida* and *Trichophyton*.

- *Candida* are yeast that cause **candidiasis**, commonly called a "yeast infection." The yeast can infect the mouth or the vagina. If yeast enter the blood, they cause a potentially life threatening illness. However, this is rare, except in people with a depressed immune system.
- *Trichophyton* are fungi that cause **ringworm**. This is a skin infection characterized by a ring-shaped rash. The rash may occur on the arms, legs, head, neck, or trunk. The same fungi cause **athlete's foot** when they infect the skin between the toes.

Athlete's foot is the second most common skin disease in the U.S.

Figure below shows signs of these two infections.



Ringworm Athlete's Foot

Ringworm produces a ring-shaped rash, but it isn't caused by a worm. It's caused by the same fungus that causes athlete's foot.

Fungal Allergies

Mold allergies are very common. They are caused by airborne mold spores. When the spores enter the respiratory tract, the immune system responds to them as though they were harmful microbes. Symptoms may include sneezing, coughing, and difficulty breathing. The symptoms are likely to be more severe in people with asthma or other respiratory diseases. Long-term exposure to mold spores may also weaken the immune system.

Molds grow indoors as well as out. Indoors, they grow in showers, basements, and other damp places. Homes damaged in floods and hurricanes may have mold growing just about everywhere (see **Figure** below). Indoor mold may cause more health problems than outdoor mold because of the closed, confined space. Most people also spend more time indoors than out.



The mold growing on the walls and ceiling of this storm-damaged home may be harmful to human health.

Summary

- Fungi cause three different types of human illness: poisonings, parasitic infections, and allergies.
- Many poisonous mushrooms are eaten by mistake because they look like edible mushrooms.
- Parasitic yeasts cause candidiasis, ringworm, and athlete's foot.
- Mold allergies are very common.

Review

1. Explain why you should never eat mushrooms you find in the woods unless you know for certain which type of mushrooms they are.

2. Compare and contrast ringworm and athlete’s foot.
3. How does mold cause allergies?
4. State why indoor mold may cause more health problems than outdoor mold.

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31.5: Basidomycota- The Club (Basidium) Fungi

Learning Objectives

- Describe the ecology and reproduction of the Basidiomycota

Basidiomycota: The Club Fungi

The fungi in the Phylum Basidiomycota are easily recognizable under a light microscope by their club-shaped fruiting bodies called basidia (singular, basidium), which are the swollen terminal cell of a hypha. The basidia, which are the reproductive organs of these fungi, are often contained within the familiar mushroom, commonly seen in fields after rain, on the supermarket shelves, and growing on your lawn. These mushroom-producing basidiomyces are sometimes referred to as “gill fungi” because of the presence of gill-like structures on the underside of the cap. The “gills” are actually compacted hyphae on which the basidia are borne. This group also includes shelf fungus, which cling to the bark of trees like small shelves. In addition, the basidiomycota includes smuts and rusts, which are important plant pathogens, and toadstools. Most edible fungi belong to the Phylum Basidiomycota; however, some basidiomycetes produce deadly toxins. For example, *Cryptococcus neoformans* causes severe respiratory illness.



Figure **31.5.1**: Fruiting bodies of a basidiomycete: The fruiting bodies of a basidiomycete form a ring in a meadow, commonly called “fairy ring.” The best-known fairy ring fungus has the scientific name *Marasmius oreades*. The body of this fungus, its mycelium, is underground and grows outward in a circle. As it grows, the mycelium depletes the soil of nitrogen, causing the mycelia to grow away from the center, leading to the “fairy ring” of fruiting bodies where there is adequate soil nitrogen.

The lifecycle of basidiomycetes includes alternation of generations. Spores are generally produced through sexual reproduction, rather than asexual reproduction. The club-shaped basidium carries spores called basidiospores. In the basidium, nuclei of two different mating strains fuse (karyogamy), giving rise to a diploid zygote that then undergoes meiosis. The haploid nuclei migrate into basidiospores, which germinate and generate monokaryotic hyphae. The mycelium that results is called a primary mycelium. Mycelia of different mating strains can combine and produce a secondary mycelium that contains haploid nuclei of two different mating strains. This is the dikaryotic stage of the basidiomyces lifecyle and it is the dominant stage. Eventually, the secondary mycelium generates a basidiocarp, which is a fruiting body that protrudes from the ground; this is what we think of as a mushroom. The basidiocarp bears the developing basidia on the gills under its cap.

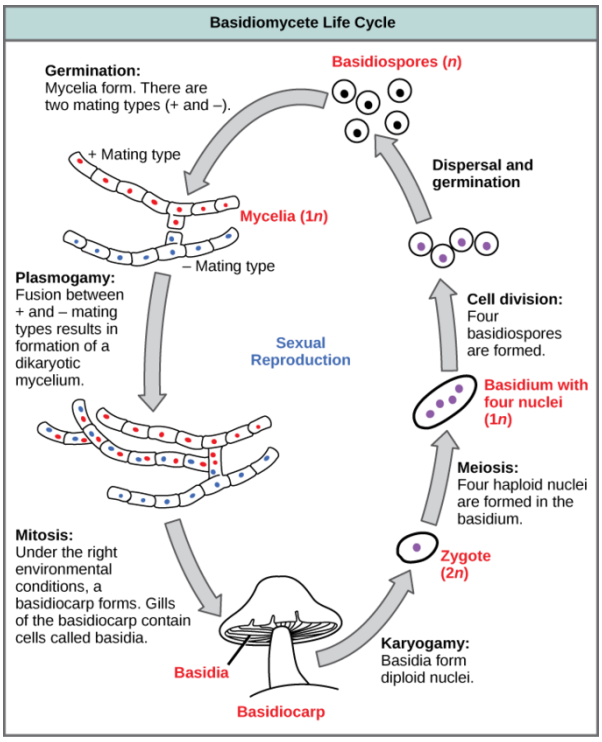


Figure **31.5.1**: Lifecycle of a basidiomycete: The lifecycle of a basidiomycete alternates generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae.

Key Points

- The majority of edible fungi belong to the Phylum Basidiomycota.
- The basidiomycota includes shelf fungus, toadstools, and smuts and rusts.
- Unlike most fungi, basidiomycota reproduce sexually as opposed to asexually.
- Two different mating strains are required for the fusion of genetic material in the basidium which is followed by meiosis producing haploid basidiospores.
- Mycelia of different mating strains combine to produce a secondary mycelium that contains haploid basidiospores in what is called the dikaryotic stage, where the fungi remains until a basidiocarp (mushroom) is generated with the developing basidia on the gills under its cap.

Key Terms

- **basidiocarp**: a fruiting body that protrudes from the ground, known as a mushroom, which has a developing basidia on the gills under its cap
- **basidiomycete**: a fungus of the phylum Basidiomycota, which produces sexual spores on a basidium
- **Basidiomycota**: a taxonomic division within the kingdom Fungi: 30,000 species of fungi that produce spores from a basidium
- **basidium**: a small structure, shaped like a club, found in the Basidiomycota phylum of fungi, that bears four spores at the tips of small projections
- **basidiospore**: a sexually-reproductive spore produced by fungi of the phylum Basidiomycota

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31.6: Ascomycota- The Sac (Ascus) Fungi

Learning Objectives

- Describe the ecology and the reproduction of Ascomycetes

The majority of known fungi belong to the Phylum Ascomycota, which is characterized by the formation of an ascus (plural, asci), a sac-like structure that contains haploid ascospores. Many ascomycetes are of commercial importance. Some play a beneficial role, such as the yeasts used in baking, brewing, and wine fermentation, plus truffles and morels, which are held as gourmet delicacies. *Aspergillus oryzae* is used in the fermentation of rice to produce sake. Other ascomycetes parasitize plants and animals, including humans. For example, fungal pneumonia poses a significant threat to AIDS patients who have a compromised immune system. Ascomycetes not only infest and destroy crops directly, they also produce poisonous secondary metabolites that make crops unfit for consumption. Filamentous ascomycetes produce hyphae divided by perforated septa, allowing streaming of cytoplasm from one cell to the other. Conidia and asci, which are used respectively for asexual and sexual reproductions, are usually separated from the vegetative hyphae by blocked (non-perforated) septa.

Asexual reproduction is frequent and involves the production of conidiophores that release haploid conidiospores. Sexual reproduction starts with the development of special hyphae from either one of two types of mating strains. The “male” strain produces an antheridium (plural: antheridia) and the “female” strain develops an ascogonium (plural: ascogonia). At fertilization, the antheridium and the ascogonium combine in plasmogamy without nuclear fusion. Special ascogenous hyphae arise, in which pairs of nuclei migrate: one from the “male” strain and one from the “female” strain. In each ascus, two or more haploid ascospores fuse their nuclei in karyogamy. During sexual reproduction, thousands of asci fill a fruiting body called the ascocarp. The diploid nucleus gives rise to haploid nuclei by meiosis. The ascospores are then released, germinate, and form hyphae that are disseminated in the environment and start new mycelia.

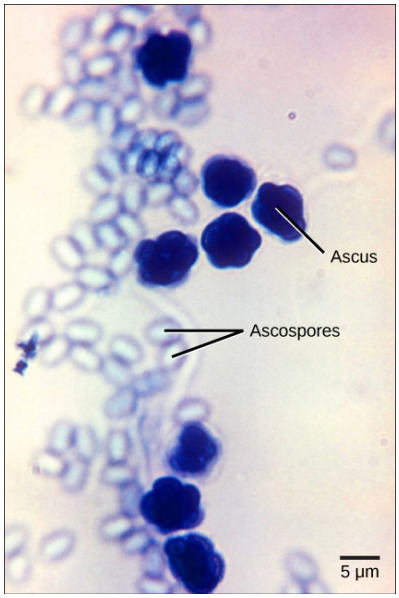


Figure **31.6.1**: Release of ascospores: The bright field light micrograph shows ascospores being released from asci in the fungus Talaromyces flavus var. flavus.

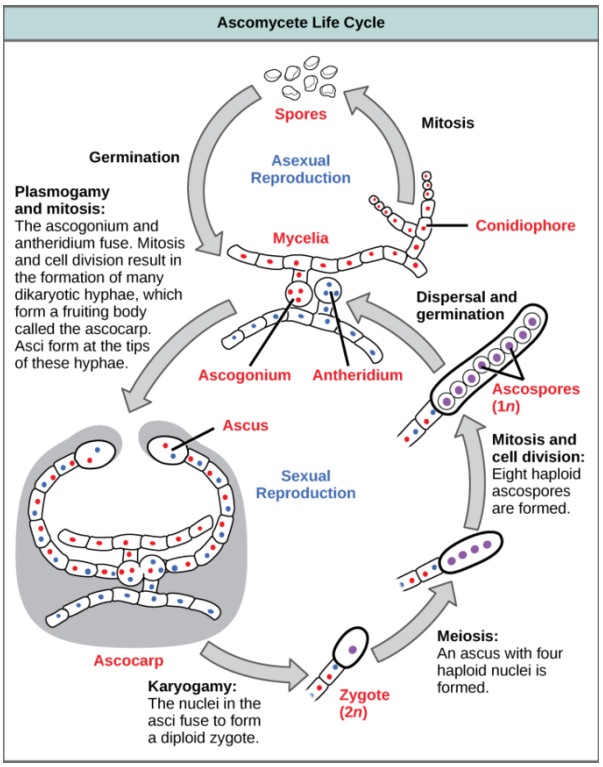


Figure **31.6.1**: Lifecycle of an ascomycete: The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle.

Key Points

- Ascomycota fungi are the yeasts used in baking, brewing, and wine fermentation, plus delicacies such as truffles and morels.
- Ascomycetes are filamentous and produce hyphae divided by perforated septa.
- Ascomycetes frequently reproduce asexually which leads to the production of conidiophores that release haploid conidiospores.
- Two types of mating strains, a “male” strain which produces an antheridium and a “female” strain which develops an ascogonium, are required for sexual reproduction.
- The antheridium and the ascogonium combine in plasmogamy at the time of fertilization, followed by nuclei fusion in the asci.
- In the ascocarp, a fruiting body, thousands of asci undergo meiosis to generate haploid ascospores ready to be released to the world.

Key Terms

- **plasmogamy**: stage of sexual reproduction joining the cytoplasm of two parent mycelia without the fusion of nuclei
- **Ascomycota**: a taxonomic division within the kingdom Fungi; those fungi that produce spores in a microscopic sporangium called an ascus
- **ascus**: a sac-shaped cell present in ascomycete fungi; it is a reproductive cell in which meiosis and an additional cell division produce eight spores
- **ascospore**: a sexually-produced spore from the ascus of an Ascomycetes fungus
- **conidia**: asexual, non-motile spores of a fungus, named after the Greek word for dust, conia; also known as conidiospores and mitospores
- **antheridia**: a haploid structure or organ producing and containing male gametes (called antherozoids or sperm) present in lower plants like mosses and ferns, primitive vascular psilotophytes, and fungi
- **ascogonium**: a haploid structure or organ producing and containing female gametes in certain Ascomycota fungi
- **ascocarp**: the sporocarp of an ascomycete, typically bowl-shaped
- **ascomycete**: any fungus of the phylum Ascomycota, characterized by the production of a sac, or ascus, which contains non-motile spores

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31.7: Glomeromycota- Asexual Plant Symbionts

Learning Objectives

- Describe the ecology and reproduction of Glomeromycetes

In the kingdom Fungi, the Glomeromycota is a newly-established phylum comprised of about 230 species that live in close association with the roots of trees and plants. Fossil records indicate that trees and their root symbionts share a long evolutionary history. It appears that most members of this family form arbuscular mycorrhizae: the hyphae interact with the root cells forming a mutually-beneficial association where the plants supply the carbon source and energy in the form of carbohydrates to the fungus while the fungus supplies essential minerals from the soil to the plant. This association is termed biotrophic. The Glomeromycota species that have arbuscular mycorrhizal are terrestrial and widely distributed in soils worldwide where they form symbioses with the roots of the majority of plant species. They can also be found in wetlands, including salt-marshes, and are associated with epiphytic plants.

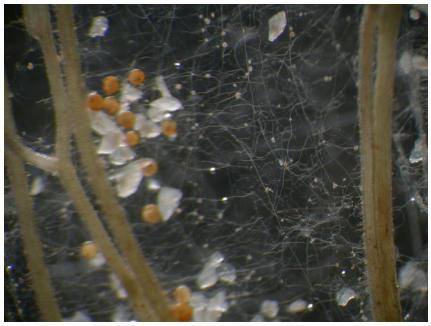


Figure **31.7.1**: Glyomeromycetes and tree roots: This image illustrates the bitrophic relationship between a glomeromycota (Gigaspora margarita) and the roots of a plant (Lotus corniculatus).

The glomeromycetes do not reproduce sexually and cannot survive without the presence of plant roots. They have coenocytic hyphae and reproduce asexually, producing glomerospores. The biochemical and genetic characterization of the Glomeromycota has been hindered by their biotrophic nature, which impedes laboratory culturing. This obstacle was eventually surpassed with the use of root cultures. With the advent of molecular techniques, such as gene sequencing, the phylogenetic classification of Glomeromycota has become clearer. The first mycorrhizal gene to be sequenced was the small-subunit ribosomal RNA (SSU rRNA). This gene is highly conserved and commonly used in phylogenetic studies so it was isolated from spores of each taxonomic group. Using a molecular clock approach based on the substitution rates of SSU sequences, scientists were able to estimate the time of divergence of the fungi. This analysis shows that all glomeromycetes probably descended from a common ancestor 462 and 353 million years ago, making them a monophyletic lineage. A long-held theory is that Glomeromycota were instrumental in the colonization of land by plants.

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Key Points

- Most glomeromycetes form arbuscular mycorrhizae, a type of symbiotic relationship between a fungus and plant roots; the plants supply a source of energy to the fungus while the fungus supplies essential minerals to the plant.
- Glomeromycota that have arbuscular mycorrhizal are mostly terrestrial, but can also be found in wetlands.
- The glomeromycetes reproduce asexually by producing glomerospores and cannot survive without the presence of plant roots.
- DNA analysis shows that all glomeromycetes probably descended from a common ancestor 462 and 353 million years ago.
- The classification of fungi as Glomeromycota has been redefined with adoption of molecular techniques.

Key Terms

- **biotrophic**: describing a parasite that needs its host to stay alive
- **arbuscular mycorrhizae**: a type of symbiotic relationship between a fungus and the roots of a plant where the plants supply a source of energy to the fungus while the fungus supplies essential minerals to the plant
- **glomeromycete**: an organism of the phylum Glomeromycota

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31.8: Zygomycota- Zygote-Producing Fungi

Learning Objectives

- Describe the ecology and reproduction of Zygomycetes

The zygomycetes are a relatively small group in the fungi kingdom and belong to the Phylum Zygomycota. They include the familiar bread mold, *Rhizopus stolonifer*, which rapidly propagates on the surfaces of breads, fruits, and vegetables. They are mostly terrestrial in habitat, living in soil or on plants and animals. Most species are saprobes meaning they live off decaying organic material. Some are parasites of plants, insects, and small animals, while others form symbiotic relationships with plants. Zygomycetes play a considerable commercial role. The metabolic products of other species of *Rhizopus* are intermediates in the synthesis of semi-synthetic steroid hormones.

Zygomycetes have a thallus of coenocytic hyphae in which the nuclei are haploid when the organism is in the vegetative stage. The fungi usually reproduce asexually by producing sporangiospores. The black tips of bread mold, *Rhizopus stolonifer*, are the swollen sporangia packed with black spores. When spores land on a suitable substrate, they germinate and produce a new mycelium.

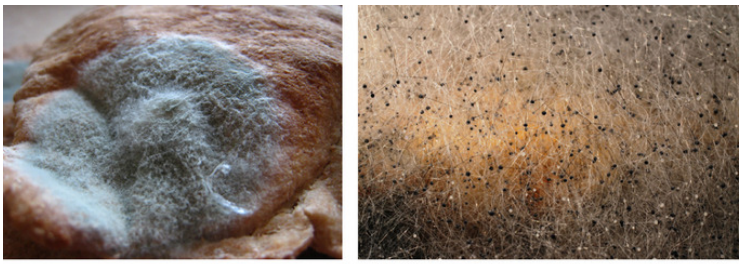


Figure **31.8.1**: Sporangia of bread mold: Sporangia grow at the end of stalks, which appear as (a) white fuzz seen on this bread mold, *Rhizopus stolonifer*. The (b) tips of bread mold are the spore-containing sporangia.

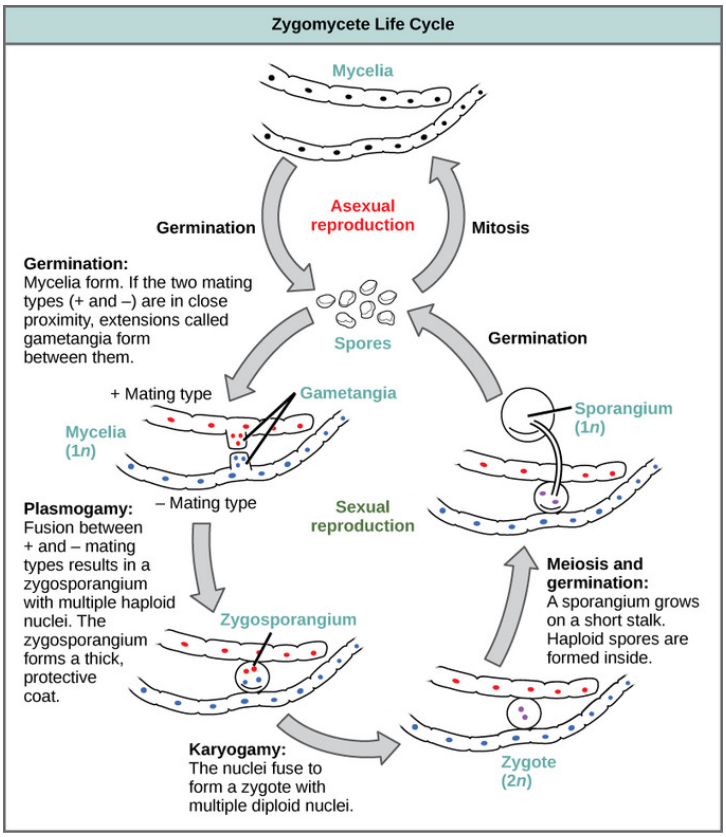


Figure **31.8.1**: Zygomycete life cycle: Zygomycetes have asexual and sexual life cycles. In the sexual life cycle, plus and minus mating types conjugate to form a zygosporangium.

Sexual reproduction starts when conditions become unfavorable. Two opposing mating strains (type + and type –) must be in close proximity for gametangia (singular: gametangium) from the hyphae to be produced and fuse, leading to karyogamy. The developing diploid zygospores have thick coats that protect them from desiccation and other hazards. They may remain dormant until environmental conditions become favorable. When the zygospore germinates, it undergoes meiosis and produces haploid spores, which will, in turn, grow into a new organism. This form of sexual reproduction in fungi is called conjugation (although it differs markedly from conjugation in bacteria and protists), giving rise to the name “conjugated fungi”.

Key Points

- Most zygomycota are saprobes, while a few species are parasites.
- Zygomycota usually reproduce asexually by producing sporangiospores.
- Zygomycota reproduce sexually when environmental conditions become unfavorable.
- To reproduce sexually, two opposing mating strains must fuse or conjugate, thereby, sharing genetic content and creating zygospores.
- The resulting diploid zygospores remain dormant and protected by thick coats until environmental conditions have improved.
- When conditions become favorable, zygospores undergo meiosis to produce haploid spores, which will eventually grow into a new organism.

Key Terms

- **zygomycete**: an organism of the phylum Zygomycota
- **karyogamy**: the fusion of two nuclei within a cell
- **zygospore**: a spore formed by the union of several zoospores
- **conjugation**: the temporary fusion of organisms, especially as part of sexual reproduction

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31.9: Chytridmycota and Relatives- Fungi with Zoospores

Learning Objectives

- Describe the ecology and reproduction of chytrids

Chytridiomycota: The Chytrids

The kingdom Fungi contains five major phyla, which were established according to their mode of sexual reproduction or use of molecular data. The Phylum Chytridiomycota (chytrids) is one of the five true phyla of fungi. There is only one class in the Phylum Chytridiomycota, the Chytridiomycetes. The chytrids are the simplest and most primitive Eumycota, or true fungi. The evolutionary record shows that the first, recognizable chytrids appeared during the late pre-Cambrian period, more than 500 million years ago. Like all fungi, chytrids have chitin in their cell walls, but one group of chytrids has both cellulose and chitin in the cell wall. Most chytrids are unicellular; a few form multicellular organisms and hyphae, which have no septa between cells (coenocytic). They reproduce both sexually and asexually; the asexual spores are called diploid zoospores. Their gametes are the only fungal cells known to have a flagellum.

The ecological habitat and cell structure of chytrids have much in common with protists. Chytrids usually live in aquatic environments, although some species live on land. Some species thrive as parasites on plants, insects, or amphibians, while others are saprobes. Some chytrids cause diseases in many species of amphibians, resulting in species decline and extinction. An example of a harmful parasitic chytrid is *Batrachochytrium dendrobatidis*, which is known to cause skin disease. Another chytrid species, *Allomyces*, is well characterized as an experimental organism. Its reproductive cycle includes both asexual and sexual phases. *Allomyces* produces diploid or haploid flagellated zoospores in a sporangium.

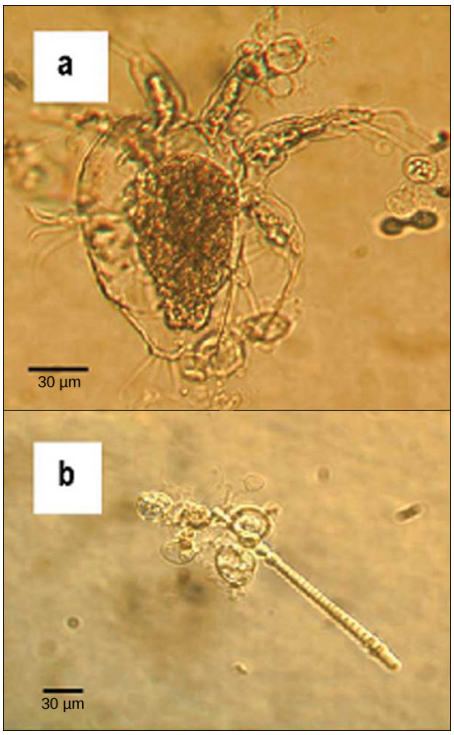


Figure **31.9.1**: Parasitic chytrids: The chytrid *Batrachochytrium dendrobatidis*is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod and (b) algae. This chytrid causes skin diseases in many species of amphibians, resulting in species decline and extinction.

Key Points

- The first recognizable chytrids appeared more than 500 million years ago during the late pre-Cambrian period.
- Like protists, chytrids usually live in aquatic environments, but some species live on land.
- Some chytrids are saprobes while others are parasites that may be harmful to amphibians and other animals.

- Chytrids reproduce both sexually and asexually, which leads to the production of zoospores.
- Chytrids have chitin in their cell walls; one unique group also has cellulose along with chitin.
- Chytrids are mostly unicellular, but multicellular organisms do exist.

Key Terms

- **chytridiomycete**: an organism of the phylum Chytridiomycota
- **zoospore**: an asexual spore of some algae and fungi
- **flagellum**: a flagellum is a lash-like appendage that protrudes from the cell body of certain prokaryotic and eukaryotic cells
- **coenocytic**: a multinucleate cell that can result from multiple nuclear divisions without their accompanying cytokinesis

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31.10: Microsporidia- Unicellular Parasites

Learning Objectives

- Summarize the general characteristics of unicellular eukaryotic parasites
- Describe the general life cycles and modes of reproduction in unicellular eukaryotic parasites
- Identify challenges associated with classifying unicellular eukaryotes
- Explain the taxonomic scheme used for unicellular eukaryotes
- Give examples of infections caused by unicellular eukaryotes

Clinical Focus: Part 1

Upon arriving home from school, 7-year-old Sarah complains that a large spot on her arm will not stop itching. She keeps scratching at it, drawing the attention of her parents. Looking more closely, they see that it is a red circular spot with a raised red edge (Figure **31.10.1**). The next day, Sarah's parents take her to their doctor, who examines the spot using a Wood's lamp. A Wood's lamp produces ultraviolet light that causes the spot on Sarah's arm to fluoresce, which confirms what the doctor already suspected: Sarah has a case of ringworm.

Sarah's mother is mortified to hear that her daughter has a "worm." How could this happen?

Exercise **31.10.1**

What are some likely ways that Sarah might have contracted ringworm?



Figure **31.10.1**: Ringworm presents as a raised, red ring on the skin. (credit: Centers for Disease Control and Prevention)

Eukaryotic microbes are an extraordinarily diverse group, including species with a wide range of life cycles, morphological specializations, and nutritional needs. Although more diseases are caused by viruses and bacteria than by microscopic eukaryotes, these eukaryotes are responsible for some diseases of great public health importance. For example, the protozoal disease malaria was responsible for 584,000 deaths worldwide (primarily children in Africa) in 2013, according to the World Health Organization (WHO). The protist parasite *Giardia* causes a diarrheal illness (giardiasis) that is easily transmitted through contaminated water supplies. In the United States, *Giardia* is the most common human intestinal parasite (Figure **31.10.2**). Although it may seem surprising, parasitic worms are included within the study of microbiology because identification depends on observation of microscopic adult worms or eggs. Even in developed countries, these worms are important parasites of humans and of domestic animals. There are fewer fungal pathogens, but these are important causes of illness, as well. On the other hand, fungi have been important in producing antimicrobial substances such as penicillin. In this chapter, we will examine characteristics of protists, worms, and fungi while considering their roles in causing disease.

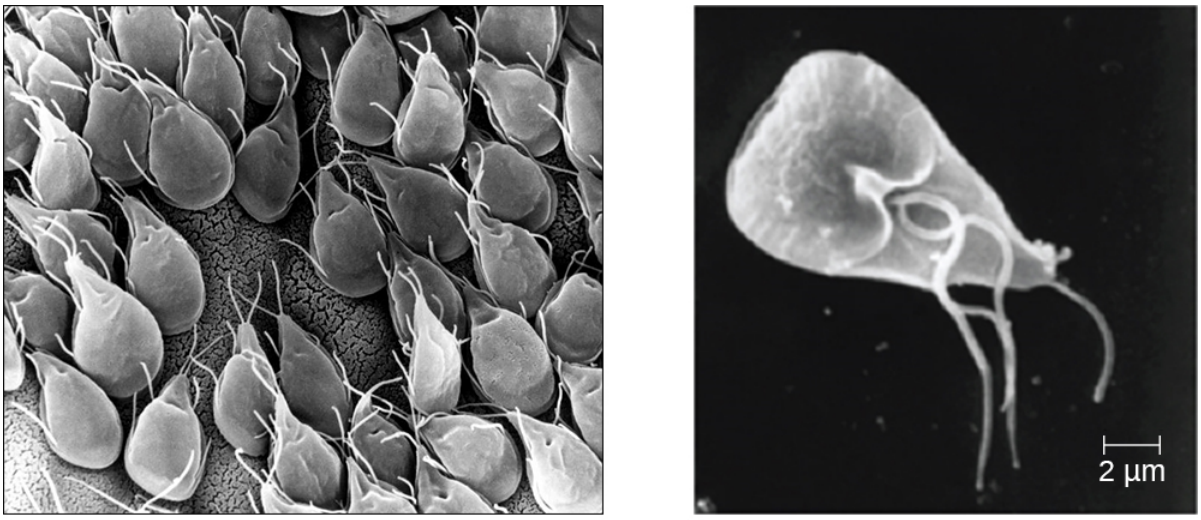


Figure **31.10.2**: (a) A scanning electron micrograph shows many *Giardia* parasites in the trophozoite, or feeding stage, in a gerbil intestine. (b) An individual trophozoite of *G. lamblia*, visualized here in a scanning electron micrograph. This waterborne protist causes severe diarrhea when ingested. (credit a, b: modification of work by Centers for Disease Control and Prevention)

Characteristics of Protists

The word *protist* is a historical term that is now used informally to refer to a diverse group of microscopic eukaryotic organisms. It is not considered a formal taxonomic term because the organisms it describes do not have a shared evolutionary origin. Historically, the protists were informally grouped into the "animal-like" protozoans, the "plant-like" algae, and the "fungus-like" protists such as water molds. These three groups of protists differ greatly in terms of their basic characteristics. For example, algae are photosynthetic organisms that can be unicellular or multicellular. Protozoa, on the other hand, are nonphotosynthetic, motile organisms that are always unicellular. Other informal terms may also be used to describe various groups of protists. For example, microorganisms that drift or float in water, moved by currents, are referred to as plankton. Types of plankton include zooplankton, which are motile and nonphotosynthetic, and phytoplankton, which are photosynthetic.

Protozoans inhabit a wide variety of habitats, both aquatic and terrestrial. Many are free-living, while others are parasitic, carrying out a life cycle within a host or hosts and potentially causing illness. There are also beneficial symbionts that provide metabolic services to their hosts. During the feeding and growth part of their life cycle, they are called trophozoites; these feed on small particulate food sources such as bacteria. While some types of protozoa exist exclusively in the trophozoite form, others can develop from trophozoite to an encapsulated cyst stage when environmental conditions are too harsh for the trophozoite. A cyst is a cell with a protective wall, and the process by which a trophozoite becomes a cyst is called encystment. When conditions become more favorable, these cysts are triggered by environmental cues to become active again through excystment.

One protozoan genus capable of encystment is *Eimeria*, which includes some human and animal pathogens. Figure **31.10.3** illustrates the life cycle of *Eimeria*.

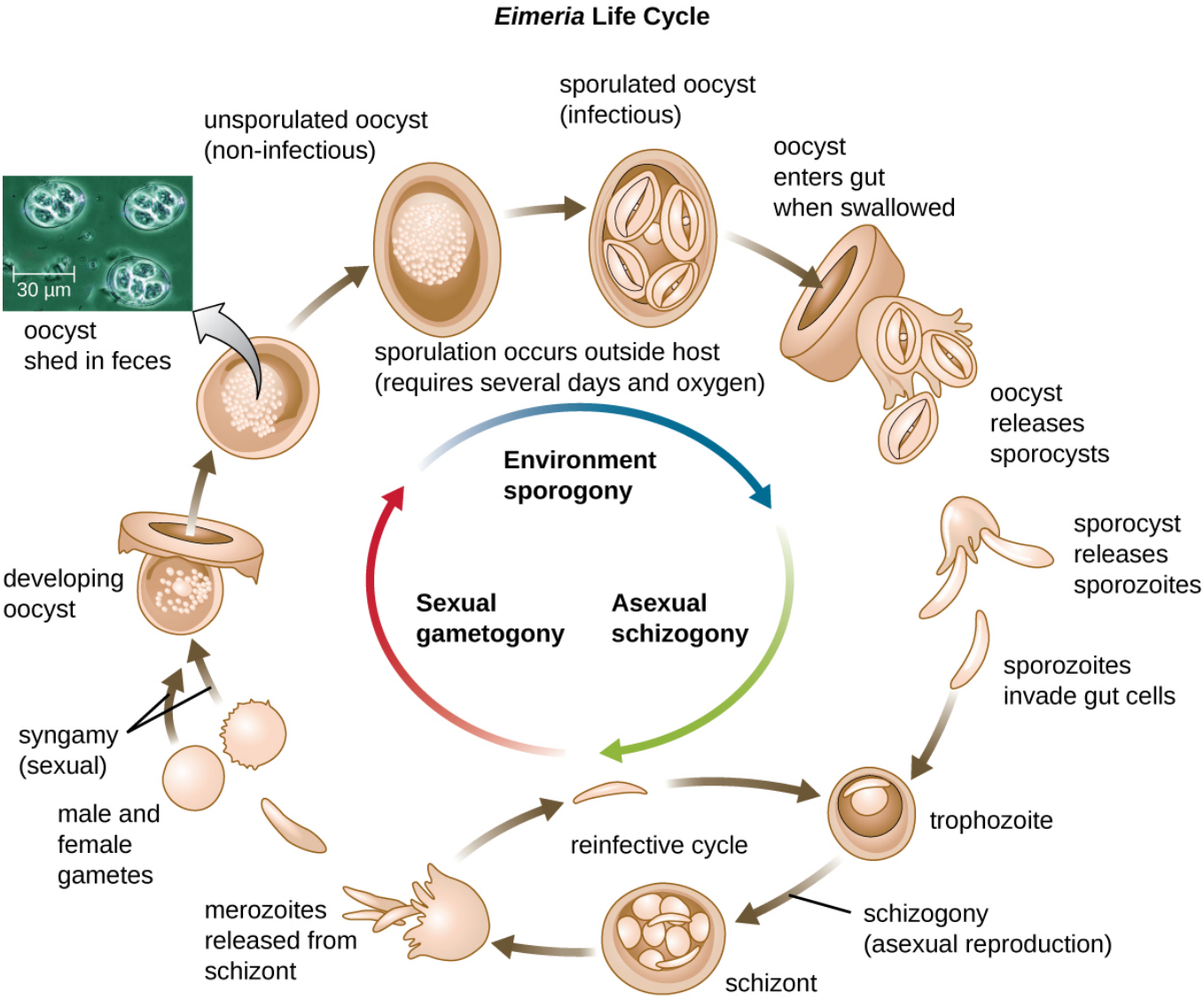


Figure **31.10.3**: In the sexual/asexual life cycle of Eimeria, oocysts (inset) are shed in feces and may cause disease when ingested by a new host. (credit "life cycle," "micrograph": modification of work by USDA)

Protozoans have a variety of reproductive mechanisms. Some protozoans reproduce asexually and others reproduce sexually; still others are capable of both sexual and asexual reproduction. In protozoans, asexual reproduction occurs by binary fission, budding, or schizogony. In schizogony, the nucleus of a cell divides multiple times before the cell divides into many smaller cells. The products of schizogony are called merozoites and they are stored in structures known as schizonts. Protozoans may also reproduce sexually, which increases genetic diversity and can lead to complex life cycles. Protozoans can produce haploid gametes that fuse through syngamy. However, they can also exchange genetic material by joining to exchange DNA in a process called conjugation. This is a different process than the conjugation that occurs in bacteria. The term protist conjugation refers to a true form of eukaryotic sexual reproduction between two cells of different mating types. It is found in ciliates, a group of protozoans, and is described later in this subsection.

All protozoans have a plasma membrane, or plasmalemma, and some have bands of protein just inside the membrane that add rigidity, forming a structure called the pellicle. Some protists, including protozoans, have distinct layers of cytoplasm under the membrane. In these protists, the outer gel layer (with microfilaments of actin) is called the ectoplasm. Inside this layer is a sol (fluid) region of cytoplasm called the endoplasm. These structures contribute to complex cell shapes in some protozoans, whereas others (such as amoebas) have more flexible shapes (Figure **31.10.4**).

Different groups of protozoans have specialized feeding structures. They may have a specialized structure for taking in food through phagocytosis, called a cytostome, and a specialized structure for the exocytosis of wastes called a cytoproct. Oral grooves

leading to cytostomes are lined with hair-like cilia to sweep in food particles. Protozoans are heterotrophic. Protozoans that are holozoic ingest whole food particles through phagocytosis. Forms that are saprozoic ingest small, soluble food molecules.

Many protists have whip-like flagella or hair-like cilia made of microtubules that can be used for locomotion (Figure **31.10.4**). Other protists use cytoplasmic extensions known as pseudopodia ("false feet") to attach the cell to a surface; they then allow cytoplasm to flow into the extension, thus moving themselves forward.

Protozoans have a variety of unique organelles and sometimes lack organelles found in other cells. Some have contractile vacuoles, organelles that can be used to move water out of the cell for osmotic regulation (salt and water balance) (Figure **31.10.4**). Mitochondria may be absent in parasites or altered to kinetoplastids (modified mitochondria) or hydrogenosomes (see Unique Characteristics of Eukaryotic Cells for more discussion of these structures).

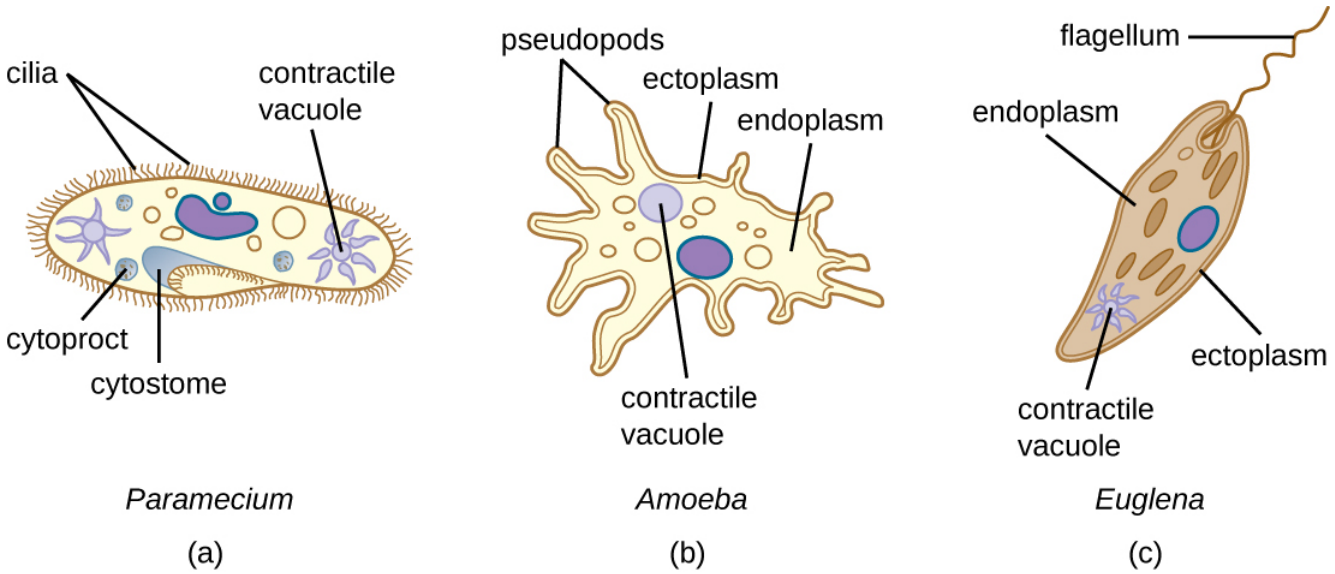


Figure **31.10.4**: (a) *Paramecium* spp. have hair-like appendages called cilia for locomotion. (b) *Amoeba* spp. use lobe-like pseudopodia to anchor the cell to a solid surface and pull forward. (c) *Euglena* spp. use a whip-like structure called a flagellum to propel the cell.

? Exercise 31.10.2

What is the sequence of events in reproduction by schizogony and what are the cells produced called?

Taxonomy of Protists

The protists are a polyphyletic group, meaning they lack a shared evolutionary origin. Since the current taxonomy is based on evolutionary history (as determined by biochemistry, morphology, and genetics), protists are scattered across many different taxonomic groups within the domain Eukarya. Eukarya is currently divided into six supergroups that are further divided into subgroups, as illustrated in (Figure **31.10.5**). In this section, we will primarily be concerned with the supergroups Amoebozoa, Excavata, and Chromalveolata; these supergroups include many protozoans of clinical significance. The supergroups Opisthokonta and Rhizaria also include some protozoans, but few of clinical significance. In addition to protozoans, Opisthokonta also includes animals and fungi, some of which we will discuss in Parasitic Helminths and Fungi. Some examples of the Archaeplastida will be discussed in Algae. Figure **31.10.6** and Figure **31.10.7** summarize the characteristics of each supergroup and subgroup and list representatives of each.

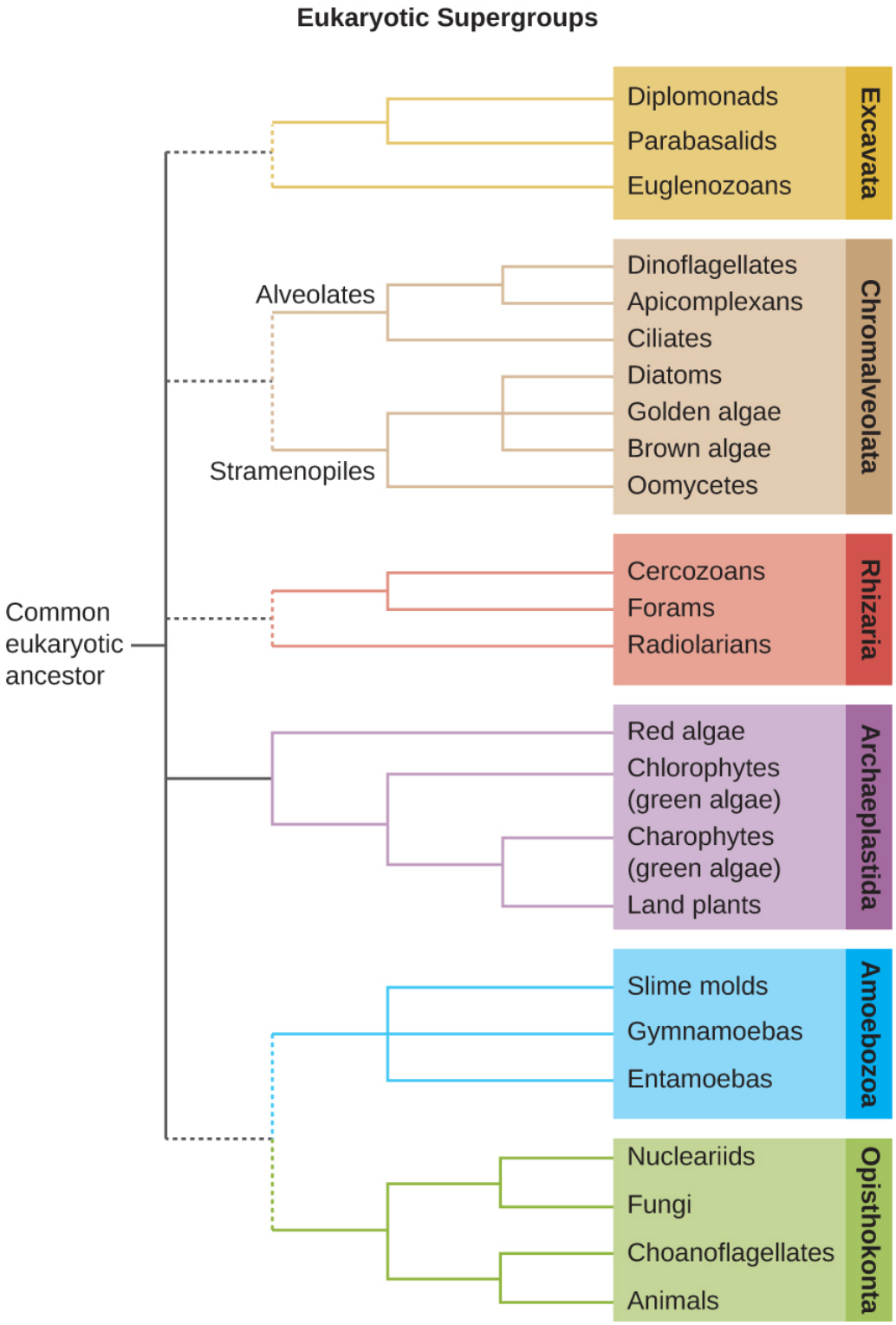


Figure **31.10.5**: This tree shows a proposed classification of the domain Eukarya based on evolutionary relationships. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

The Eukaryote Supergroups and Some Examples				
Supergroup	**Subgroups**	**Distinguishing Features**	**Examples**	**Clinical Notes**
Excavata	Fornicata	Form cysts Pair of equal nuclei No mitochondria Often parasitic Four free flagella	*Giardia lamblia*	Giardiasis
	Parabasalids	No mitochondria Four free flagella One attached flagellum No cysts Parasitic or symbiotic Basal bodies Kinetoplastids	*Trichomonas*	Trichomoniasis
	Euglenozoans	Photosynthetic or heterotrophic Flagella	*Euglena*	N/a
			Trypanosoma	African sleeping sickness, Chagas disease
			Leishmania	Leishmaniasis
Chromalveolata	Dinoflagellates	Cellulose theca Two dissimilar flagella	*Gonyaulax*	Red tides
			Alexandrium	Paralytic shellfish poisoning
			Pfiesteria	Harmful algal blooms
	Apicomplexans	Intracellular parasite Apical organelles	*Plasmodium*	Malaria
			Cryptosporidium	Cryptosporidiosis
			Theileria (Babesia)	Babesiosis
			Toxoplasma	Toxoplasmosis
	Ciliates	Cilia	*Balantidium*	Balantidiasis
			Paramecium	N/a
			Stentor	N/a
	Öomycetes/ peronosporomy-cetes	“Water molds” Generally diploid Cellulose cell walls	*Phytophthora*	Diseases in crops

Figure **31.10.6**

The Eukaryote Supergroups and Some Examples (continued)				
Supergroup	**Subgroups**	**Distinguishing Features**	**Examples**	**Clinical Notes**
Rhizaria	Foraminifera	Amoeboid Threadlike pseudopodia Calcium carbonate shells	*Astrolonche*	N/a
	Radiolaria	Amoeboid Threadlike pseudopodia Silica shells	*Actinomma*	N/a
	Cercozoa	Amoeboid Threadlike pseudopodia Complex shells Parasitic forms	*Spongospora subterranea*	Powdery scab (potato disease)
			Plasmodiophora brassicae	Cabbage clubroot
Archaeplastida	Red algae	Chlorophyll *a* Phycoerythrin Phycocyanin Floridean starch Agar in cell walls	*Gelidium*	Source of agar
			Gracilaria	Source of agar
	Chlorophytes	Chlorophyll *a* Chlorophyll *b* Cellulose cell walls Starch storage	*Acetabularia*	N/a
			Ulva	N/a
Amoebozoa	Slime molds	Plasmodial and cellular forms	*Dictyostelium*	N/a
	Entamoebas	Trophozoites Form cysts	*Entamoeba*	Amoebiasis
			Naegleria	Primary amoebic meningoencephalitis
			Acanthamoeba	Keratitis, granulomatous amoebic encephalitis
Opisthokonta	Fungi	Chitin cell walls Unicellular or multicellular Often hyphae	Zygomycetes	Zygomycosis
			Ascomycetes	Candidiasis
			Basidiomycetes	Cryptococcosis
			Microsporidia	Microsporidiosis
	Animals	Multicellular heterotrophs No cell walls	Nematoda	Trichinosis; hookworm and pinworm infections
			Trematoda	Schistosomiasis
			Cestoda	Tapeworm infections

Figure **31.10.7**

? Exercise 31.10.3

Which supergroups contain the clinically significant protists?

Amoebozoa

The supergroup Amoebozoa includes protozoans that use amoeboid movement. Actin microfilaments produce pseudopodia, into which the remainder of the protoplasm flows, thereby moving the organism. The genus *Entamoeba*includes commensal or parasitic

species, including the medically important *E. histolytica*, which is transmitted by cysts in feces and is the primary cause of amoebic dysentery. The notorious “brain-eating amoeba,” *Naegleria fowleri*, is also classified within the Amoebozoa. This deadly parasite is found in warm, fresh water and causes primary amoebic meningoencephalitis (PAM). Another member of this group is *Acanthamoeba*, which can cause keratitis (corneal inflammation) and blindness.

The Eumycetozoa are an unusual group of organisms called slime molds, which have previously been classified as animals, fungi, and plants (Figure **31.10.8**). Slime molds can be divided into two types: cellular slime molds and plasmodial slime molds. The cellular slime molds exist as individual amoeboid cells that periodically aggregate into a mobile slug. The aggregate then forms a fruiting body that produces haploid spores. Plasmodial slime molds exist as large, multinucleate amoeboid cells that form reproductive stalks to produce spores that divide into gametes. One cellular slime mold, *Dictyostelium discoideum*, has been an important study organism for understanding cell differentiation, because it has both single-celled and multicelled life stages, with the cells showing some degree of differentiation in the multicelled form. Figure **31.10.9** and Figure **31.10.10** illustrate the life cycles of cellular and plasmodial slime molds, respectively.



(a) (b)

Figure **31.10.8**: (a) The cellular slime mold *Dictyostelium discoideum* can be grown on agar in a Petri dish. In this image, individual amoeboid cells (visible as small spheres) are streaming together to form an aggregation that is beginning to rise in the upper right corner of the image. The primitively multicellular aggregation consists of individual cells that each have their own nucleus. (b) *Fuligo septica* is a plasmodial slime mold. This brightly colored organism consists of a large cell with many nuclei.

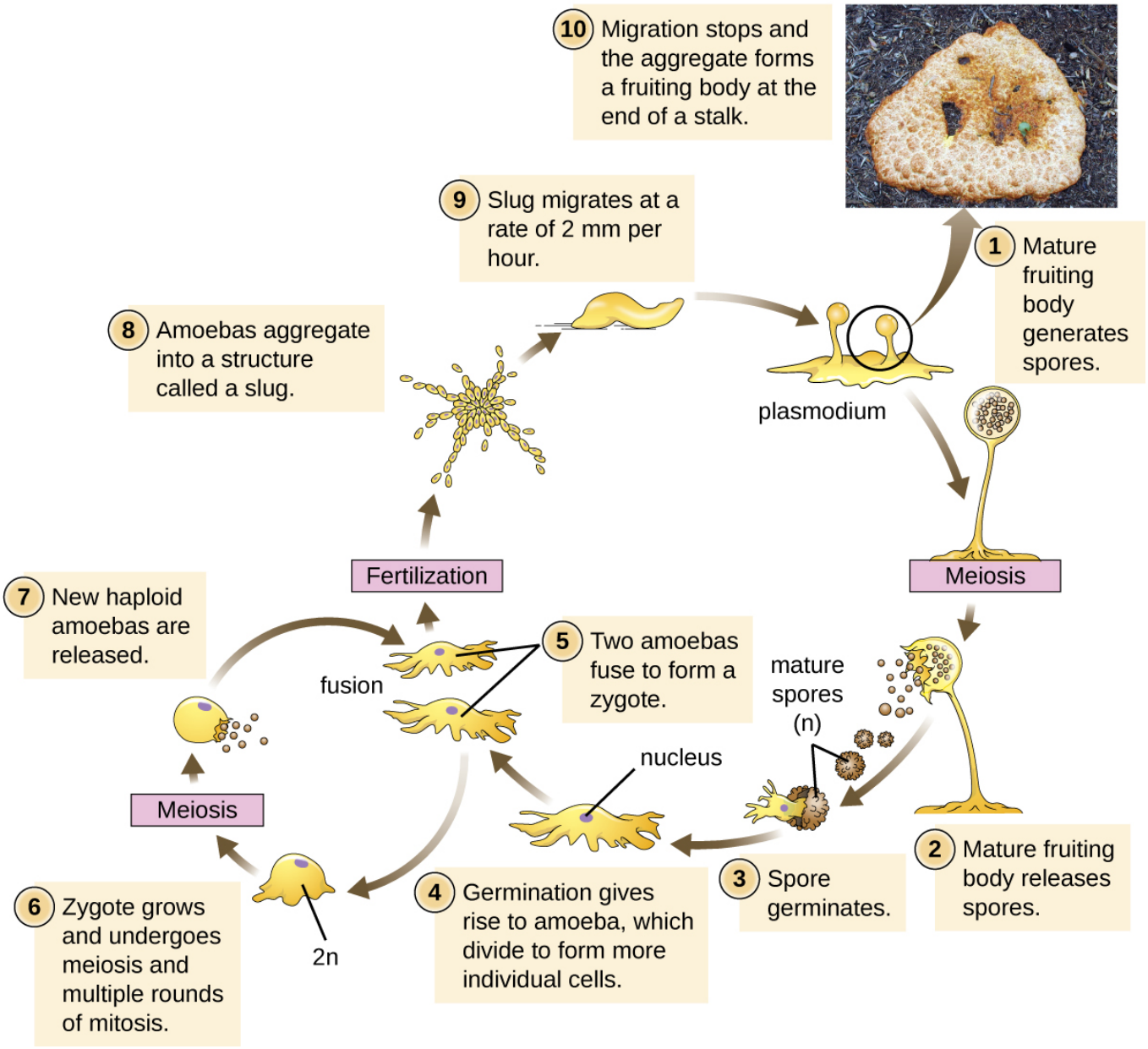


Figure **31.10.9**: The life cycle of the cellular slime mold *Dictyostelium discoideum* primarily involves individual amoebas but includes the formation of a multinucleate plasmodium formed from a uninucleate zygote (the result of the fusion of two individual amoeboid cells). The plasmodium is able to move and forms a fruiting body that generates haploid spores. (credit "photo": modification of work by "thatredhead4"/Flickr)

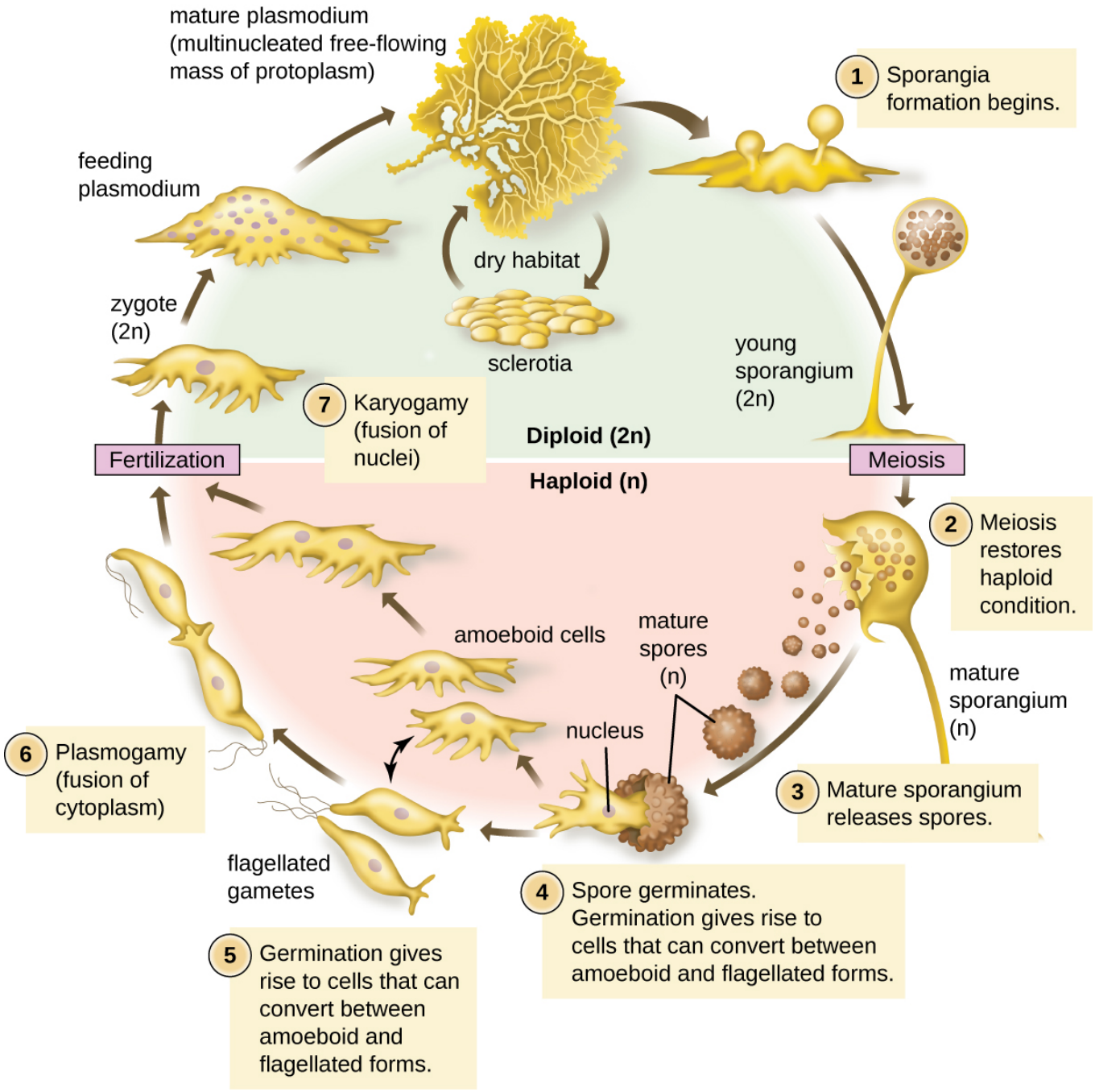


Figure **31.10.1**: Plasmodial slime molds exist as large multinucleate amoeboid cells that form reproductive stalks to produce spores that divide into gametes.

Chromalveolata

The supergroup Chromalveolata is united by similar origins of its members' plastids and includes the apicomplexans, ciliates, diatoms, and dinoflagellates, among other groups (we will cover the diatoms and dinoflagellates in Algae). The apicomplexans are intra- or extracellular parasites that have an apical complex at one end of the cell. The apical complex is a concentration of organelles, vacuoles, and microtubules that allows the parasite to enter host cells (Figure **31.10.11**). Apicomplexans have complex life cycles that include an infective sporozoite that undergoes schizogony to make many merozoites (see the example in Figure **31.10.3**). Many are capable of infecting a variety of animal cells, from insects to livestock to humans, and their life cycles often depend on transmission between multiple hosts. The genus *Plasmodium* is an example of this group.

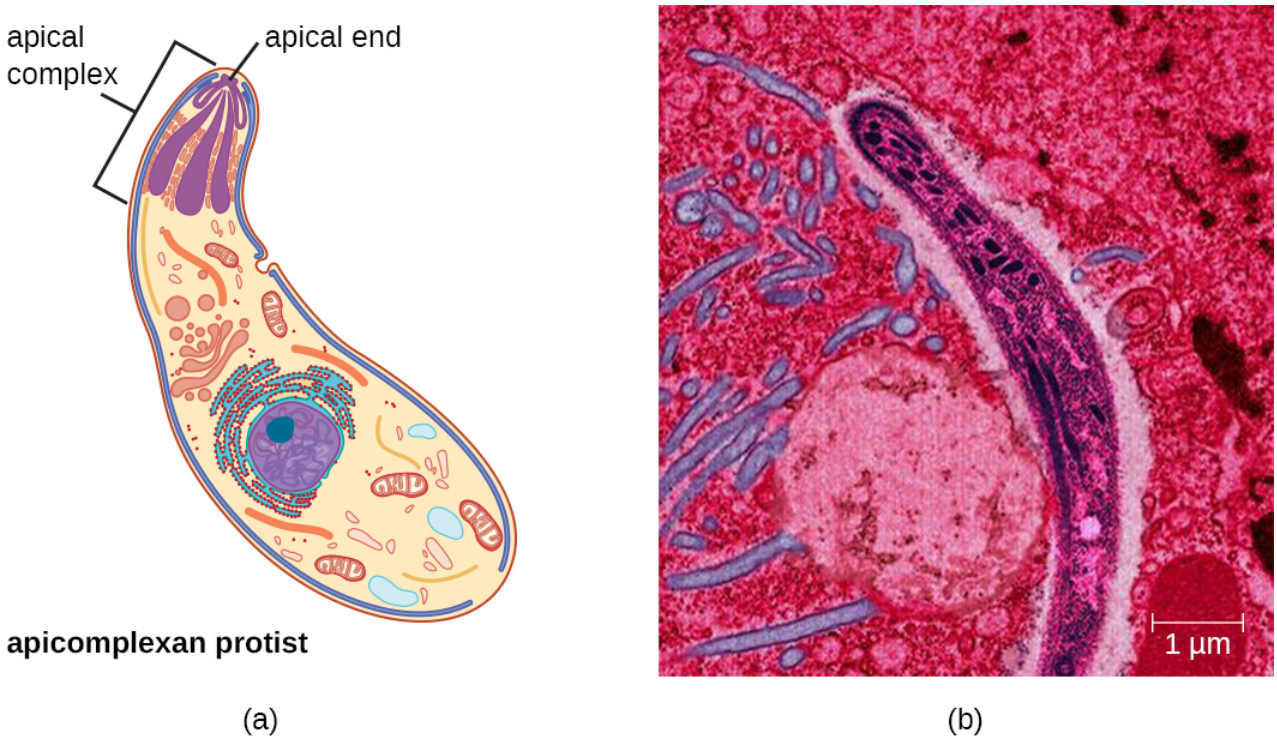


Figure **31.10.11**: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) A colorized electron microscope image of a *Plasmodium* sporozoite. (credit b: modification of work by Ute Frevert)

Other apicomplexans are also medically important. *Cryptosporidium parvum* causes intestinal symptoms and can cause epidemic diarrhea when the cysts contaminate drinking water. *Theileria (Babesia) microti*, transmitted by the tick *Ixodes scapularis*, causes recurring fever that can be fatal and is becoming a common transfusion-transmitted pathogen in the United States (*Theileria* and *Babesia* are closely related genera and there is some debate about the best classification). Finally, *Toxoplasma gondii* causes toxoplasmosis and can be transmitted from cat feces, unwashed fruit and vegetables, or from undercooked meat. Because toxoplasmosis can be associated with serious birth defects, pregnant women need to be aware of this risk and use caution if they are exposed to the feces of potentially infected cats. A national survey found the frequency of individuals with antibodies for toxoplasmosis (and thus who presumably have a current latent infection) in the United States to be 11%. Rates are much higher in other countries, including some developed countries.[1] There is also evidence and a good deal of theorizing that the parasite may be responsible for altering infected humans' behavior and personality traits.[2]

The ciliates (Ciliaphora), also within the Chromalveolata, are a large, very diverse group characterized by the presence of cilia on their cell surface. Although the cilia may be used for locomotion, they are often used for feeding, as well, and some forms are nonmotile. *Balantidium coli* (Figure **31.10.12**) is the only parasitic ciliate that affects humans by causing intestinal illness, although it rarely causes serious medical issues except in the immunocompromised (those having a weakened immune system). Perhaps the most familiar ciliate is *Paramecium*, a motile organism with a clearly visible cytostomeand cytoproct that is often studied in biology laboratories (Figure **31.10.13**). Another ciliate, *Stentor*, is sessile and uses its cilia for feeding (Figure **31.10.14**). Generally, these organisms have a micronucleus that is diploid, somatic, and used for sexual reproduction by conjugation. They also have a macronucleus that is derived from the micronucleus; the macronucleus becomes polyploid (multiple sets of duplicate chromosomes), and has a reduced set of metabolic genes.

Ciliates are able to reproduce through conjugation, in which two cells attach to each other. In each cell, the diploid micronuclei undergo meiosis, producing eight haploid nuclei each. Then, all but one of the haploid micronuclei and the macronucleus disintegrate; the remaining (haploid) micronucleus undergoes mitosis. The two cells then exchange one micronucleus each, which fuses with the remaining micronucleus present to form a new, genetically different, diploid micronucleus. The diploid micronucleus undergoes two mitotic divisions, so each cell has four micronuclei, and two of the four combine to form a new macronucleus. The chromosomes in the macronucleus then replicate repeatedly, the macronucleus reaches its polyploid state, and the two cells separate. The two cells are now genetically different from each other and from their previous versions.



Figure **31.10.12**: This specimen of the ciliate *Balantidium coli* is a trophozoite form isolated from the gut of a primate. *B. coli* is the only ciliate capable of parasitizing humans. (credit: modification of work by Kouassi RYW, McGraw SW, Yao PK, Abou-Bacar A, Brunet J, Pesson B, Bonfoh B, N'goran EK & Candolfi E)

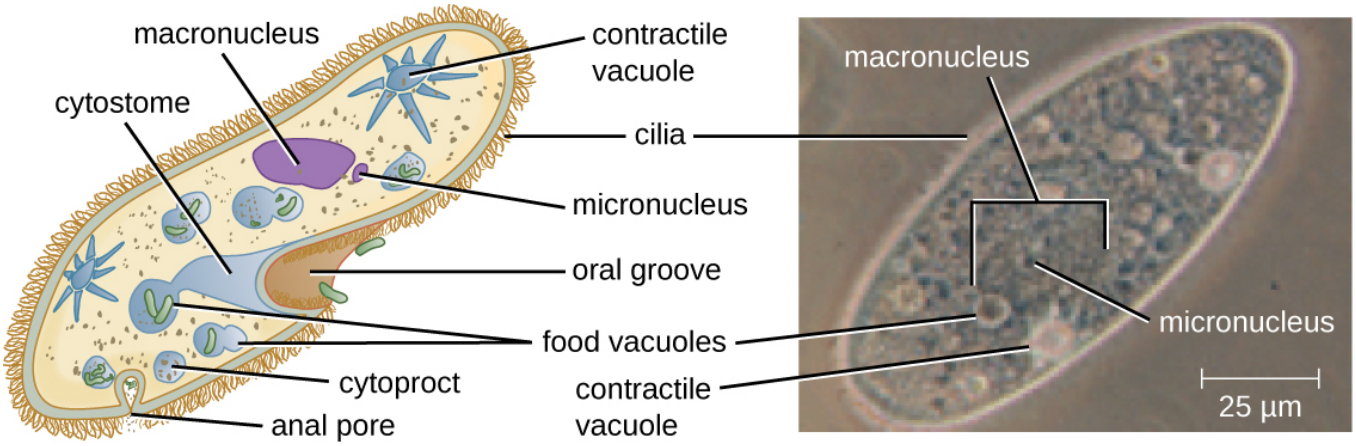


Figure **31.10.13**: Paramecium has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move.

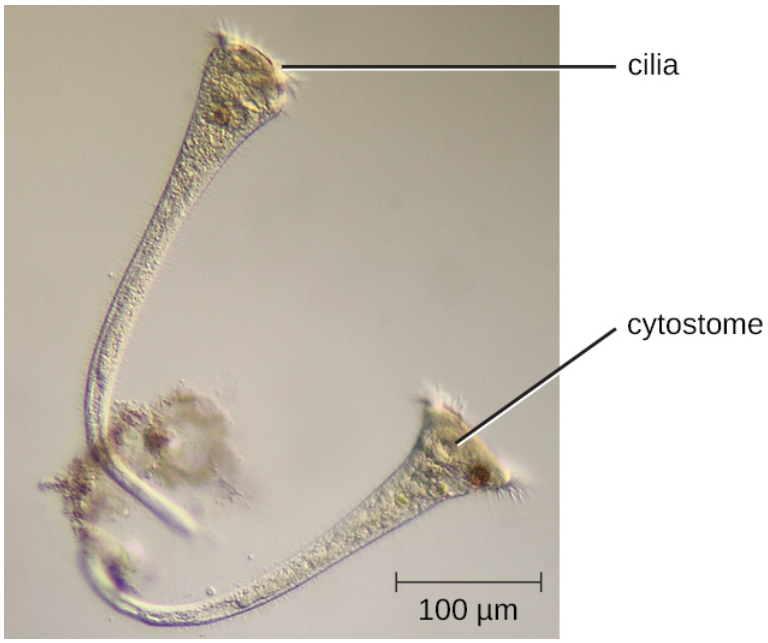


Figure **31.10.14**: This differential interference contrast micrograph (magnification: ×65) of *Stentor roeselie* shows cilia present on the margins of the structure surrounding the cytostome; the cilia move food particles. (credit: modification of work by "picturepest"/Flickr)

Öomycetes have similarities to fungi and were once classified with them. They are also called water molds. However, they differ from fungi in several important ways. Öomycetes have cell walls of cellulose (unlike the chitinous cell walls of fungi) and they are generally diploid, whereas the dominant life forms of fungi are typically haploid. *Phytophthora*, the plant pathogen found in the soil that caused the Irish potato famine, is classified within this group (Figure **31.10.15**).



Figure **31.10.15**: A saprobic oomycete, or water mold, engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Link to Learning

This video shows the feeding of *Stentor*.

Excavata

The third and final supergroup to be considered in this section is the Excavata, which includes primitive eukaryotes and many parasites with limited metabolic abilities. These organisms have complex cell shapes and structures, often including a depression on the surface of the cell called an excavate. The group Excavata includes the subgroups Fornicata, Parabasalia, and Euglenozoa. The Fornicata lack mitochondria but have flagella. This group includes *Giardia lamblia* (also known as *G. intestinalis* or *G. duodenalis)*, a widespread pathogen that causes diarrheal illness and can be spread through cysts from feces that contaminate water supplies (Figure **31.10.2**). Parabasalia are frequent animal endosymbionts; they live in the guts of animals like termites and cockroaches. They have basal bodies and modified mitochondria (kinetoplastids). They also have a large, complex cell structure with an undulating membrane and often have many flagella. The trichomonads (a subgroup of the Parabasalia) include pathogens such as *Trichomonas vaginalis*, which causes the human sexually transmitted disease trichomoniasis. Trichomoniasis often does not cause symptoms in men, but men are able to transmit the infection. In women, it causes vaginal discomfort and discharge and may cause complications in pregnancy if left untreated.

The Euglenozoa are common in the environment and include photosynthetic and nonphotosynthetic species. Members of the genus *Euglena* are typically not pathogenic. Their cells have two flagella, a pellicle, a stigma (eyespot) to sense light, and chloroplasts for photosynthesis (Figure **31.10.16**). The pellicle of *Euglena* is made of a series of protein bands surrounding the cell; it supports the cell membrane and gives the cell shape.

The Euglenozoa also include the trypanosomes, which are parasitic pathogens. The genus *Trypanosoma* includes *T. brucei*, which causes African trypanosomiasis (African sleeping sickness and *T. cruzi*, which causes American trypanosomiasis (Chagas disease). These tropical diseases are spread by insect bites. In African sleeping sickness, *T. brucei* colonizes the blood and the brain after being transmitted via the bite of a tsetse fly (*Glossina* spp.) (Figure **31.10.17**). The early symptoms include confusion, difficulty sleeping, and lack of coordination. Left untreated, it is fatal.

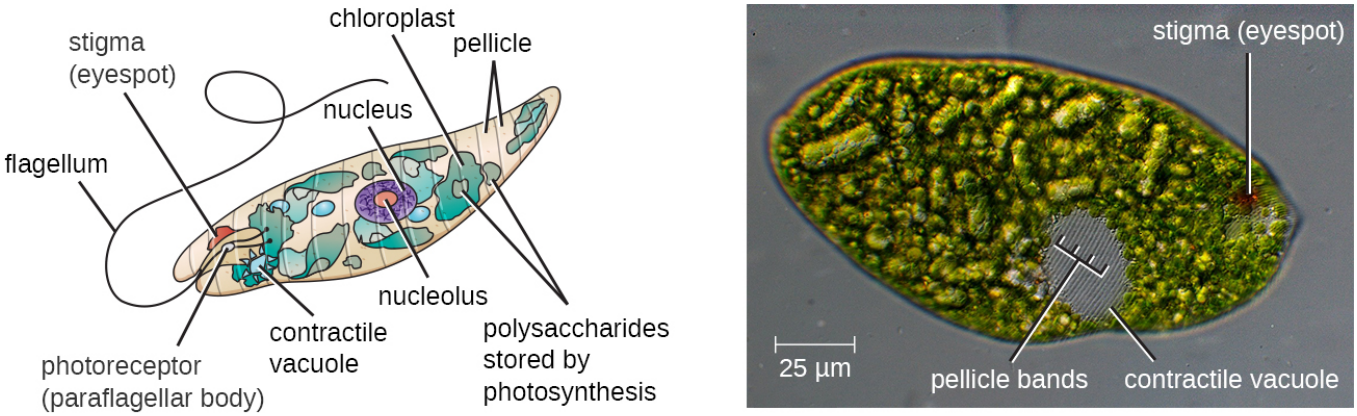


Figure **31.10.16**: (a) This illustration of a *Euglena* shows the characteristic structures, such as the stigma and flagellum. (b) The pellicle, under the cell membrane, gives the cell its distinctive shape and is visible in this image as delicate parallel striations over the surface of the entire cell (especially visible over the grey contractile vacuole). (credit a: modification of work by Claudio Miklos; credit b: modification of work by David Shykind)

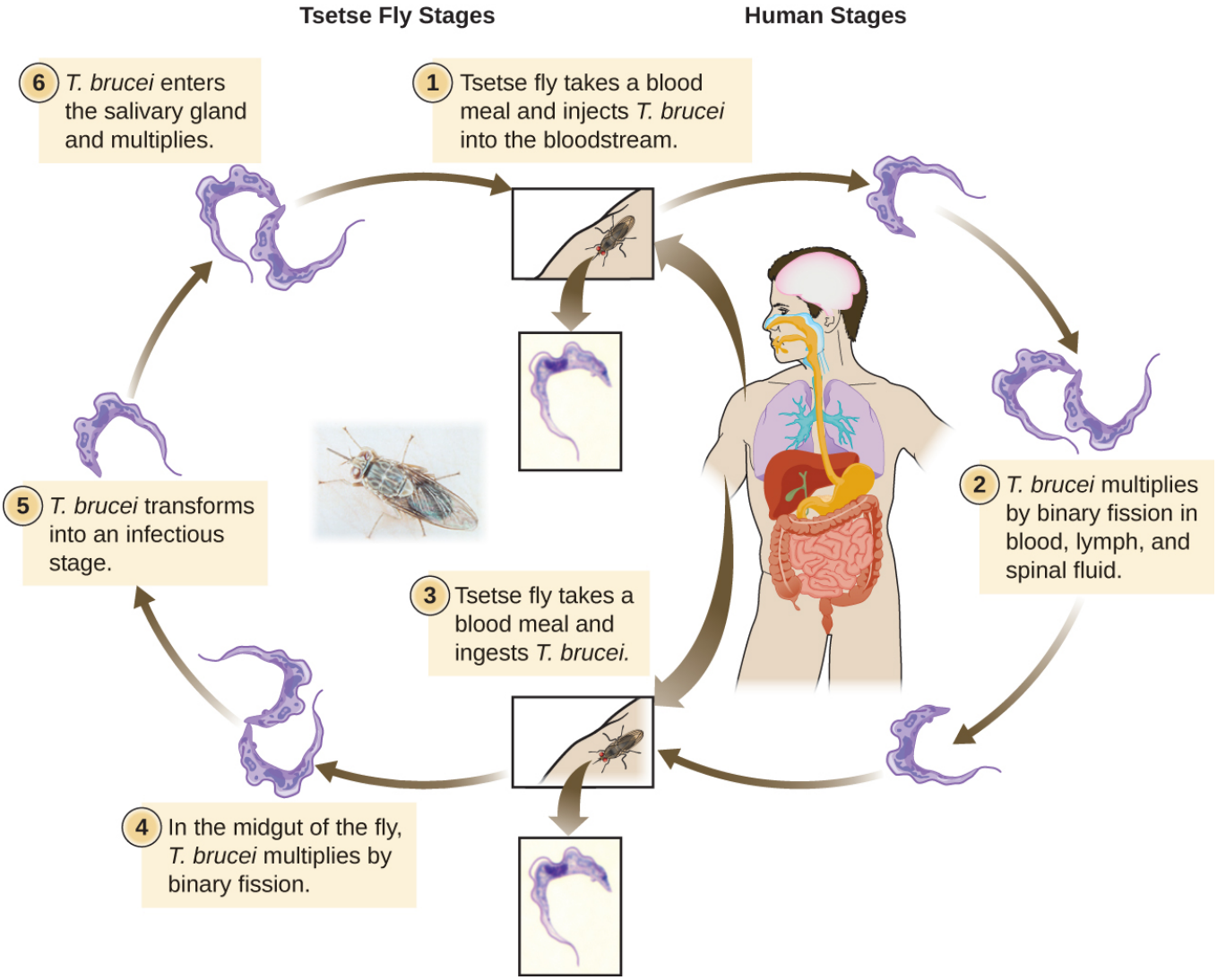


Figure **31.10.17**: Trypanosoma brucei, the causative agent of African trypanosomiasis, spends part of its life cycle in the tsetse fly and part in humans. (credit "illustration": modification of work by Centers for Disease Control and Prevention; credit "photo": DPDx/Centers for Disease Control and Prevention)

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Chagas' disease originated and is most common in Latin America. The disease is transmitted by *Triatoma* spp., insects often called "kissing bugs," and affects either the heart tissue or tissues of the digestive system. Untreated cases can eventually lead to heart failure or significant digestive or neurological disorders.

The genus *Leishmania* includes trypanosomes that cause disfiguring skin disease and sometimes systemic illness as well.

Neglected Parasites

The Centers for Disease Control and Prevention (CDC) is responsible for identifying public health priorities in the United States and developing strategies to address areas of concern. As part of this mandate, the CDC has officially identified five parasitic diseases it considers to have been neglected (i.e., not adequately studied). These neglected parasitic infections (NPIs) include toxoplasmosis, Chagas disease, toxocariasis (a nematode infection transmitted primarily by infected dogs), cysticercosis (a disease caused by a tissue infection of the tapeworm *Taenia solium*), and trichomoniasis (a sexually transmitted disease caused by the parabasalid *Trichomonas vaginalis*).

The decision to name these specific diseases as NPIs means that the CDC will devote resources toward improving awareness and developing better diagnostic testing and treatment through studies of available data. The CDC may also advise on treatment of these diseases and assist in the distribution of medications that might otherwise be difficult to obtain.3

Of course, the CDC does not have unlimited resources, so by prioritizing these five diseases, it is effectively deprioritizing others. Given that many Americans have never heard of many of these NPIs, it is fair to ask what criteria the CDC used in prioritizing diseases. According to the CDC, the factors considered were the number of people infected, the severity of the illness, and whether the illness can be treated or prevented. Although several of these NPIs may seem to be more common outside the United States, the CDC argues that many cases in the United States likely go undiagnosed and untreated because so little is known about these diseases.4

What criteria should be considered when prioritizing diseases for purposes of funding or research? Are those identified by the CDC reasonable? What other factors could be considered? Should government agencies like the CDC have the same criteria as private pharmaceutical research labs? What are the ethical implications of deprioritizing other potentially neglected parasitic diseases such as leishmaniasis?

Key Concepts and Summary

- **Protists** are a diverse, **polyphyletic** group of eukaryotic organisms.
- Protists may be unicellular or multicellular. They vary in how they get their nutrition, morphology, method of locomotion, and mode of reproduction.
- Important structures of protists include **contractile vacuoles**, cilia, flagella, **pellicles**, and pseudopodia; some lack organelles such as mitochondria.
- Taxonomy of protists is changing rapidly as relationships are reassessed using newer techniques.
- The protists include important pathogens and parasites.

Footnotes

1. 1 J. Flegr et al. "Toxoplasmosis—A Global Threat. Correlation of Latent Toxoplasmosis With Specific Disease Burden in a Set of 88 Countries." *PloS ONE* 9 no. 3 (2014):e90203.
2. 2 J. Flegr. "Effects of Toxoplasma on Human Behavior." *Schizophrenia Bull* 33, no. 3 (2007):757–760.
3. 3 Centers for Disease Control and Prevention. "Neglected Parasitic Infections (NPIs) in the United States." http://www.cdc.gov/parasites/npi/. Last updated July 10, 2014.
4. 4 Centers for Disease Control and Prevention. "Fact Sheet: Neglected Parasitic Infections in the United States." www.cdc.gov/parasites/resourc..._factsheet.pdf

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CHAPTER OVERVIEW

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32.1: Some General Features of Animals

Skills to Develop

- List the features that distinguish the kingdom Animalia from other kingdoms
- Explain the processes of animal reproduction and embryonic development
- Describe the roles that Hox genes play in development

Even though members of the animal kingdom are incredibly diverse, most animals share certain features that distinguish them from organisms in other kingdoms. All animals are eukaryotic, multicellular organisms, and almost all animals have a complex tissue structure with differentiated and specialized tissues. Most animals are motile, at least during certain life stages. All animals require a source of food and are therefore heterotrophic, ingesting other living or dead organisms; this feature distinguishes them from autotrophic organisms, such as most plants, which synthesize their own nutrients through photosynthesis. As heterotrophs, animals may be carnivores, herbivores, omnivores, or parasites (Figure 32.1.1). Most animals reproduce sexually, and the offspring pass through a series of developmental stages that establish a determined and fixed body plan. The body plan refers to the morphology of an animal, determined by developmental cues.



(a) (b)

Figure 32.1.1: All animals are heterotrophs that derive energy from food. The (a) black bear is an omnivore, eating both plants and animals. The (b) heartworm *Dirofilaria immitis* is a parasite that derives energy from its hosts. It spends its larval stage in mosquitoes and its adult stage infesting the heart of dogs and other mammals, as shown here. (credit a: modification of work by USDA Forest Service; credit b: modification of work by Clyde Robinson)

Complex Tissue Structure

As multicellular organisms, animals differ from plants and fungi because their cells don't have cell walls, their cells may be embedded in an extracellular matrix (such as bone, skin, or connective tissue), and their cells have unique structures for intercellular communication (such as gap junctions). In addition, animals possess unique tissues, absent in fungi and plants, which allow coordination (nerve tissue) of motility (muscle tissue). Animals are also characterized by specialized connective tissues that provide structural support for cells and organs. This connective tissue constitutes the extracellular surroundings of cells and is made up of organic and inorganic materials. In vertebrates, bone tissue is a type of connective tissue that supports the entire body structure. The complex bodies and activities of vertebrates demand such supportive tissues. Epithelial tissues cover, line, protect, and secrete. Epithelial tissues include the epidermis of the integument, the lining of the digestive tract and trachea, and make up the ducts of the liver and glands of advanced animals.

The animal kingdom is divided into Parazoa (sponges) and Eumetazoa (all other animals). As very simple animals, the organisms in group Parazoa ("beside animal") do not contain true specialized tissues; although they do possess specialized cells that perform different functions, those cells are not organized into tissues. These organisms are considered animals since they lack the ability to make their own food. Animals with true tissues are in the group Eumetazoa ("true animals"). When we think of animals, we usually think of Eumetazoans, since most animals fall into this category.

The different types of tissues in true animals are responsible for carrying out specific functions for the organism. This differentiation and specialization of tissues is part of what allows for such incredible animal diversity. For example, the evolution of nerve tissues and muscle tissues has resulted in animals' unique ability to rapidly sense and respond to changes in their environment. This allows animals to survive in environments where they must compete with other species to meet their nutritional demands.

Link to Learning

Watch a presentation by biologist E.O. Wilson on the importance of diversity.

Animal Reproduction and Development

Most animals are diploid organisms, meaning that their body (somatic) cells are diploid and haploid reproductive (gamete) cells are produced through meiosis. Some exceptions exist: For example, in bees, wasps, and ants, the male is haploid because it develops from unfertilized eggs. Most animals undergo sexual reproduction: This fact distinguishes animals from fungi, protists, and bacteria, where asexual reproduction is common or exclusive. However, a few groups, such as cnidarians, flatworm, and roundworms, undergo asexual reproduction, although nearly all of those animals also have a sexual phase to their life cycle.

Processes of Animal Reproduction and Embryonic Development

During sexual reproduction, the haploid gametes of the male and female individuals of a species combine in a process called fertilization. Typically, the small, motile male sperm fertilizes the much larger, sessile female egg. This process produces a diploid fertilized egg called a zygote.

Some animal species—including sea stars and sea anemones, as well as some insects, reptiles, and fish—are capable of asexual reproduction. The most common forms of asexual reproduction for stationary aquatic animals include budding and fragmentation, where part of a parent individual can separate and grow into a new individual. In contrast, a form of asexual reproduction found in certain insects and vertebrates is called parthenogenesis (or "virgin beginning"), where unfertilized eggs can develop into new male offspring. This type of parthenogenesis is called haplodiploidy. These types of asexual reproduction produce genetically identical offspring, which is disadvantageous from the perspective of evolutionary adaptability because of the potential buildup of deleterious mutations. However, for animals that are limited in their capacity to attract mates, asexual reproduction can ensure genetic propagation.

After fertilization, a series of developmental stages occur during which primary germ layers are established and reorganize to form an embryo. During this process, animal tissues begin to specialize and organize into organs and organ systems, determining their future morphology and physiology. Some animals, such as grasshoppers, undergo incomplete metamorphosis, in which the young resemble the adult. Other animals, such as some insects, undergo complete metamorphosis where individuals enter one or more larval stages that may in differ in structure and function from the adult (Figure **32.1.2**). For the latter, the young and the adult may have different diets, limiting competition for food between them. Regardless of whether a species undergoes complete or incomplete metamorphosis, the series of developmental stages of the embryo remains largely the same for most members of the animal kingdom.

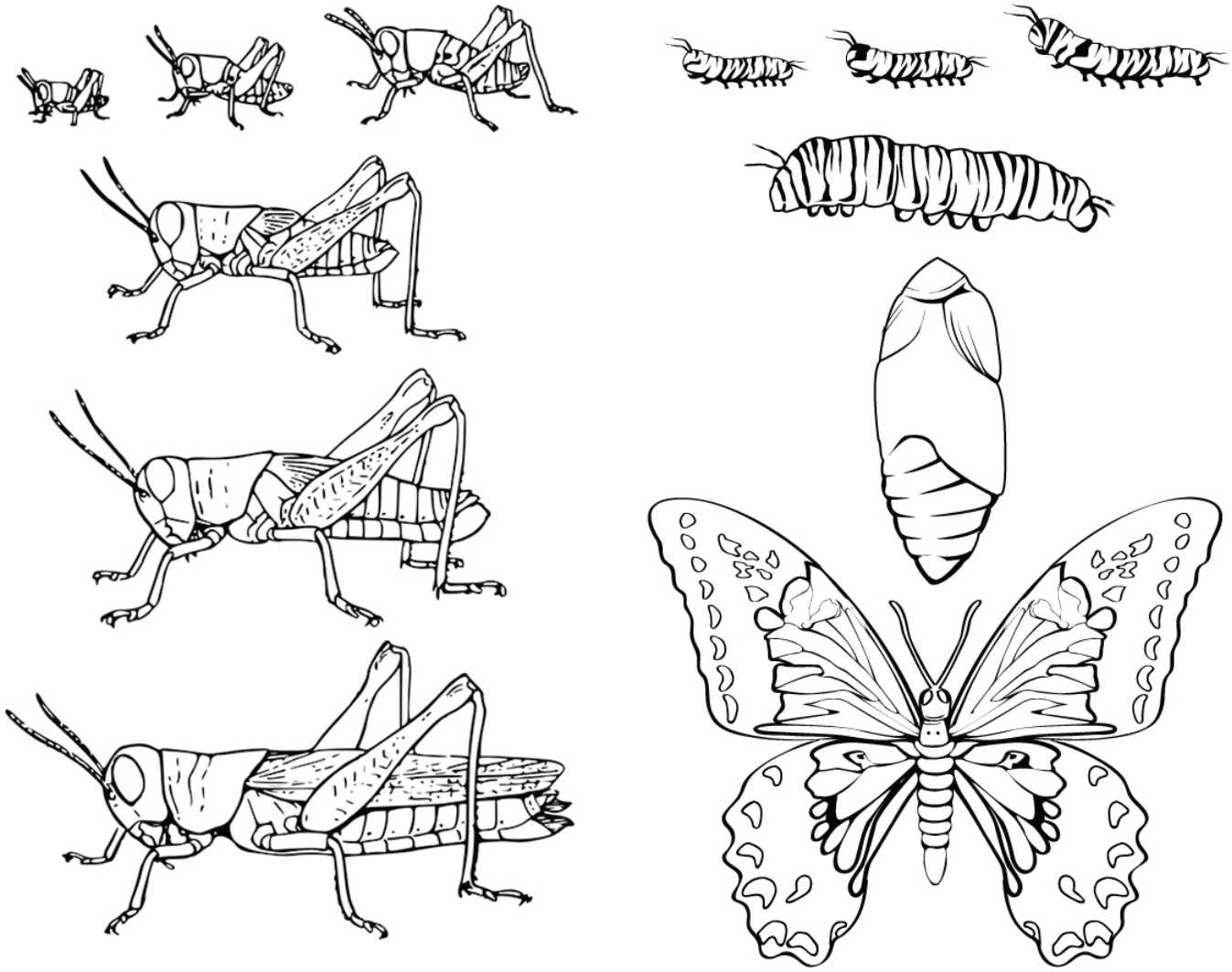


Figure 32.1.2: (a) The grasshopper undergoes incomplete metamorphosis. (b) The butterfly undergoes complete metamorphosis. (credit: S.E. Snodgrass, USDA)

The process of animal development begins with the cleavage, or series of mitotic cell divisions, of the zygote (Figure 32.1.3). Three cell divisions transform the single-celled zygote into an eight-celled structure. After further cell division and rearrangement of existing cells, a 6–32-celled hollow structure called a blastula is formed. Next, the blastula undergoes further cell division and cellular rearrangement during a process called gastrulation. This leads to the formation of the next developmental stage, the gastrula, in which the future digestive cavity is formed. Different cell layers (called germ layers) are formed during gastrulation. These germ layers are programmed to develop into certain tissue types, organs, and organ systems during a process called organogenesis.

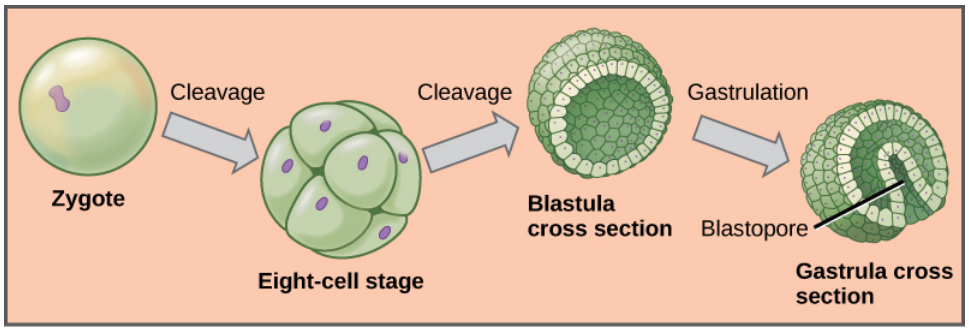


Figure **32.1.3**: During embryonic development, the zygote undergoes a series of mitotic cell divisions, or cleavages, to form an eight-cell stage, then a hollow blastula. During a process called gastrulation, the blastula folds inward to form a cavity in the gastrula.

Link to Learning



Watch the following video to see how human embryonic development (after the blastula and gastrula stages of development) reflects evolution.

The Role of Homeobox (*Hox*) Genes in Animal Development

Since the early 19th century, scientists have observed that many animals, from the very simple to the complex, shared similar embryonic morphology and development. Surprisingly, a human embryo and a frog embryo, at a certain stage of embryonic development, look remarkably alike. For a long time, scientists did not understand why so many animal species looked similar during embryonic development but were very different as adults. They wondered what dictated the developmental direction that a fly, mouse, frog, or human embryo would take. Near the end of the 20th century, a particular class of genes was discovered that had this very job. These genes that determine animal structure are called "homeotic genes," and they contain DNA sequences called homeoboxes. The animal genes containing homeobox sequences are specifically referred to as *Hox* genes. This family of genes is responsible for determining the general body plan, such as the number of body segments of an animal, the number and placement of appendages, and animal head-tail directionality. The first *Hox* genes to be sequenced were those from the fruit fly (*Drosophila melanogaster*). A single *Hox* mutation in the fruit fly can result in an extra pair of wings or even appendages growing from the "wrong" body part.

While there are a great many genes that play roles in the morphological development of an animal, what makes *Hox* genes so powerful is that they serve as master control genes that can turn on or off large numbers of other genes. *Hox* genes do this by coding transcription factors that control the expression of numerous other genes. *Hox* genes are homologous in the animal kingdom, that is, the genetic sequences of *Hox* genes and their positions on chromosomes are remarkably similar across most animals because of their presence in a common ancestor, from worms to flies, mice, and humans (Figure **32.1.4**). One of the contributions to increased animal body complexity is that *Hox* genes have undergone at least two duplication events during animal evolution, with the additional genes allowing for more complex body types to evolve.

Art Connection

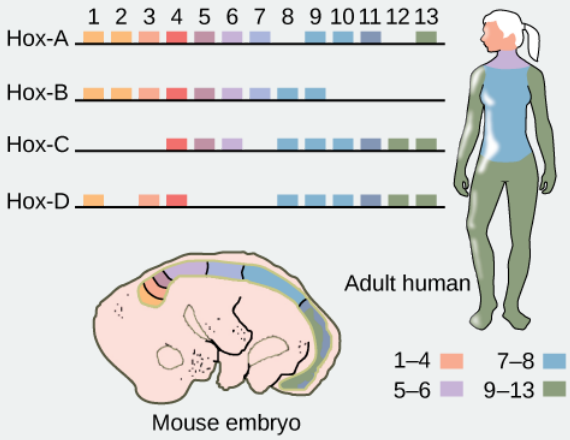


Figure **32.1.4**: *Hox* genes are highly conserved genes encoding transcription factors that determine the course of embryonic development in animals. In vertebrates, the genes have been duplicated into four clusters: *Hox-A*, *Hox-B*, *Hox-C*, and *Hox-D*. Genes within these clusters are expressed in certain body segments at certain stages of development. Shown here is the homology between *Hox* genes in mice and humans. Note how Hox gene expression, as indicated with orange, pink, blue and green shading, occurs in the same body segments in both the mouse and the human.

If a *Hox 13* gene in a mouse was replaced with a *Hox 1* gene, how might this alter animal development?

Summary

Animals constitute an incredibly diverse kingdom of organisms. Although animals range in complexity from simple sea sponges to human beings, most members of the animal kingdom share certain features. Animals are eukaryotic, multicellular, heterotrophic organisms that ingest their food and usually develop into motile creatures with a fixed body plan. A major characteristic unique to the animal kingdom is the presence of differentiated tissues, such as nerve, muscle, and connective tissues, which are specialized to perform specific functions. Most animals undergo sexual reproduction, leading to a series of developmental embryonic stages that are relatively similar across the animal kingdom. A class of transcriptional control genes called *Hox* genes directs the organization of the major animal body plans, and these genes are strongly homologous across the animal kingdom.

Art Connections

Figure **32.1.4**: If a *Hox 13* gene in a mouse was replaced with a *Hox 1* gene, how might this alter animal development?

Answer

The animal might develop two heads and no tail.

Glossary

blastula

16–32 cell stage of development of an animal embryo

body plan

morphology or constant shape of an organism

cleavage

cell division of a fertilized egg (zygote) to form a multicellular embryo

gastrula

stage of animal development characterized by the formation of the digestive cavity

germ layer

collection of cells formed during embryogenesis that will give rise to future body tissues, more pronounced in vertebrate embryogenesis

Hox gene

(also, homeobox gene) master control gene that can turn on or off large numbers of other genes during embryogenesis

organogenesis

formation of organs in animal embryogenesis

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32.2: Evolution of the Animal Body Plan

Skills to Develop

- Explain the differences in animal body plans that support basic animal classification
- Compare and contrast the embryonic development of protostomes and deuterostomes

Scientists have developed a classification scheme that categorizes all members of the animal kingdom, although there are exceptions to most "rules" governing animal classification (Figure **32.2.1**). Animals are primarily classified according to morphological and developmental characteristics, such as a body plan. One of the most prominent features of the body plan of true animals is that they are morphologically symmetrical. This means that their distribution of body parts is balanced along an axis. Additional characteristics include the number of tissue layers formed during development, the presence or absence of an internal body cavity, and other features of embryological development, such as the origin of the mouth and anus.

Art Connection

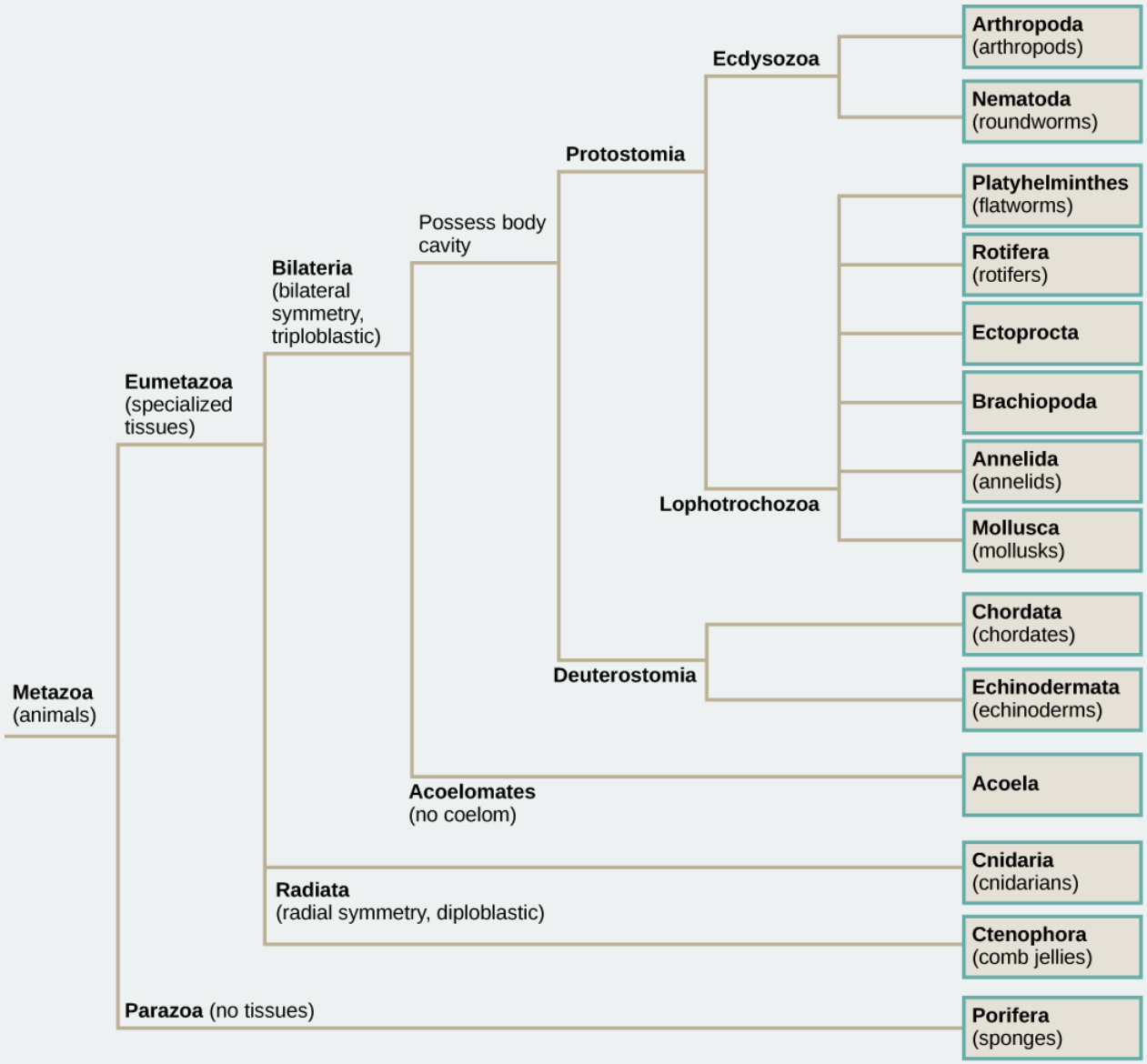


Figure **32.2.1**: The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

Which of the following statements is false?

A. Eumetazoans have specialized tissues and parazoans don't

A. Eumetazoans have specialized tissues and parazoans don't.
B. Lophotrochozoa and Ecdysozoa are both Bilataria.
C. Acoela and Cnidaria both possess radial symmetry.
D. Arthropods are more closely related to nematodes than they are to annelids.

Animal Characterization Based on Body Symmetry

At a very basic level of classification, true animals can be largely divided into three groups based on the type of symmetry of their body plan: radially symmetrical, bilaterally symmetrical, and asymmetrical. Asymmetry is a unique feature of Parazoa (Figure **32.2.2**). Only a few animal groups display radial symmetry. All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.

Radial symmetry is the arrangement of body parts around a central axis, as is seen in a drinking glass or pie. It results in animals having top and bottom surfaces but no left and right sides, or front or back. The two halves of a radially symmetrical animal may be described as the side with a mouth or "oral side," and the side without a mouth (the "aboral side"). This form of symmetry marks the body plans of animals in the phyla Ctenophora and Cnidaria, including jellyfish and adult sea anemones (Figure 27.2.2). Radial symmetry equips these sea creatures (which may be sedentary or only capable of slow movement or floating) to experience the environment equally from all directions.



Figure **32.2.2**: The (a) sponge is asymmetrical. The (b) jellyfish and (c) anemone are radially symmetrical, and the (d) butterfly is bilaterally symmetrical. (credit a: modification of work by Andrew Turner; credit b: modification of work by Robert Freiburger; credit c: modification of work by Samuel Chow; credit d: modification of work by Cory Zanker)

Bilateral symmetry involves the division of the animal through a sagittal plane, resulting in two mirror image, right and left halves, such as those of a butterfly (Figure **32.2.2**), crab, or human body. Animals with bilateral symmetry have a “head” and “tail” (anterior vs. posterior), front and back (dorsal vs. ventral), and right and left sides (Figure **32.2.3**). All true animals except those with radial symmetry are bilaterally symmetrical. The evolution of bilateral symmetry that allowed for the formation of anterior and posterior (head and tail) ends promoted a phenomenon called cephalization, which refers to the collection of an organized nervous system at the animal’s anterior end. In contrast to radial symmetry, which is best suited for stationary or limited-motion lifestyles, bilateral symmetry allows for streamlined and directional motion. In evolutionary terms, this simple form of symmetry promoted active mobility and increased sophistication of resource-seeking and predator-prey relationships.

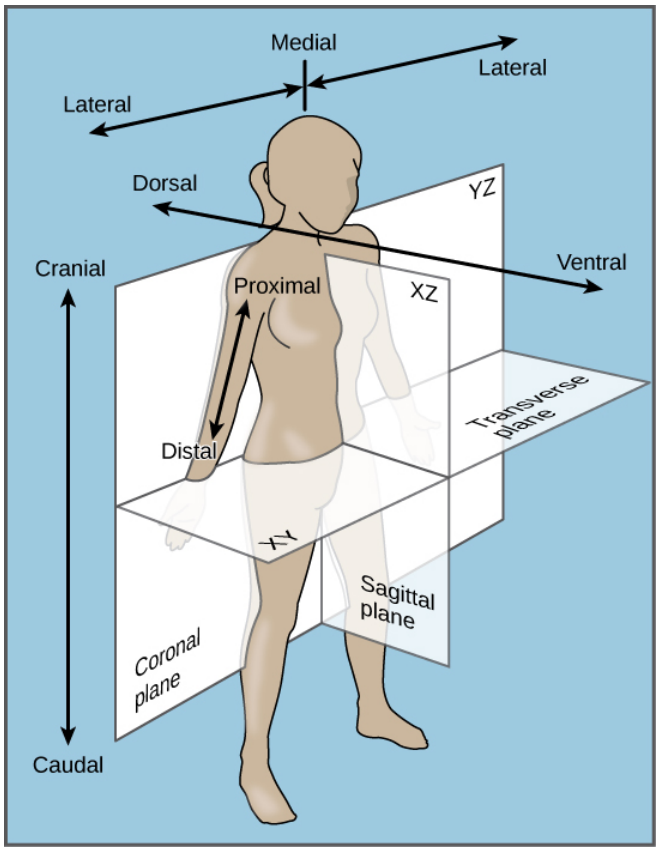
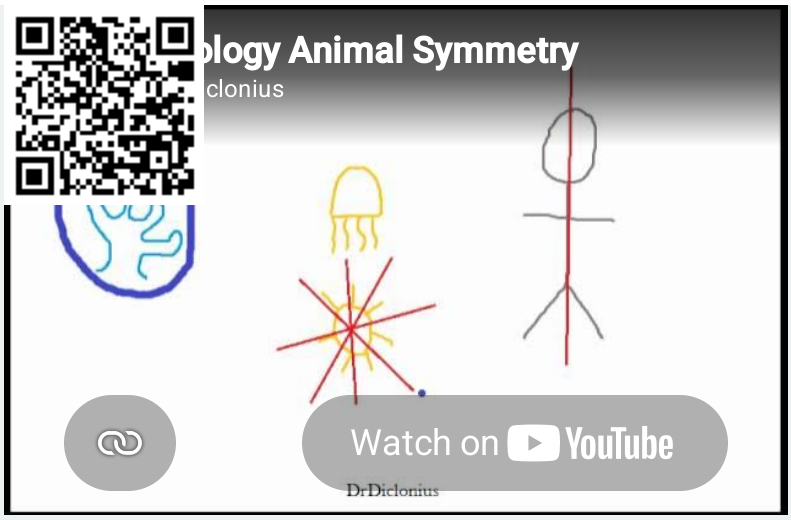


Figure **32.2.3**: The bilaterally symmetrical human body can be divided into planes.

Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display radial symmetry as adults, but their larval stages exhibit bilateral symmetry. This is termed secondary radial symmetry. They are believed to have evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.

Link to Learning



Watch this video to see a quick sketch of the different types of body symmetry.

Animal Characterization Based on Features of Embryological Development

Most animal species undergo a separation of tissues into germ layers during embryonic development. Recall that these germ layers are formed during gastrulation, and that they are predetermined to develop into the animal's specialized tissues and organs. Animals develop either two or three embryonic germs layers (Figure **32.2.4**). The animals that display radial symmetry develop two germ layers, an inner layer (endoderm) and an outer layer (ectoderm). These animals are called diploblasts. Diploblasts have a non-living layer between the endoderm and ectoderm. More complex animals (those with bilateral symmetry) develop three tissue layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm). Animals with three tissue layers are called triploblasts.

Art Connection

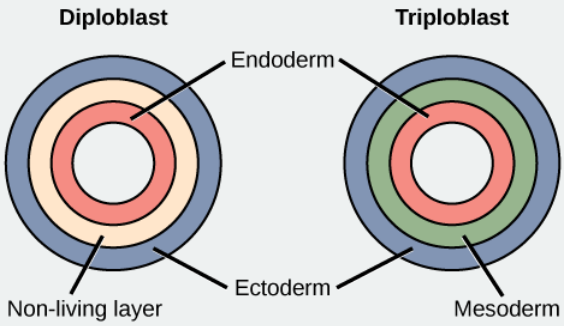


Figure **32.2.4**: During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

Which of the following statements about diploblasts and triploblasts is false?

A. Animals that display radial symmetry are diploblasts.
B. Animals that display bilateral symmetry are triploblasts.
C. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
D. The mesoderm gives rise to the central nervous system.

Each of the three germ layers is programmed to give rise to particular body tissues and organs. The endoderm gives rise to the lining of the digestive tract (including the stomach, intestines, liver, and pancreas), as well as to the lining of the trachea, bronchi, and lungs of the respiratory tract, along with a few other structures. The ectoderm develops into the outer epithelial covering of the body surface, the central nervous system, and a few other structures. The mesoderm is the third germ layer; it forms between the endoderm and ectoderm in triploblasts. This germ layer gives rise to all muscle tissues (including the cardiac tissues and muscles of

the intestines), connective tissues such as the skeleton and blood cells, and most other visceral organs such as the kidneys and the spleen.

Presence or Absence of a Coelom

Further subdivision of animals with three germ layers (triploblasts) results in the separation of animals that may develop an internal body cavity derived from mesoderm, called a coelom, and those that do not. This epithelial cell-lined coelomic cavity represents a space, usually filled with fluid, which lies between the visceral organs and the body wall. It houses many organs such as the digestive system, kidneys, reproductive organs, and heart, and contains the circulatory system. In some animals, such as mammals, the part of the coelom called the pleural cavity provides space for the lungs to expand during breathing. The evolution of the coelom is associated with many functional advantages. Primarily, the coelom provides cushioning and shock absorption for the major organ systems. Organs housed within the coelom can grow and move freely, which promotes optimal organ development and placement. The coelom also provides space for the diffusion of gases and nutrients, as well as body flexibility, promoting improved animal motility.

Triploblasts that do not develop a coelom are called acoelomates, and their mesoderm region is completely filled with tissue, although they do still have a gut cavity. Examples of acoelomates include animals in the phylum Platyhelminthes, also known as flatworms. Animals with a true coelom are called eucoelomates (or coelomates) (Figure **32.2.5**). A true coelom arises entirely within the mesoderm germ layer and is lined by an epithelial membrane. This membrane also lines the organs within the coelom, connecting and holding them in position while allowing them some free motion. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. A third group of triploblasts has a slightly different coelom derived partly from mesoderm and partly from endoderm, which is found between the two layers. Although still functional, these are considered false coeloms, and those animals are called pseudocoelomates. The phylum Nematoda (roundworms) is an example of a pseudocoelomate. True coelomates can be further characterized based on certain features of their early embryological development.

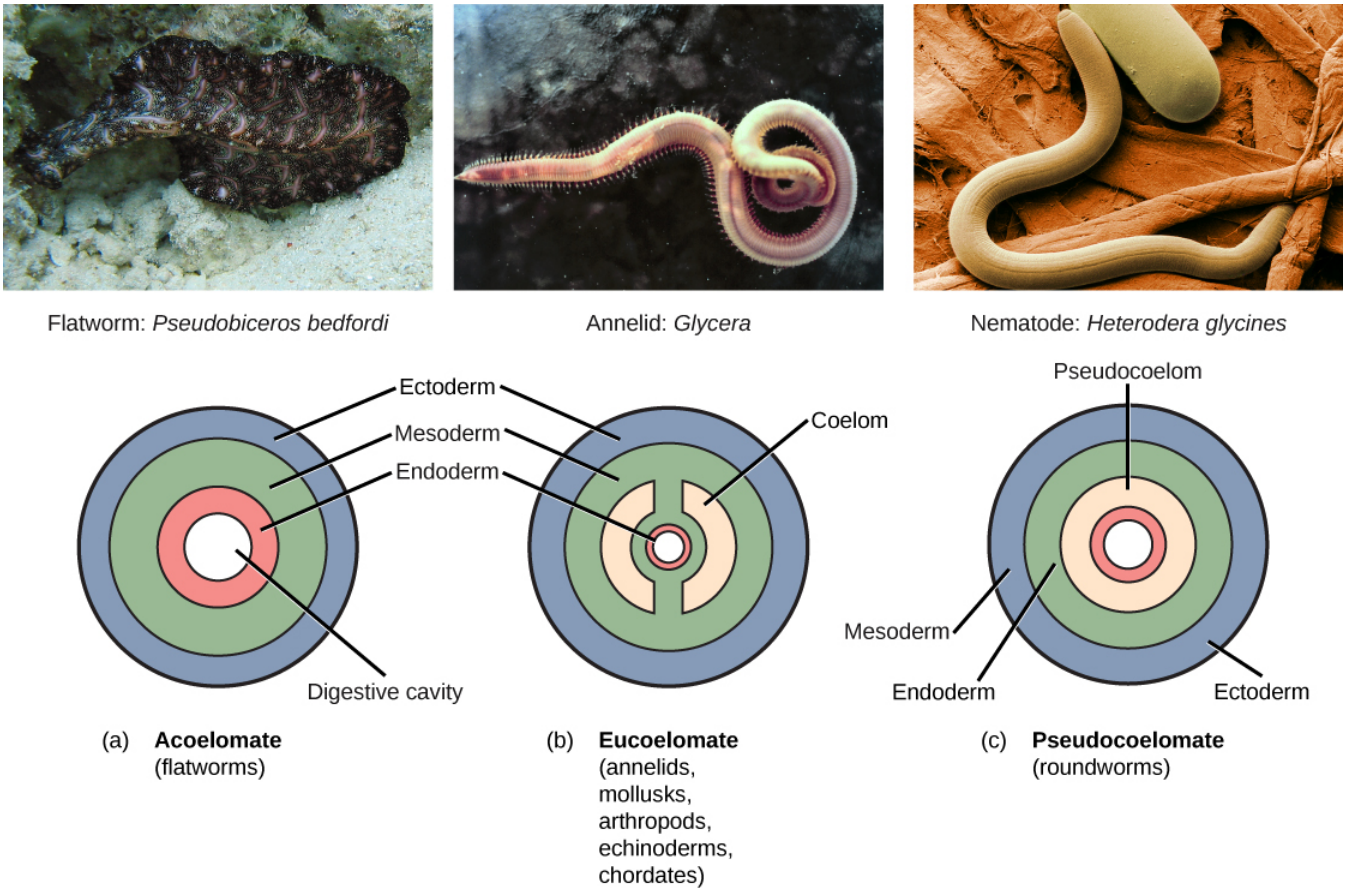


Figure **32.2.5**: Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm. Pseudocoelomates also have a body cavity, but it is sandwiched between the endoderm and mesoderm. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS)

Embryonic Development of the Mouth

Bilaterally symmetrical, tribloblastic eucoelomates can be further divided into two groups based on differences in their early embryonic development. Protostomes include arthropods, mollusks, and annelids. Deuterostomes include more complex animals such as chordates but also some simple animals such as echinoderms. These two groups are separated based on which opening of the digestive cavity develops first: mouth or anus. The word protostome comes from the Greek word meaning “mouth first,” and deuterostome originates from the word meaning “mouth second” (in this case, the anus develops first). The mouth or anus develops from a structure called the blastopore (Figure **32.2.6**). The blastopore is the indentation formed during the initial stages of gastrulation. In later stages, a second opening forms, and these two openings will eventually give rise to the mouth and anus (Figure **32.2.6**). It has long been believed that the blastopore develops into the mouth of protostomes, with the second opening developing into the anus; the opposite is true for deuterostomes. Recent evidence has challenged this view of the development of the blastopore of protostomes, however, and the theory remains under debate.

Another distinction between protostomes and deuterostomes is the method of coelom formation, beginning from the gastrula stage. The coelom of most protostomes is formed through a process called schizocoely, meaning that during development, a solid mass of the mesoderm splits apart and forms the hollow opening of the coelom. Deuterostomes differ in that their coelom forms through a process called enterocoely. Here, the mesoderm develops as pouches that are pinched off from the endoderm tissue. These pouches eventually fuse to form the mesoderm, which then gives rise to the coelom.

The earliest distinction between protostomes and deuterostomes is the type of cleavage undergone by the zygote. Protostomes undergo spiral cleavage, meaning that the cells of one pole of the embryo are rotated, and thus misaligned, with respect to the cells of the opposite pole. This is due to the oblique angle of the cleavage. Deuterostomes undergo radial cleavage, where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the alignment of the cells between the two poles.

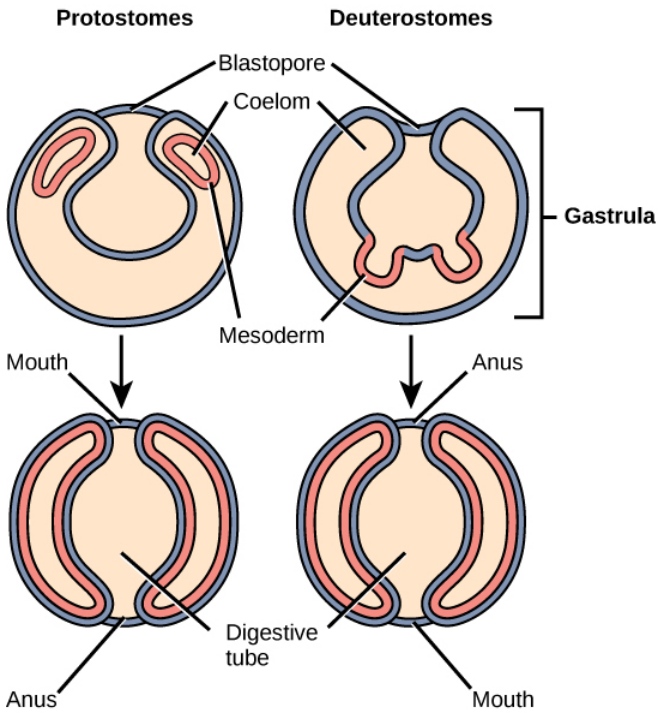


Figure 32.2.6: Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely. It was long believed that the blastopore developed into the mouth in protostomes and into the anus in deuterostomes, but recent evidence challenges this belief.

There is a second distinction between the types of cleavage in protostomes and deuterostomes. In addition to spiral cleavage, protostomes also undergo determinate cleavage. This means that even at this early stage, the developmental fate of each embryonic cell is already determined. A cell does not have the ability to develop into any cell type. In contrast, deuterostomes undergo indeterminate cleavage, in which cells are not yet pre-determined at this early stage to develop into specific cell types. These cells are referred to as undifferentiated cells. This characteristic of deuterostomes is reflected in the existence of familiar embryonic stem cells, which have the ability to develop into any cell type until their fate is programmed at a later developmental stage.

Evolution Connection: The Evolution of the Coelom

One of the first steps in the classification of animals is to examine the animal's body. Studying the body parts tells us not only the roles of the organs in question but also how the species may have evolved. One such structure that is used in classification of animals is the coelom. A coelom is a body cavity that forms during early embryonic development. The coelom allows for compartmentalization of the body parts, so that different organ systems can evolve and nutrient transport is possible. Additionally, because the coelom is a fluid-filled cavity, it protects the organs from shock and compression. Simple animals, such as worms and jellyfish, do not have a coelom. All vertebrates have a coelom that helped them evolve complex organ systems.

Animals that do not have a coelom are called acoelomates. Flatworms and tapeworms are examples of acoelomates. They rely on passive diffusion for nutrient transport across their body. Additionally, the internal organs of acoelomates are not protected from crushing.

Animals that have a true coelom are called eucoelomates; all vertebrates are eucoelomates. The coelom evolves from the mesoderm during embryogenesis. The abdominal cavity contains the stomach, liver, gall bladder, and other digestive organs. Another category of invertebrates animals based on body cavity is pseudocoelomates. These animals have a pseudo-cavity that is not completely lined by mesoderm. Examples include nematode parasites and small worms. These animals are thought to have evolved from coelomates and may have lost their ability to form a coelom through genetic mutations. Thus, this step in early embryogenesis—the formation of the coelom—has had a large evolutionary impact on the various species of the animal kingdom.

Summary

Organisms in the animal kingdom are classified based on their body morphology and development. True animals are divided into those with radial versus bilateral symmetry. Generally, the simpler and often non-motile animals display radial symmetry. Animals with radial symmetry are also generally characterized by the development of two embryological germ layers, the endoderm and ectoderm, whereas animals with bilateral symmetry are generally characterized by the development of a third embryological germ layer, the mesoderm. Animals with three germ layers, called triploblasts, are further characterized by the presence or absence of an internal body cavity called a coelom. The presence of a coelom affords many advantages, and animals with a coelom may be termed true coelomates or pseudocoelomates, depending on which tissue gives rise to the coelom. Coelomates are further divided into one of two groups called protostomes and deuterostomes, based on a number of developmental characteristics, including differences in zygote cleavage and method of coelom formation.

Art Connections

Figure **32.2.1**: Which of the following statements is false?

A. Eumetazoans have specialized tissues and parazoans don't.
B. Lophotrochozoa and Ecdysozoa are both Bilataria.
C. Acoela and Cnidaria both possess radial symmetry.
D. Arthropods are more closely related to nematodes than they are to annelids.

Answer

C

Figure **32.2.4**: Which of the following statements about diploblasts and triploblasts is false?

A. Animals that display radial symmetry are diploblasts.
B. Animals that display bilateral symmetry are triploblasts.
C. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
D. The mesoderm gives rise to the central nervous system.

Answer

D

Glossary

acoelomate
animal without a body cavity

bilateral symmetry
type of symmetry in which there is only one plane of symmetry, so the left and right halves of an animal are mirror images

blastopore
indentation formed during gastrulation, evident in the gastrula stage

coelom
lined body cavity

determinate cleavage
developmental tissue fate of each embryonic cell is already determined

deuterostome
blastopore develops into the anus, with the second opening developing into the mouth

diploblast
animal that develops from two germ layers

enterocoely
mesoderm of deuterostomes develops as pouches that are pinched off from endodermal tissue, cavity contained within the pouches becomes coelom

eucoelomate
animal with a body cavity completely lined with mesodermal tissue

indeterminate cleavage
early stage of development when germ cells or “stem cells” are not yet pre-determined to develop into specific cell types

protostome
blastopore develops into the mouth of protostomes, with the second opening developing into the anus

pseudocoelomate
animal with a body cavity located between the mesoderm and endoderm

radial cleavage
cleavage axes are parallel or perpendicular to the polar axis, resulting in the alignment of cells between the two poles

radial symmetry
type of symmetry with multiple planes of symmetry, with body parts (rays) arranged around a central disk

schizocoely
during development of protostomes, a solid mass of mesoderm splits apart and forms the hollow opening of the coelom

spiral cleavage
cells of one pole of the embryo are rotated or misaligned with respect to the cells of the opposite pole

triploblast
animal that develops from three germ layers

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SECTION OVERVIEW

32.3: Animal Phylogeny

Skills to Develop

- Explain the differences in animal body plans that support basic animal classification
- Compare and contrast the embryonic development of protostomes and deuterostomes

Scientists have developed a classification scheme that categorizes all members of the animal kingdom, although there are exceptions to most “rules” governing animal classification (Figure **32.3.1**). Animals are primarily classified according to morphological and developmental characteristics, such as a body plan. One of the most prominent features of the body plan of true animals is that they are morphologically symmetrical. This means that their distribution of body parts is balanced along an axis. Additional characteristics include the number of tissue layers formed during development, the presence or absence of an internal body cavity, and other features of embryological development, such as the origin of the mouth and anus.

Art Connection

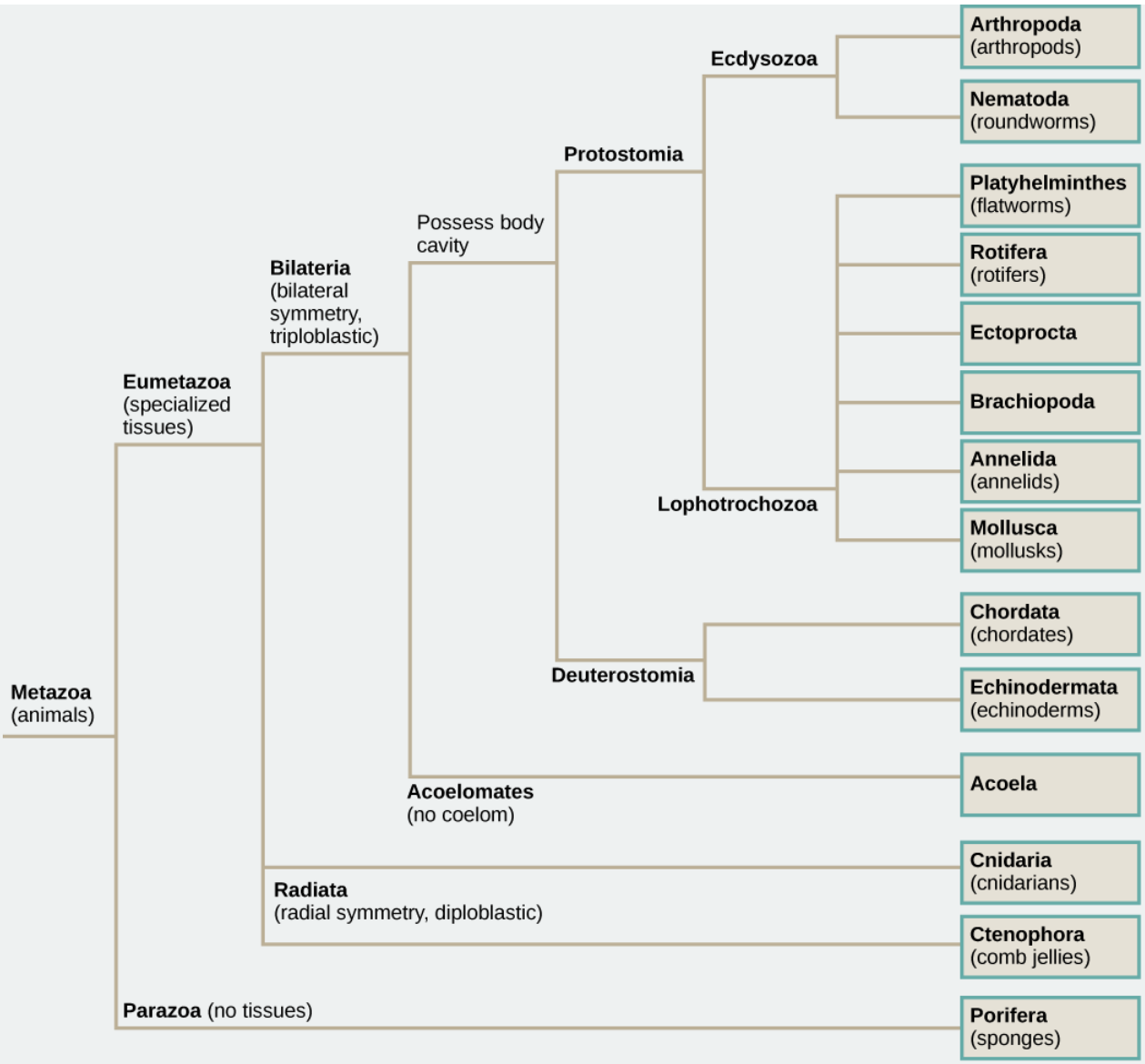


Figure **32.3.1**: The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

Which of the following statements is false?

A. Eumetazoans have specialized tissues and parazoans don't.
B. Lophotrochozoa and Ecdysozoa are both Bilataria.
C. Acoela and Cnidaria both possess radial symmetry.
D. Arthropods are more closely related to nematodes than they are to annelids.

Animal Characterization Based on Body Symmetry

At a very basic level of classification, true animals can be largely divided into three groups based on the type of symmetry of their body plan: radially symmetrical, bilaterally symmetrical, and asymmetrical. Asymmetry is a unique feature of Parazoa (Figure **32.3.2**). Only a few animal groups display radial symmetry. All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.

Radial symmetry is the arrangement of body parts around a central axis, as is seen in a drinking glass or pie. It results in animals having top and bottom surfaces but no left and right sides, or front or back. The two halves of a radially symmetrical animal may be described as the side with a mouth or "oral side," and the side without a mouth (the "aboral side"). This form of symmetry marks the body plans of animals in the phyla Ctenophora and Cnidaria, including jellyfish and adult sea anemones (Figure 27.2.2). Radial

symmetry equips these sea creatures (which may be sedentary or only capable of slow movement or floating) to experience the environment equally from all directions.



Figure **32.3.2**: The (a) sponge is asymmetrical. The (b) jellyfish and (c) anemone are radially symmetrical, and the (d) butterfly is bilaterally symmetrical. (credit a: modification of work by Andrew Turner; credit b: modification of work by Robert Freiburger; credit c: modification of work by Samuel Chow; credit d: modification of work by Cory Zanker)

Bilateral symmetry involves the division of the animal through a sagittal plane, resulting in two mirror image, right and left halves, such as those of a butterfly (Figure **32.3.2**), crab, or human body. Animals with bilateral symmetry have a “head” and “tail” (anterior vs. posterior), front and back (dorsal vs. ventral), and right and left sides (Figure **32.3.3**). All true animals except those with radial symmetry are bilaterally symmetrical. The evolution of bilateral symmetry that allowed for the formation of anterior and posterior (head and tail) ends promoted a phenomenon called cephalization, which refers to the collection of an organized nervous system at the animal’s anterior end. In contrast to radial symmetry, which is best suited for stationary or limited-motion lifestyles, bilateral symmetry allows for streamlined and directional motion. In evolutionary terms, this simple form of symmetry promoted active mobility and increased sophistication of resource-seeking and predator-prey relationships.

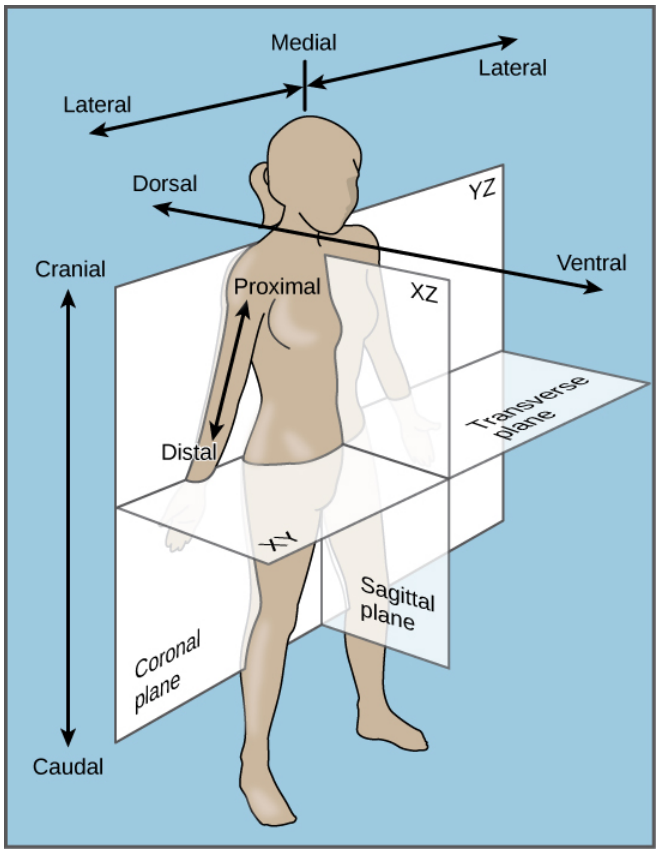
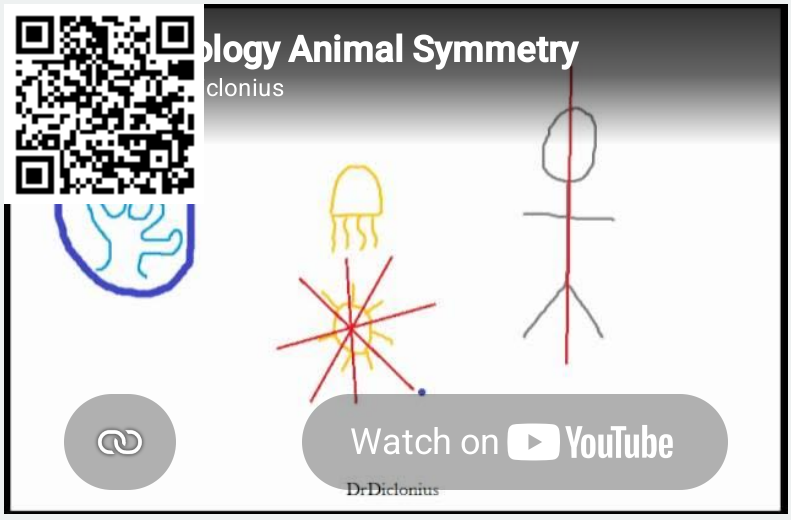


Figure **32.3.3**: The bilaterally symmetrical human body can be divided into planes.

Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display radial symmetry as adults, but their larval stages exhibit bilateral symmetry. This is termed secondary radial symmetry. They are believed to have evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.

Link to Learning



Watch this video to see a quick sketch of the different types of body symmetry.

Animal Characterization Based on Features of Embryological Development

Most animal species undergo a separation of tissues into germ layers during embryonic development. Recall that these germ layers are formed during gastrulation, and that they are predetermined to develop into the animal's specialized tissues and organs. Animals

develop either two or three embryonic germs layers (Figure **32.3.4**). The animals that display radial symmetry develop two germ layers, an inner layer (endoderm) and an outer layer (ectoderm). These animals are called diploblasts. Diploblasts have a non-living layer between the endoderm and ectoderm. More complex animals (those with bilateral symmetry) develop three tissue layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm). Animals with three tissue layers are called triploblasts.

Art Connection

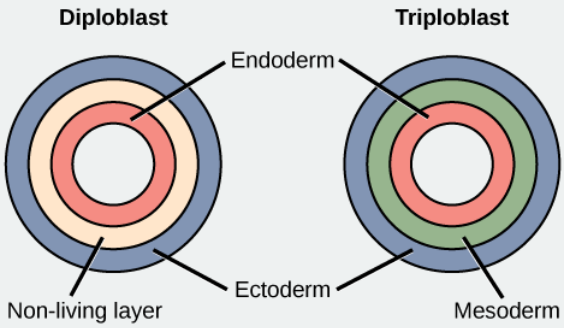


Figure **32.3.4**: During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

Which of the following statements about diploblasts and triploblasts is false?

A. Animals that display radial symmetry are diploblasts.
B. Animals that display bilateral symmetry are triploblasts.
C. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
D. The mesoderm gives rise to the central nervous system.

Each of the three germ layers is programmed to give rise to particular body tissues and organs. The endoderm gives rise to the lining of the digestive tract (including the stomach, intestines, liver, and pancreas), as well as to the lining of the trachea, bronchi, and lungs of the respiratory tract, along with a few other structures. The ectoderm develops into the outer epithelial covering of the body surface, the central nervous system, and a few other structures. The mesoderm is the third germ layer; it forms between the endoderm and ectoderm in triploblasts. This germ layer gives rise to all muscle tissues (including the cardiac tissues and muscles of the intestines), connective tissues such as the skeleton and blood cells, and most other visceral organs such as the kidneys and the spleen.

Presence or Absence of a Coelom

Further subdivision of animals with three germ layers (triploblasts) results in the separation of animals that may develop an internal body cavity derived from mesoderm, called a coelom, and those that do not. This epithelial cell-lined coelomic cavity represents a space, usually filled with fluid, which lies between the visceral organs and the body wall. It houses many organs such as the digestive system, kidneys, reproductive organs, and heart, and contains the circulatory system. In some animals, such as mammals, the part of the coelom called the pleural cavity provides space for the lungs to expand during breathing. The evolution of the coelom is associated with many functional advantages. Primarily, the coelom provides cushioning and shock absorption for the major organ systems. Organs housed within the coelom can grow and move freely, which promotes optimal organ development and placement. The coelom also provides space for the diffusion of gases and nutrients, as well as body flexibility, promoting improved animal motility.

Triploblasts that do not develop a coelom are called acoelomates, and their mesoderm region is completely filled with tissue, although they do still have a gut cavity. Examples of acoelomates include animals in the phylum Platyhelminthes, also known as flatworms. Animals with a true coelom are called eucoelomates (or coelomates) (Figure **32.3.5**). A true coelom arises entirely within the mesoderm germ layer and is lined by an epithelial membrane. This membrane also lines the organs within the coelom, connecting and holding them in position while allowing them some free motion. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. A third group of triploblasts has a slightly different coelom derived partly from mesoderm and partly from endoderm, which is found between the two layers. Although still functional, these are considered false coeloms, and

those animals are called pseudocoelomates. The phylum Nematoda (roundworms) is an example of a pseudocoelomate. True coelomates can be further characterized based on certain features of their early embryological development.

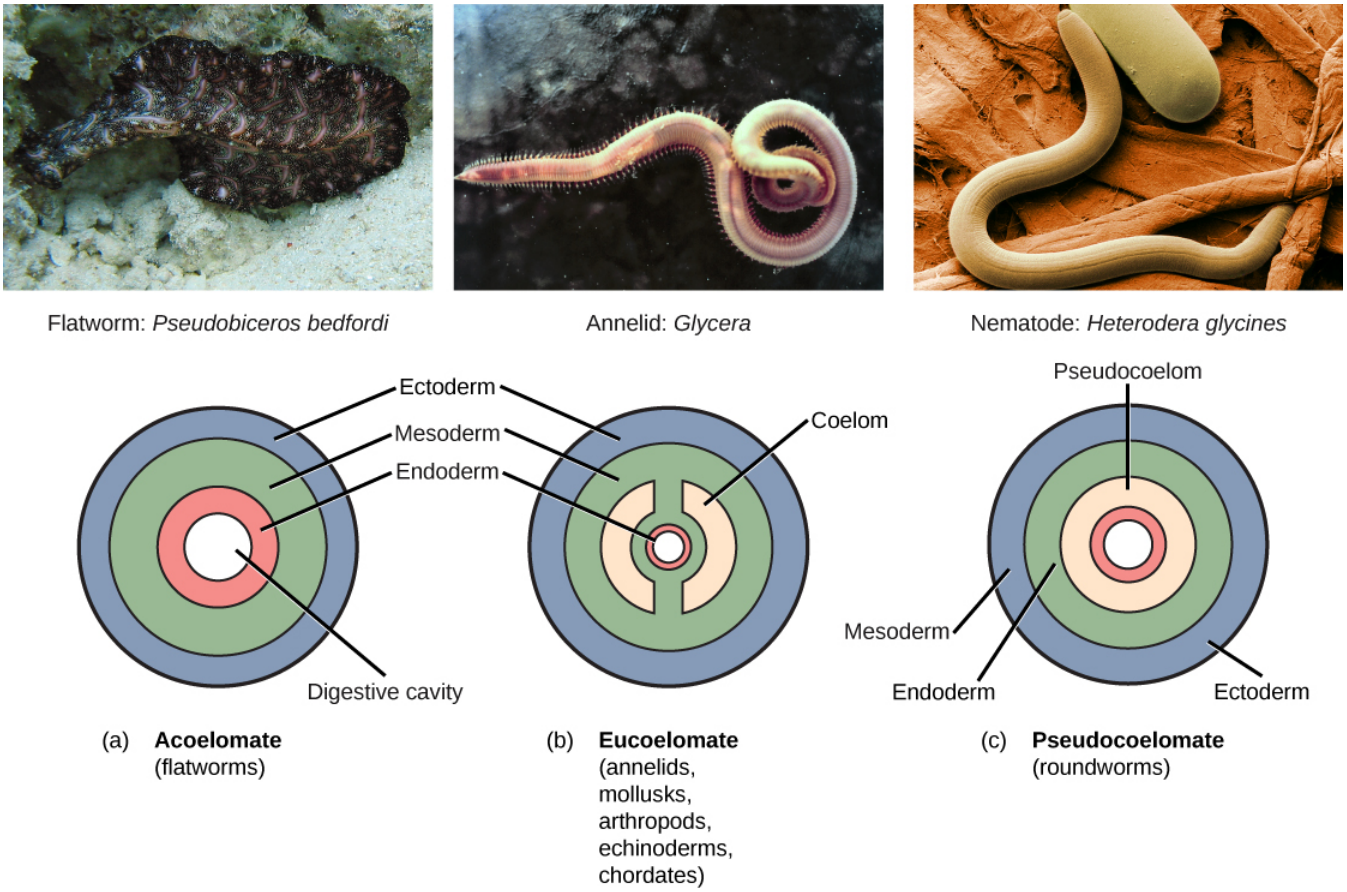


Figure **32.3.5**: Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm. Pseudocoelomates also have a body cavity, but it is sandwiched between the endoderm and mesoderm. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS)

Embryonic Development of the Mouth

Bilaterally symmetrical, tribloblastic eucoelomates can be further divided into two groups based on differences in their early embryonic development. Protostomes include arthropods, mollusks, and annelids. Deuterostomes include more complex animals such as chordates but also some simple animals such as echinoderms. These two groups are separated based on which opening of the digestive cavity develops first: mouth or anus. The word protostome comes from the Greek word meaning “mouth first,” and deuterostome originates from the word meaning “mouth second” (in this case, the anus develops first). The mouth or anus develops from a structure called the blastopore (Figure **32.3.6**). The blastopore is the indentation formed during the initial stages of gastrulation. In later stages, a second opening forms, and these two openings will eventually give rise to the mouth and anus (Figure **32.3.6**). It has long been believed that the blastopore develops into the mouth of protostomes, with the second opening developing into the anus; the opposite is true for deuterostomes. Recent evidence has challenged this view of the development of the blastopore of protostomes, however, and the theory remains under debate.

Another distinction between protostomes and deuterostomes is the method of coelom formation, beginning from the gastrula stage. The coelom of most protostomes is formed through a process called schizocoely, meaning that during development, a solid mass of the mesoderm splits apart and forms the hollow opening of the coelom. Deuterostomes differ in that their coelom forms through a process called enterocoely. Here, the mesoderm develops as pouches that are pinched off from the endoderm tissue. These pouches eventually fuse to form the mesoderm, which then gives rise to the coelom.

The earliest distinction between protostomes and deuterostomes is the type of cleavage undergone by the zygote. Protostomes undergo spiral cleavage, meaning that the cells of one pole of the embryo are rotated, and thus misaligned, with respect to the cells of the opposite pole. This is due to the oblique angle of the cleavage. Deuterostomes undergo radial cleavage, where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the alignment of the cells between the two poles.

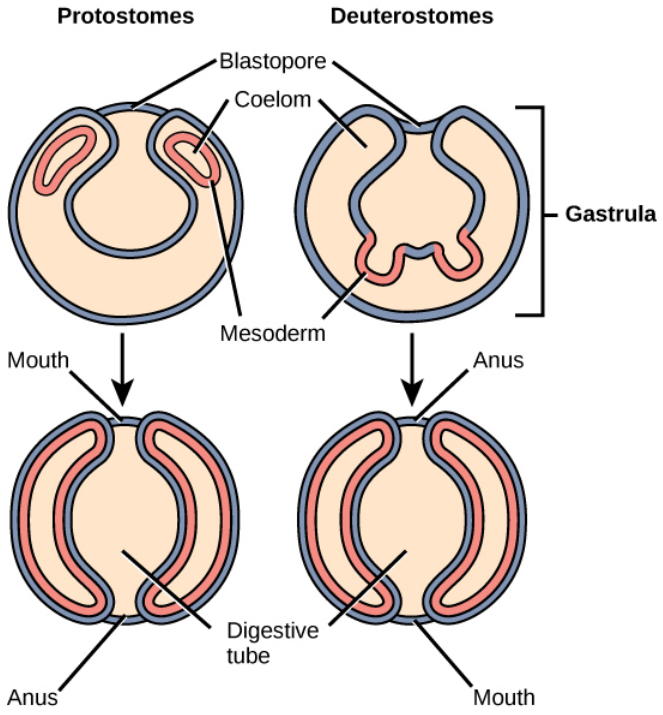


Figure 32.3.6: Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely. It was long believed that the blastopore developed into the mouth in protostomes and into the anus in deuterostomes, but recent evidence challenges this belief.

There is a second distinction between the types of cleavage in protostomes and deuterostomes. In addition to spiral cleavage, protostomes also undergo determinate cleavage. This means that even at this early stage, the developmental fate of each embryonic cell is already determined. A cell does not have the ability to develop into any cell type. In contrast, deuterostomes undergo indeterminate cleavage, in which cells are not yet pre-determined at this early stage to develop into specific cell types. These cells are referred to as undifferentiated cells. This characteristic of deuterostomes is reflected in the existence of familiar embryonic stem cells, which have the ability to develop into any cell type until their fate is programmed at a later developmental stage.

Evolution Connection: The Evolution of the Coelom

One of the first steps in the classification of animals is to examine the animal's body. Studying the body parts tells us not only the roles of the organs in question but also how the species may have evolved. One such structure that is used in classification of animals is the coelom. A coelom is a body cavity that forms during early embryonic development. The coelom allows for compartmentalization of the body parts, so that different organ systems can evolve and nutrient transport is possible. Additionally, because the coelom is a fluid-filled cavity, it protects the organs from shock and compression. Simple animals, such as worms and jellyfish, do not have a coelom. All vertebrates have a coelom that helped them evolve complex organ systems.

Animals that do not have a coelom are called acoelomates. Flatworms and tapeworms are examples of acoelomates. They rely on passive diffusion for nutrient transport across their body. Additionally, the internal organs of acoelomates are not protected from crushing.

Animals that have a true coelom are called eucoelomates; all vertebrates are eucoelomates. The coelom evolves from the mesoderm during embryogenesis. The abdominal cavity contains the stomach, liver, gall bladder, and other digestive organs. Another category of invertebrates animals based on body cavity is pseudocoelomates. These animals have a pseudo-cavity that

is not completely lined by mesoderm. Examples include nematode parasites and small worms. These animals are thought to have evolved from coelomates and may have lost their ability to form a coelom through genetic mutations. Thus, this step in early embryogenesis—the formation of the coelom—has had a large evolutionary impact on the various species of the animal kingdom.

Summary

Organisms in the animal kingdom are classified based on their body morphology and development. True animals are divided into those with radial versus bilateral symmetry. Generally, the simpler and often non-motile animals display radial symmetry. Animals with radial symmetry are also generally characterized by the development of two embryological germ layers, the endoderm and ectoderm, whereas animals with bilateral symmetry are generally characterized by the development of a third embryological germ layer, the mesoderm. Animals with three germ layers, called triploblasts, are further characterized by the presence or absence of an internal body cavity called a coelom. The presence of a coelom affords many advantages, and animals with a coelom may be termed true coelomates or pseudocoelomates, depending on which tissue gives rise to the coelom. Coelomates are further divided into one of two groups called protostomes and deuterostomes, based on a number of developmental characteristics, including differences in zygote cleavage and method of coelom formation.

Art Connections

Figure **32.3.1**: Which of the following statements is false?

A. Eumetazoans have specialized tissues and parazoans don't.
B. Lophotrochozoa and Ecdysozoa are both Bilataria.
C. Acoela and Cnidaria both possess radial symmetry.
D. Arthropods are more closely related to nematodes than they are to annelids.

Answer

C

Figure **32.3.4**: Which of the following statements about diploblasts and triploblasts is false?

A. Animals that display radial symmetry are diploblasts.
B. Animals that display bilateral symmetry are triploblasts.
C. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
D. The mesoderm gives rise to the central nervous system.

Answer

D

Glossary

acoelomate

animal without a body cavity

bilateral symmetry

type of symmetry in which there is only one plane of symmetry, so the left and right halves of an animal are mirror images

blastopore

indentation formed during gastrulation, evident in the gastrula stage

coelom

lined body cavity

determinate cleavage
developmental tissue fate of each embryonic cell is already determined

deuterostome
blastopore develops into the anus, with the second opening developing into the mouth

diploblast
animal that develops from two germ layers

enterocoely
mesoderm of deuterostomes develops as pouches that are pinched off from endodermal tissue, cavity contained within the pouches becomes coelom

eucoelomate
animal with a body cavity completely lined with mesodermal tissue

indeterminate cleavage
early stage of development when germ cells or “stem cells” are not yet pre-determined to develop into specific cell types

protostome
blastopore develops into the mouth of protostomes, with the second opening developing into the anus

pseudocoelomate
animal with a body cavity located between the mesoderm and endoderm

radial cleavage
cleavage axes are parallel or perpendicular to the polar axis, resulting in the alignment of cells between the two poles

radial symmetry
type of symmetry with multiple planes of symmetry, with body parts (rays) arranged around a central disk

schizocoely
during development of protostomes, a solid mass of mesoderm splits apart and forms the hollow opening of the coelom

spiral cleavage
cells of one pole of the embryo are rotated or misaligned with respect to the cells of the opposite pole

triploblast
animal that develops from three germ layers

32.3.1: Animal Phylogeny

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32.3.1: Animal Phylogeny

Skills to Develop

- Interpret the metazoan phylogenetic tree
- Describe the types of data that scientists use to construct and revise animal phylogeny
- List some of the relationships within the modern phylogenetic tree that have been discovered as a result of modern molecular data

Biologists strive to understand the evolutionary history and relationships of members of the animal kingdom, and all of life, for that matter. The study of phylogeny aims to determine the evolutionary relationships between phyla. Currently, most biologists divide the animal kingdom into 35 to 40 phyla. Scientists develop phylogenetic trees, which serve as hypotheses about which species have evolved from which ancestors

Recall that until recently, only morphological characteristics and the fossil record were used to determine phylogenetic relationships among animals. Scientific understanding of the distinctions and hierarchies between anatomical characteristics provided much of this knowledge. Used alone, however, this information can be misleading. Morphological characteristics may evolve multiple times, and independently, through evolutionary history. Analogous characteristics may appear similar between animals, but their underlying evolution may be very different. With the advancement of molecular technologies, modern phylogenetics is now informed by genetic and molecular analyses, in addition to traditional morphological and fossil data. With a growing understanding of genetics, the animal evolutionary tree has changed substantially and continues to change as new DNA and RNA analyses are performed on additional animal species.

Constructing an Animal Phylogenetic Tree

The current understanding of evolutionary relationships between animal, or Metazoa, phyla begins with the distinction between “true” animals with true differentiated tissues, called Eumetazoa, and animal phyla that do not have true differentiated tissues (such as the sponges), called Parazoa. Both Parazoa and Eumetazoa evolved from a common ancestral organism that resembles the modern-day protists called choanoflagellates. These protist cells strongly resemble the sponge choanocyte cells today (Figure **32.3.1.1**).

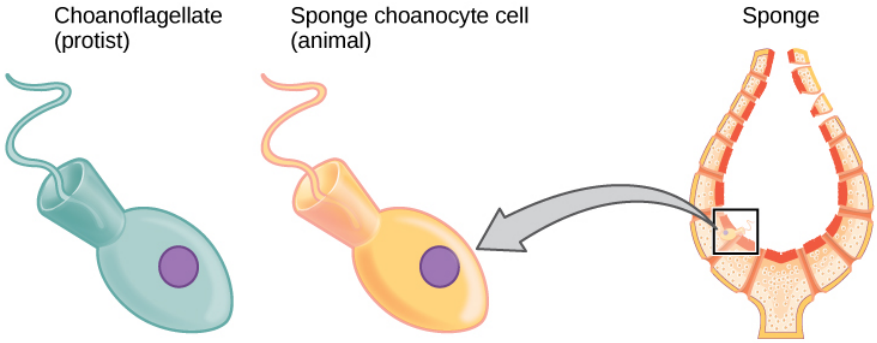


Figure **32.3.1.1**: Cells of the protist choanoflagellate resemble sponge choanocyte cells. Beating of choanocyte flagella draws water through the sponge so that nutrients can be extracted and waste removed.

Eumetazoa are subdivided into radially symmetrical animals and bilaterally symmetrical animals, and are thus classified into clade Bilateria or Radiata, respectively. As mentioned earlier, the cnidarians and ctenophores are animal phyla with true radial symmetry. All other Eumetazoa are members of the Bilateria clade. The bilaterally symmetrical animals are further divided into deuterostomes (including chordates and echinoderms) and two distinct clades of protostomes (including ecdysozoans and lophotrochozoans) (Figure **32.3.1.2**). Ecdysozoa includes nematodes and arthropods; they are so named for a commonly found characteristic among the group: exoskeletal molting (termed ecdysis). Lophotrochozoa is named for two structural features, each common to certain phyla within the clade. Some lophotrochozoan phyla are characterized by a larval stage called trochophore larvae, and other phyla are characterized by the presence of a feeding structure called a lophophore.



(a) (b)

Figure **32.3.1.2**: Animals that molt their exoskeletons, such as these (a) Madagascar hissing cockroaches, are in the clade Ecdysozoa. (b) Phoronids are in the clade Lophotrochozoa. The tentacles are part of a feeding structure called a lophophore. (credit a: modification of work by Whitney Cranshaw, Colorado State University, Bugwood.org; credit b: modification of work by NOAA)

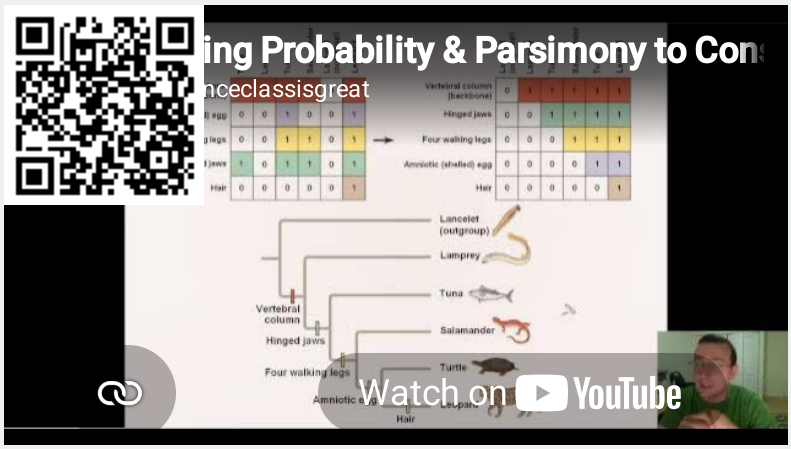
Link to Learning

Explore an interactive tree of life here. Zoom and click to learn more about the organisms and their evolutionary relationships.

Modern Advances in Phylogenetic Understanding Come from Molecular Analyses

The phylogenetic groupings are continually being debated and refined by evolutionary biologists. Each year, new evidence emerges that further alters the relationships described by a phylogenetic tree diagram.

Link to Learning



Watch the following video to learn how biologists use genetic data to determine relationships among organisms.

Nucleic acid and protein analyses have greatly informed the modern phylogenetic animal tree. These data come from a variety of molecular sources, such as mitochondrial DNA, nuclear DNA, ribosomal RNA (rRNA), and certain cellular proteins. Many

evolutionary relationships in the modern tree have only recently been determined due to molecular evidence. For example, a previously classified group of animals called lophophorates, which included brachiopods and bryozoans, were long-thought to be primitive deuterostomes. Extensive molecular analysis using rRNA data found these animals to be protostomes, more closely related to annelids and mollusks. This discovery allowed for the distinction of the protostome clade, the lophotrochozoans. Molecular data have also shed light on some differences within the lophotrochozoan group, and some scientists believe that the phyla Platyhelminthes and Rotifera within this group should actually belong to their own group of protostomes termed Platyzoa.

Molecular research similar to the discoveries that brought about the distinction of the lophotrochozoan clade has also revealed a dramatic rearrangement of the relationships between mollusks, annelids, arthropods, and nematodes, and a new ecdysozoan clade was formed. Due to morphological similarities in their segmented body types, annelids and arthropods were once thought to be closely related. However, molecular evidence has revealed that arthropods are actually more closely related to nematodes, now comprising the ecdysozoan clade, and annelids are more closely related to mollusks, brachiopods, and other phyla in the lophotrochozoan clade. These two clades now make up the protostomes.

Another change to former phylogenetic groupings because of molecular analyses includes the emergence of an entirely new phylum of worm called Acoelomorpha. These acoel flatworms were long thought to belong to the phylum Platyhelminthes because of their similar “flatworm” morphology. However, molecular analyses revealed this to be a false relationship and originally suggested that acoels represented living species of some of the earliest divergent bilaterians. More recent research into the acoelomorphs has called this hypothesis into question and suggested a closer relationship with deuterostomes. The placement of this new phylum remains disputed, but scientists agree that with sufficient molecular data, their true phylogeny will be determined.

Summary

Scientists are interested in the evolutionary history of animals and the evolutionary relationships among them. There are three main sources of data that scientists use to create phylogenetic evolutionary tree diagrams that illustrate such relationships: morphological information (which includes developmental morphologies), fossil record data, and, most recently, molecular data. The details of the modern phylogenetic tree change frequently as new data are gathered, and molecular data has recently contributed to many substantial modifications of the understanding of relationships between animal phyla.

Glossary

Ecdysozoa
clade of protostomes that exhibit exoskeletal molting (ecdysis)

Eumetazoa
group of animals with true differentiated tissues

Lophotrochozoa
clade of protostomes that exhibit a trochophore larvae stage or a lophophore feeding structure

Metazoa
group containing all animals

Parazoa
group of animals without true differentiated tissues

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32.4: Parazoa- Animals that Lack Specialized Tissues

Skills to Develop

- Describe the organizational features of the simplest multicellular organisms
- Explain the various body forms and bodily functions of sponges

The invertebrates, or invertebrata, are animals that do not contain bony structures, such as the cranium and vertebrae. The simplest of all the invertebrates are the Parazoans, which include only the phylum Porifera: the sponges (Figure **32.4.1**). Parazoans ("beside animals") do not display tissue-level organization, although they do have specialized cells that perform specific functions. Sponge larvae are able to swim; however, adults are non-motile and spend their life attached to a substratum. Since water is vital to sponges for excretion, feeding, and gas exchange, their body structure facilitates the movement of water through the sponge. Structures such as canals, chambers, and cavities enable water to move through the sponge to nearly all body cells.

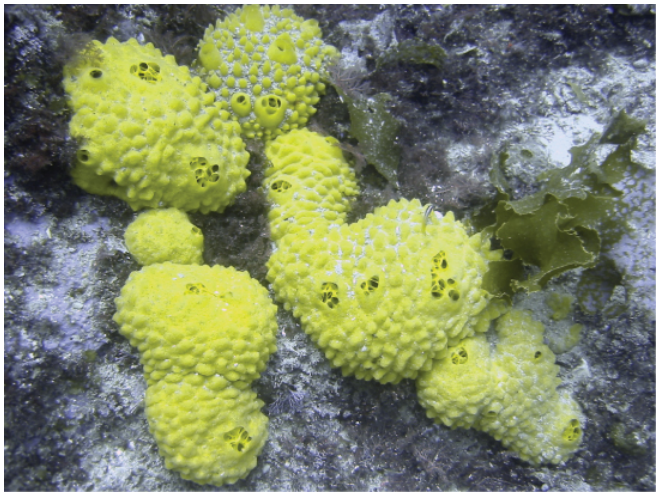


Figure **32.4.1**: Sponges are members of the Phylum Porifera, which contains the simplest invertebrates. (credit: Andrew Turner)

Morphology of Sponges

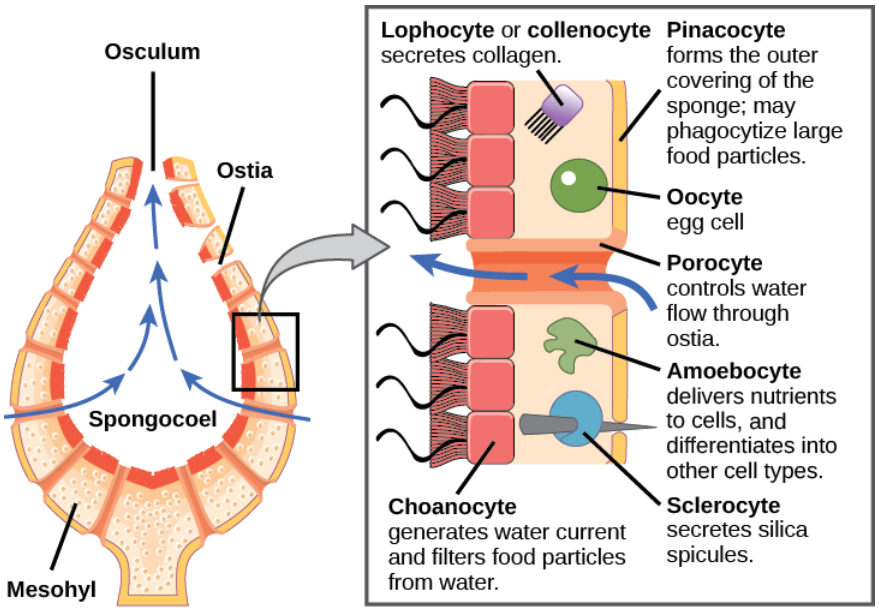
The morphology of the simplest sponges takes the shape of a cylinder with a large central cavity, the spongocoel, occupying the inside of the cylinder. Water can enter into the spongocoel from numerous pores in the body wall. Water entering the spongocoel is extruded via a large common opening called the osculum. However, sponges exhibit a range of diversity in body forms, including variations in the size of the spongocoel, the number of osculi, and where the cells that filter food from the water are located.

While sponges (excluding the hexactinellids) do not exhibit tissue-layer organization, they do have different cell types that perform distinct functions. Pinacocytes, which are epithelial-like cells, form the outermost layer of sponges and enclose a jelly-like substance called mesohyl. Mesohyl is an extracellular matrix consisting of a collagen-like gel with suspended cells that perform various functions. The gel-like consistency of mesohyl acts like an endoskeleton and maintains the tubular morphology of sponges. In addition to the osculum, sponges have multiple pores called ostia on their bodies that allow water to enter the sponge. In some sponges, ostia are formed by porocytes, single tube-shaped cells that act as valves to regulate the flow of water into the spongocoel. In other sponges, ostia are formed by folds in the body wall of the sponge.

Choanocytes ("collar cells") are present at various locations, depending on the type of sponge, but they always line the inner portions of some space through which water flows (the spongocoel in simple sponges, canals within the body wall in more complex sponges, and chambers scattered throughout the body in the most complex sponges). Whereas pinacocytes line the outside of the sponge, choanocytes tend to line certain inner portions of the sponge body that surround the mesohyl. The structure of a choanocyte is critical to its function, which is to generate a water current through the sponge and to trap and ingest food particles by phagocytosis. Note the similarity in appearance between the sponge choanocyte and choanoflagellates (Protista). This similarity suggests that sponges and choanoflagellates are closely related and likely share a recent common ancestry. The cell body is embedded in mesohyl and contains all organelles required for normal cell function, but protruding into the "open space" inside of

the sponge is a mesh-like collar composed of microvilli with a single flagellum in the center of the column. The cumulative effect of the flagella from all choanocytes aids the movement of water through the sponge: drawing water into the sponge through the numerous ostia, into the spaces lined by choanocytes, and eventually out through the osculum (or osculi). In the meantime, food particles, including waterborne bacteria and algae, are trapped by the sieve-like collar of the choanocytes, slide down into the body of the cell, are ingested by phagocytosis, and become encased in a food vacuole. Lastly, choanocytes will differentiate into sperm for sexual reproduction, where they will become dislodged from the mesohyl and leave the sponge with expelled water through the osculum.

The second crucial cells in sponges are called amoebocytes (or archaeocytes), named for the fact that they move throughout the mesohyl in an amoeba-like fashion. Amoebocytes have a variety of functions: delivering nutrients from choanocytes to other cells within the sponge, giving rise to eggs for sexual reproduction (which remain in the mesohyl), delivering phagocytized sperm from choanocytes to eggs, and differentiating into more-specific cell types. Some of these more-specific cell types include collencytes and lophocytes, which produce the collagen-like protein to maintain the mesohyl, sclerocytes, which produce spicules in some sponges, and spongocytes, which produce the protein spongin in the majority of sponges. These cells produce collagen to maintain the consistency of the mesohyl. The different cell types in sponges are shown in Figure **32.4.2**.



(a) Basic sponge body plan (b) Some sponge cell types

Figure **32.4.2**: The sponge's (a) basic body plan and (b) some of the specialized cell types found in sponges are shown.

Exercise 32.4.1

Which of the following statements is false?

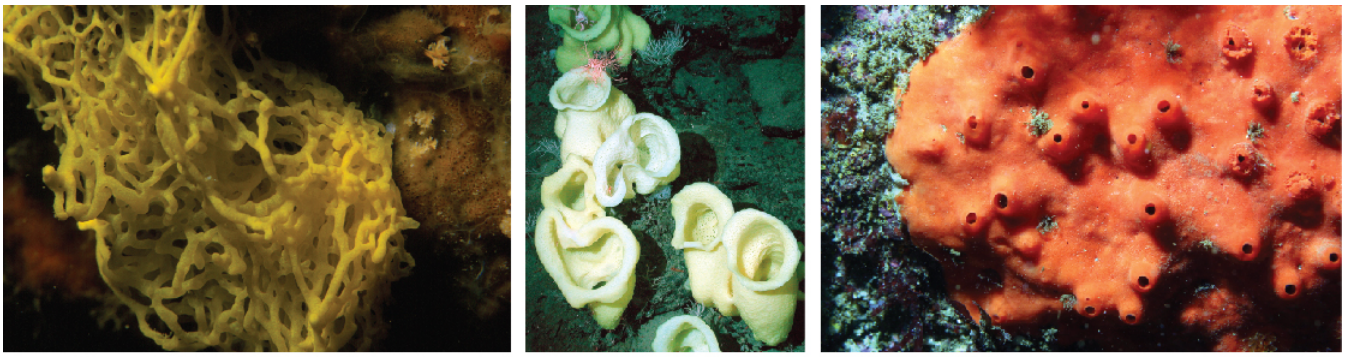
A. Choanocytes have flagella that propel water through the body.
B. Pinacocytes can transform into any cell type.
C. Lophocytes secrete collagen.
D. Porocytes control the flow of water through pores in the sponge body.

Answer

B

In some sponges, sclerocytes secrete small spicules into the mesohyl, which are composed of either calcium carbonate or silica, depending on the type of sponge. These spicules serve to provide additional stiffness to the body of the sponge. Additionally, spicules, when present externally, may ward off predators. Another type of protein, spongin, may also be present in the mesohyl of some sponges.

The presence and composition of spicules/spongin are the differentiating characteristics of the three classes of sponges (Figure **32.4.3**): Class Calcarea contains calcium carbonate spicules and no spongin, class Hexactinellida contains six-rayed siliceous spicules and no spongin, and class Demospongia contains spongin and may or may not have spicules; if present, those spicules are siliceous. Spicules are most conspicuously present in class Hexactinellida, the order consisting of glass sponges. Some of the spicules may attain giant proportions (in relation to the typical size range of glass sponges of 3 to 10 mm) as seen in *Monorhaphis chuni*, which grows up to 3 m long.



(a) (b) (c)

Figure **32.4.3**: (a) *Clathrina clathrus* belongs to class Calcarea, (b) *Staurocalyptus* spp. (common name: yellow Picasso sponge) belongs to class Hexactinellida, and (c) *Acarnus erithacus* belongs to class Demospongia. (credit a: modification of work by Parent Géry; credit b: modification of work by Monterey Bay Aquarium Research Institute, NOAA; credit c: modification of work by Sanctuary Integrated Monitoring Network, Monterey Bay National Marine Sanctuary, NOAA)

Physiological Processes in Sponges

Sponges, despite being simple organisms, regulate their different physiological processes through a variety of mechanisms. These processes regulate their metabolism, reproduction, and locomotion.

Digestion

Sponges lack complex digestive, respiratory, circulatory, reproductive, and nervous systems. Their food is trapped when water passes through the ostia and out through the osculum. Bacteria smaller than 0.5 microns in size are trapped by choanocytes, which are the principal cells engaged in nutrition, and are ingested by phagocytosis. Particles that are larger than the ostia may be phagocytized by pinacocytes. In some sponges, amoebocytes transport food from cells that have ingested food particles to those that do not. For this type of digestion, in which food particles are digested within individual cells, the sponge draws water through diffusion. The limit of this type of digestion is that food particles must be smaller than individual cells.

All other major body functions in the sponge (gas exchange, circulation, excretion) are performed by diffusion between the cells that line the openings within the sponge and the water that is passing through those openings. All cell types within the sponge obtain oxygen from water through diffusion. Likewise, carbon dioxide is released into seawater by diffusion. In addition, nitrogenous waste produced as a byproduct of protein metabolism is excreted via diffusion by individual cells into the water as it passes through the sponge.

Reproduction

Sponges reproduce by sexual as well as asexual methods. The typical means of asexual reproduction is either fragmentation (where a piece of the sponge breaks off, settles on a new substrate, and develops into a new individual) or budding (a genetically identical outgrowth grows from the parent and eventually detaches or remains attached to form a colony). An atypical type of asexual reproduction is found only in freshwater sponges and occurs through the formation of gemmules. Gemmules are environmentally resistant structures produced by adult sponges wherein the typical sponge morphology is inverted. In gemmules, an inner layer of amoebocytes is surrounded by a layer of collagen (spongin) that may be reinforced by spicules. The collagen that is normally found in the mesohyl becomes the outer protective layer. In freshwater sponges, gemmules may survive hostile environmental conditions like changes in temperature and serve to recolonize the habitat once environmental conditions stabilize. Gemmules are capable of

attaching to a substratum and generating a new sponge. Since gemmules can withstand harsh environments, are resistant to desiccation, and remain dormant for long periods, they are an excellent means of colonization for a sessile organism.

Sexual reproduction in sponges occurs when gametes are generated. Sponges are monoecious (hermaphroditic), which means that one individual can produce both gametes (eggs and sperm) simultaneously. In some sponges, production of gametes may occur throughout the year, whereas other sponges may show sexual cycles depending upon water temperature. Sponges may also become sequentially hermaphroditic, producing oocytes first and spermatozoa later. Oocytes arise by the differentiation of amoebocytes and are retained within the spongocoel, whereas spermatozoa result from the differentiation of choanocytes and are ejected via the osculum. Ejection of spermatozoa may be a timed and coordinated event, as seen in certain species. Spermatozoa carried along by water currents can fertilize the oocytes borne in the mesohyl of other sponges. Early larval development occurs within the sponge, and free-swimming larvae are then released via the osculum.

Locomotion

Sponges are generally sessile as adults and spend their lives attached to a fixed substratum. They do not show movement over large distances like other free-swimming marine invertebrates. However, sponge cells are capable of creeping along substrata via organizational plasticity. Under experimental conditions, researchers have shown that sponge cells spread on a physical support demonstrate a leading edge for directed movement. It has been speculated that this localized creeping movement may help sponges adjust to microenvironments near the point of attachment. It must be noted, however, that this pattern of movement has been documented in laboratories, but it remains to be observed in natural sponge habitats.

Summary

Animals included in phylum Porifera are Parazoans because they do not show the formation of true tissues (except in class Hexactinellida). These organisms show very simple organization, with a rudimentary endoskeleton. Sponges have multiple cell types that are geared toward executing various metabolic functions. Although these animals are very simple, they perform several complex physiological functions.

Glossary

amoebocyte
sponge cell with multiple functions, including nutrient delivery, egg formation, sperm delivery, and cell differentiation

choanocyte
(also, collar cell) sponge cell that functions to generate a water current and to trap and ingest food particles via phagocytosis

gemmule
structure produced by asexual reproduction in freshwater sponges where the morphology is inverted

invertebrata
(also, invertebrates) category of animals that do not possess a cranium or vertebral column

mesohyl
collagen-like gel containing suspended cells that perform various functions in the sponge

osculum
large opening in the sponge’s body through which water leaves

ostium
pore present on the sponge’s body through which water enters

pinacocyte
epithelial-like cell that forms the outermost layer of sponges and encloses a jelly-like substance called mesohyl

Porifera

phylum of animals with no true tissues, but a porous body with rudimentary endoskeleton

sclerocyte

cell that secretes silica spicules into the mesohyl

spicule

structure made of silica or calcium carbonate that provides structural support for sponges

spongocoel

central cavity within the body of some sponges

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SECTION OVERVIEW

32.5: Eumetazoa- Animals with True Tissues

Learning Objectives

- Describe the information needed to construct a phylogenetic tree of animals

Constructing an Animal Phylogenetic Tree

Evolutionary trees, or phylogeny, is the formal study of organisms and their evolutionary history with respect to each other. Phylogenetic trees are most-commonly used to depict the relationships that exist between species. In particular, they clarify whether certain traits are homologous (found in the common ancestor as a result of divergent evolution) or homoplasy (sometimes referred to as analogous: a character that is not found in a common ancestor, but whose function developed independently in two or more organisms through convergent evolution). Evolutionary trees are diagrams that show various biological species and their evolutionary relationships. They consist of branches that flow from lower forms of life to the higher forms of life.

Evolutionary trees differ from taxonomy which is an ordered division of organisms into categories based on a set of characteristics used to assess similarities and differences. Evolutionary trees involve biological classification and use morphology to show relationships. Phylogeny is evolutionary history shown by the relationships found when comparing polymeric molecules such as RNA, DNA, or proteins of various organisms. The evolutionary pathway is analyzed by the sequence similarity of these polymeric molecules. This is based on the assumption that the similarities of sequence result from having fewer evolutionary divergences than others. The evolutionary tree is constructed by aligning the sequences; the length of the branch is proportional to the amount of amino acid differences between the sequences.

Phylogenetic systematics informs the construction of phylogenetic trees based on shared characters. Comparing nucleic acids or other molecules to infer relationships is a valuable tool for tracing an organism's evolutionary history. The ability of molecular trees to encompass both short and long periods of time is hinged on the ability of genes to evolve at different rates, even in the same evolutionary lineage. For example, the DNA that codes for rRNA changes relatively slowly, so comparisons of DNA sequences in these genes are useful for investigating relationships between taxa that diverged a long time ago. Interestingly, 99% of the genes in humans and mice are detectably orthologous, and 50% of our genes are orthologous with those of yeast. The hemoglobin B genes in humans and in mice are orthologous. These genes serve similar functions, but their sequences have diverged since the time that humans and mice had a common ancestor.

Evolutionary pathways relating the members of a family of proteins may be deduced by examination of sequence similarity. This approach is based on the notion that sequences that are more similar to one another have had less evolutionary time to diverge than have sequences that are less similar. Evolutionary trees are used today for DNA hybridization, which determines the percentage difference of genetic material between two similar species. If there is a high resemblance of DNA between the two species, then the species are closely related. If only a small percentage is identical, then they are distantly related.

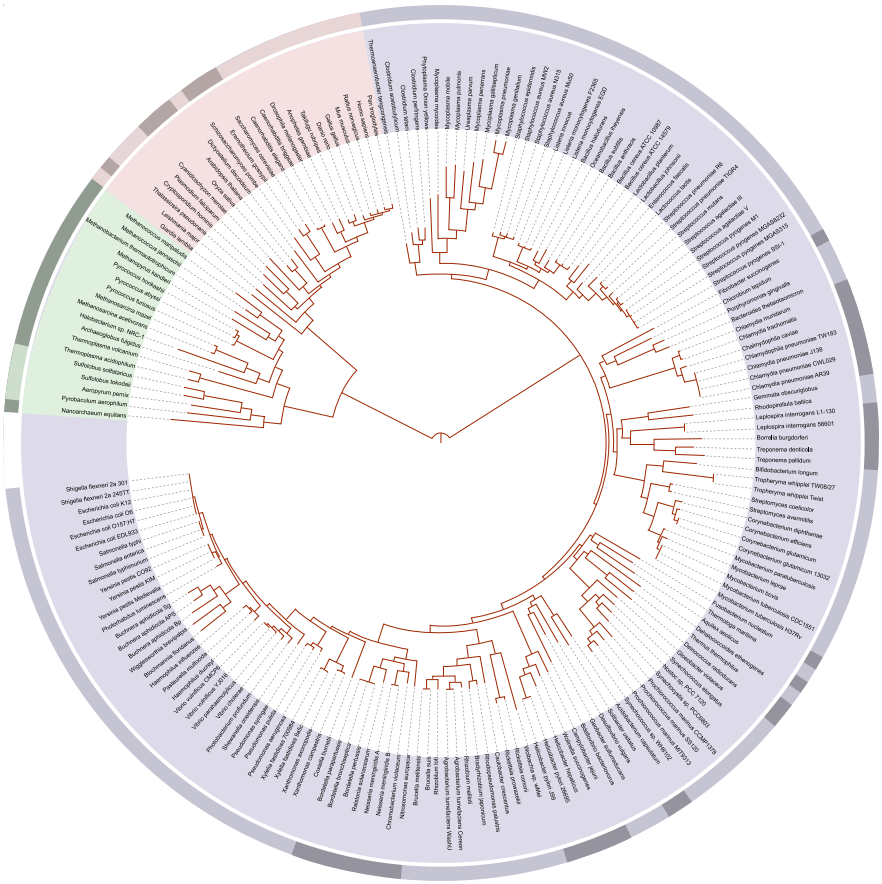


Figure 32.5.1: Phylogenetic tree of life: A phylogenetic tree of life, showing the relationship between species whose genomes had been sequenced as of 2006. The very center represents the last universal ancestor of all life on earth. The different colors represent the three domains of life: pink represents eukaryota (animals, plants, and fungi); blue represents bacteria; and green represents archaea.

Animal Phyla

The current understanding of evolutionary relationships between animal, or Metazoa, phyla begins with the distinction between “true” animals with true differentiated tissues, called Eumetazoa, and animal phyla that do not have true differentiated tissues (such as the sponges), called Parazoa. Both Parazoa and Eumetazoa evolved from a common ancestral organism that resembles the modern-day protists called choanoflagellates. These protist cells strongly resemble sponge choanocyte cells.

Eumetazoa are subdivided into radially-symmetrical animals and bilaterally-symmetrical animals and are classified into clade Radiata or Bilateria, respectively. The cnidarians and ctenophores are animal phyla with true radial symmetry. All other Eumetazoa are members of the Bilateria clade. The bilaterally-symmetrical animals are further divided into deuterostomes (including chordates and echinoderms) and two distinct clades of protostomes (including ecdysozoans and lophotrochozoans). Ecdysozoa includes nematodes and arthropods; named for a commonly-found characteristic among the group: exoskeletal molting (termed ecdysis). Lophotrochozoa is named for two structural features, each common to certain phyla within the clade. Some lophotrochozoan phyla are characterized by a larval stage called trochophore larvae, and other phyla are characterized by the presence of a feeding structure called a lophophore.

Key Points

- Phylogenetic trees are constructed using various data derived from studies on homologous traits, analagous traits, and molecular evidence that can be used to establish relationships using polymeric molecules (DNA, RNA, and proteins).
- Evolutionary relationships between animal phyla, or Metazoa, are based on the the presence or absence of differentiated tissues, referred to as Eumetazoa or Parazoa, respectively.
- Eumetazoa can be further classified into categories that are based on whether they have radial or bilateral symmetry, referred to as Radiata or Bilateria, respectively.

Key Terms

- **orthologous**: having been separated by a speciation event
- **homoplasy**: a correspondence between the parts or organs of different species acquired as the result of parallel evolution or convergence

32.5.1: Phylum Cnidaria

32.5.2: Class Anthozoa

32.5.3: Class Scyphozoa

32.5.4: Class Cubozoa and Class Hydrozoa

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32.5.1: Phylum Cnidaria

Learning Objectives

- Describe the fundamental anatomy of a Cnidarian

Introduction to Phylum Cnidaria

Phylum Cnidaria includes animals that show radial or biradial symmetry and are diploblastic: they develop from two embryonic layers. Nearly all (about 99 percent) cnidarians are marine species.

Cnidarians contain specialized cells known as cnidocytes ("stinging cells"), which contain organelles called nematocysts (stingers). These cells are present around the mouth and tentacles, serving to immobilize prey with toxins contained within the cells. Nematocysts contain coiled threads that may bear barbs. The outer wall of the cell has hairlike projections called cnidocils, which are sensitive to touch. When touched, the cells are known to fire coiled threads that can either penetrate the flesh of the prey or predators of cnidarians, or ensnare it. These coiled threads release toxins into the target that can often immobilize prey or scare away predators ().

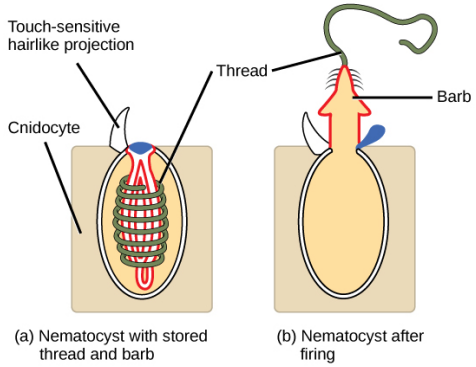


Figure **32.5.1.1**: Cnidocytes: Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

Animals in this phylum display two distinct morphological body plans: polyp or "stalk" and medusa or "bell". An example of the polyp form is *Hydra* spp.; perhaps the most well-known medusoid animals are the jellies (jellyfish). Polyp forms are sessile as adults, with a single opening to the digestive system (the mouth) facing up with tentacles surrounding it. Medusa forms are motile, with the mouth and tentacles hanging down from an umbrella-shaped bell.

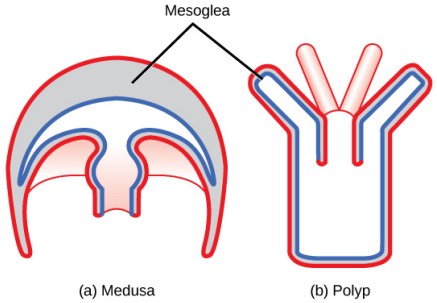


Figure **32.5.1.1**: Cnidarian morphology: Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Some cnidarians are polymorphic, having two body plans during their life cycle. An example is the colonial hydroid called an *Obelia*. The sessile polyp form has, in fact, two types of polyps. The first is the gastrozooid, which is adapted for capturing prey and feeding; the other type of polyp is the gonozooid, adapted for the asexual budding of medusa. When the reproductive buds mature, they break off and become free-swimming medusa, which are either male or female (dioecious). The male medusa makes

sperm, whereas the female medusa makes eggs. After fertilization, the zygote develops into a blastula and then into a planula larva. The larva is free swimming for a while, but eventually attaches and a new colonial reproductive polyp is formed.

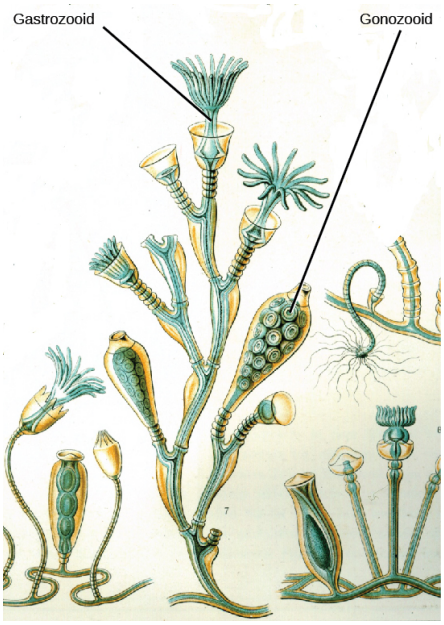


Figure **32.5.1.1**: Types of polyps in *Obelia*: The sessile form of *Obelia geniculate* has two types of polyps: gastrozooids, which are adapted for capturing prey, and gonozooids, which bud to produce medusae asexually.

All cnidarians show the presence of two membrane layers in the body that are derived from the endoderm and ectoderm of the embryo. The outer layer (from ectoderm) is called the epidermis and lines the outside of the animal, whereas the inner layer (from endoderm) is called the gastrodermis and lines the digestive cavity. Between these two membrane layers is a non-living, jelly-like mesoglea connective layer. In terms of cellular complexity, cnidarians show the presence of differentiated cell types in each tissue layer: nerve cells, contractile epithelial cells, enzyme-secreting cells, and nutrient-absorbing cells, as well as the presence of intercellular connections. However, the development of organs or organ systems is not advanced in this phylum.

The nervous system is primitive, with nerve cells scattered across the body. This nerve net may show the presence of groups of cells in the form of nerve plexi (singular: plexus) or nerve cords. The nerve cells show mixed characteristics of motor as well as sensory neurons. The predominant signaling molecules in these primitive nervous systems are chemical peptides, which perform both excitatory and inhibitory functions. Despite the simplicity of the nervous system, it coordinates the movement of tentacles, the drawing of captured prey to the mouth, the digestion of food, and the expulsion of waste.

The cnidarians perform extracellular digestion in which the food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients. The gastrovascular cavity has only one opening that serves as both a mouth and an anus; this is termed an incomplete digestive system. Cnidarian cells exchange oxygen and carbon dioxide by diffusion between cells in the epidermis with water in the environment, and between cells in the gastrodermis with water in the gastrovascular cavity. The lack of a circulatory system to move dissolved gases limits the thickness of the body wall, necessitating a non-living mesoglea between the layers. There is no excretory system or organs; nitrogenous wastes simply diffuse from the cells into the water outside the animal or in the gastrovascular cavity. There is also no circulatory system, so nutrients must move from the cells that absorb them in the lining of the gastrovascular cavity through the mesoglea to other cells.

The phylum Cnidaria contains about 10,000 described species divided into four classes: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa. The anthozoans, the sea anemones and corals, are all sessile species, whereas the scyphozoans (jellyfish) and cubozoans (box jellies) are swimming forms. The hydrozoans contain sessile forms and swimming colonial forms like the Portuguese Man O' War.

Key Points

- Cnidarians have two distinct morphological body plans known as polyp, which are sessile as adults, and medusa, which are mobile; some species exhibit both body plans in their lifecycle.

- All cnidarians have two membrane layers in the body: the epidermis and the gastrodermis; between both layers they have the mesoglea, which is a connective layer.
- Cnidarians carry out extracellular digestion, where enzymes break down the food particles and cells lining the gastrovascular cavity absorb the nutrients.
- Cnidarians have an incomplete digestive system with only one opening; the gastrovascular cavity serves as both a mouth and an anus.
- The nervous system of cnidarians, responsible for tentacle movement, drawing of captured prey to the mouth, digestion of food, and expulsion of waste, is composed of nerve cells scattered across the body.
- Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa make up the four different classes of Cnidarians.

Key Terms

- **diploblastic**: having two embryonic germ layers (the ectoderm and the endoderm)
- **cnidocyte**: a capsule, in certain cnidarians, containing a barbed, threadlike tube that delivers a paralyzing sting

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32.5.2: Class Anthozoa

Learning Objectives

- Identify the adaptive features of anthozoa

Class Anthozoa

The class Anthozoa includes all cnidarians that exhibit a polyp body plan only; in other words, there is no medusa stage within their life cycle. Examples include sea anemones, sea pens, and corals, with an estimated number of 6,100 described species. Sea anemones are usually brightly colored and can attain a size of 1.8 to 10 cm in diameter. These animals are usually cylindrical in shape and are attached to a substrate.

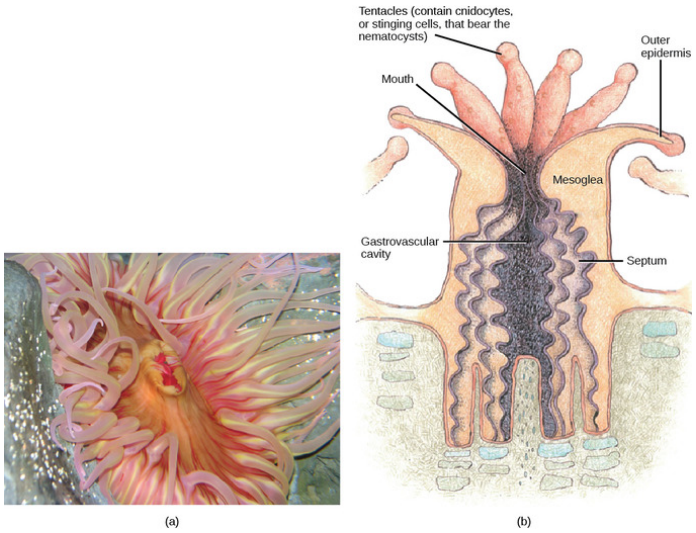


Figure **32.5.2.1**: Anthozoans: The sea anemone (a), like all anthozoans, has only a polyp body plan (b).

The mouth of a sea anemone is surrounded by tentacles that bear cnidocytes. They have slit-like mouth openings and a pharynx, which is the muscular part of the digestive system that serves to ingest as well as egest food. It may extend for up to two-thirds the length of the body before opening into the gastrovascular cavity. This cavity is divided into several chambers by longitudinal septa called mesenteries. Each mesentery consists of one ectodermal and one endodermal cell layer with the mesoglea sandwiched in between. Mesenteries do not divide the gastrovascular cavity completely; the smaller cavities coalesce at the pharyngeal opening. The adaptive benefit of the mesenteries appears to be an increase in surface area for absorption of nutrients and gas exchange.

Sea anemones feed on small fish and shrimp, usually by immobilizing their prey using the cnidocytes. Some sea anemones establish a mutualistic relationship with hermit crabs by attaching to the crab's shell. In this relationship, the anemone gets food particles from prey caught by the crab, while the crab is protected from the predators by the stinging cells of the anemone. Anemone fish, or clownfish, are able to live in the anemone since they are immune to the toxins contained within the nematocysts. Another type of anthozoan that forms an important mutualistic relationship is reef building coral. These hermatypic corals rely on a symbiotic relationship with zooxanthellae. The coral gains photosynthetic capability, while the zooxanthellae benefit by using nitrogenous waste and carbon dioxide produced by the cnidarian host.

Anthozoans remain polypoid throughout their lives. They can reproduce asexually by budding or fragmentation, or sexually by producing gametes. Both gametes are produced by the polyp, which can fuse to give rise to a free-swimming planula larva. The larva settles on a suitable substratum and develops into a sessile polyp.

Key Points

- Anthozoans include sea anemones, sea pens, and corals.
- The pharynx of anthozoans (ingesting as well as egesting food) leads to the gastrovascular cavity, which is divided by mesenteries.

- In Anthozoans, gametes are produced by the polyp; if they fuse, they will give rise to a free-swimming planula larva, which will become sessile once it finds an optimal substrate.
- Sea anemonies and coral are examples of anthozoans that form unique mutualistic relationships with other animal species; both sea anemonies and coral benefit from food availability provided by their partners.

Key Terms

- **mesentery**: in invertebrates, it describes any tissue that divides the body cavity into partitions
- **cnidocyte**: a capsule, in certain cnidarians, containing a barbed, threadlike tube that delivers a paralyzing sting
- **hermatypic**: of a coral that is a species that builds coral reefs

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32.5.3: Class Scyphozoa

Learning Objectives

- Explain the key features of scyphozoa

Class Scyphozoa

Class Scyphozoa, an exclusively marine class of animals with about 200 known species, includes all the jellies. The defining characteristic of this class is that the medusa is the prominent stage in the life cycle, although there is a polyp stage present. Members of this species range from 2 to 40 cm in length, but the largest scyphozoan species, *Cyanea capillata*, can reach a size of 2 m across. Scyphozoans display a characteristic bell-like morphology.

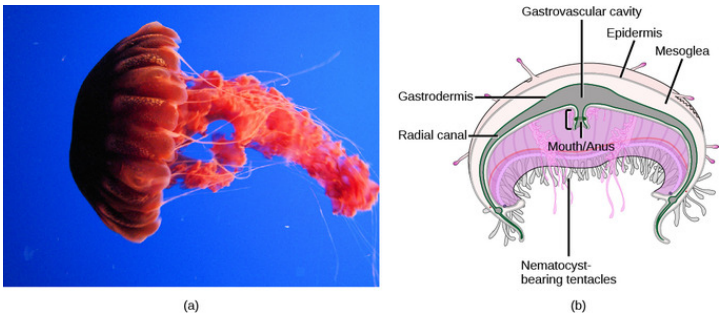


Figure **32.5.3.1**: Scyphozoans: For jellyfish (a), and all other scyphozoans, the medusa (b) is the most prominent of the two life stages.

In the jellyfish, a mouth opening, surrounded by tentacles bearing nematocysts, is present on the underside of the animal. Scyphozoans live most of their life cycle as free-swimming, solitary carnivores. The mouth leads to the gastrovascular cavity, which may be sectioned into four interconnected sacs, called diverticuli. In some species, the digestive system may be further branched into radial canals. Like the septa in anthozoans, the branched gastrovascular cells serves to increase the surface area for nutrient absorption and diffusion; thus, more cells are in direct contact with the nutrients in the gastrovascular cavity.

In scyphozoans, nerve cells are scattered over the entire body. Neurons may even be present in clusters called rhopalia. These animals possess a ring of muscles lining the dome of the body, which provides the contractile force required to swim through water. Scyphozoans are dioecious animals, having separate sexes. The gonads are formed from the gastrodermis with gametes expelled through the mouth. Planula larvae are formed by external fertilization; they settle on a substratum in a polypoid form known as scyphistoma. These forms may produce additional polyps by budding or may transform into the medusoid form. The life cycle of these animals can be described as polymorphic because they exhibit both a medusal and polypoid body plan at some point.

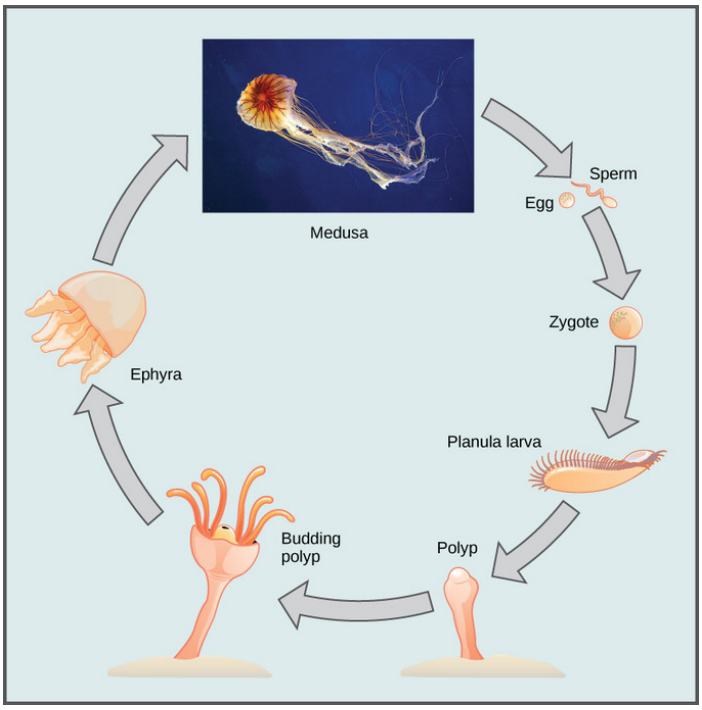


Figure **32.5.3.1**: Lifecycle of a jellyfish: The lifecycle of a jellyfish includes two stages: the medusa stage and the polyp stage. The polyp reproduces asexually by budding,while the medusa reproduces sexually.

Key Points

- Scyphozoans have a ring of muscles that lines the dome of their bodies; these structures provide them with the contractile force they need to swim through water.
- Scyphozoans have separate sexes and form planula larvae through external fertilization.
- Jellies exhibit the polyp form, known as a scyphistoma, after their larvae settle on a substrate; these forms will later bud-off and transform into their more prominenent medusa forms.

Key Terms

- **dioecious**: having the male and female reproductive organs on separate parts (of the same species)
- **rhopalia**: small sensory structures found within Scyphozoa that are characterized by clusters of neurons that can be used to sense light
- **scyphistoma**: the polypoid form of scyphozoans
- **nematocyst**: a capsule, in certain cnidarians, containing a barbed, threadlike tube that delivers a paralyzing sting

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32.5.4: Class Cubozoa and Class Hydrozoa

Learning Objectives

- Distinguish between cubozoa and hydrozoa cnidarians

Class Cubozoa

Class Cubozoa includes jellies that have a box-shaped medusa: a bell that is square in cross-section; hence, they are colloquially known as “box jellyfish.” These species may achieve sizes of 15–25 cm. Cubozoans display overall morphological and anatomical characteristics that are similar to those of the scyphozoans. A prominent difference between the two classes is the arrangement of tentacles. This is the most venomous group of all the cnidarians.

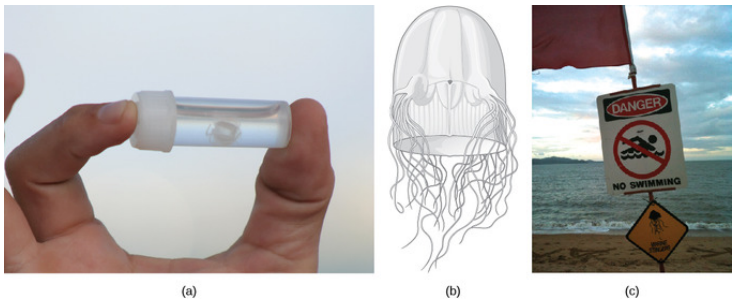


Figure **32.5.4.1**: Cubozoans: The (a) tiny cubazoan jelly *Malo kingi* is thimble shaped and, like all cubozoan jellies, (b) has four muscular pedalia to which the tentacles attach. *M. kingi* is one of two species of jellies known to cause Irukandji syndrome, a condition characterized by excruciating muscle pain, vomiting, increased heart rate, and psychological symptoms. Two people in Australia, where Irukandji jellies are most-commonly found, are believed to have died from Irukandji stings. (c) A sign on a beach in northern Australia warns swimmers of the danger.

The cubozoans contain muscular pads called pedalia at the corners of the square bell canopy, with one or more tentacles attached to each pedalium. These animals are further classified into orders based on the presence of single or multiple tentacles per pedalium. In some cases, the digestive system may extend into the pedalia. Nematocysts may be arranged in a spiral configuration along the tentacles; this arrangement helps to effectively subdue and capture prey. Cubozoans exist in a polypoid form that develops from a planula larva. These polyps show limited mobility along the substratum. As with scyphozoans, they may bud to form more polyps to colonize a habitat. Polyp forms then transform into the medusoid forms.

Class Hydrozoa

Hydrozoa includes nearly 3,200 species; most are marine, although some freshwater species are known. Animals in this class are polymorphs: most exhibit both polypoid and medusoid forms in their lifecycle, although this is variable.

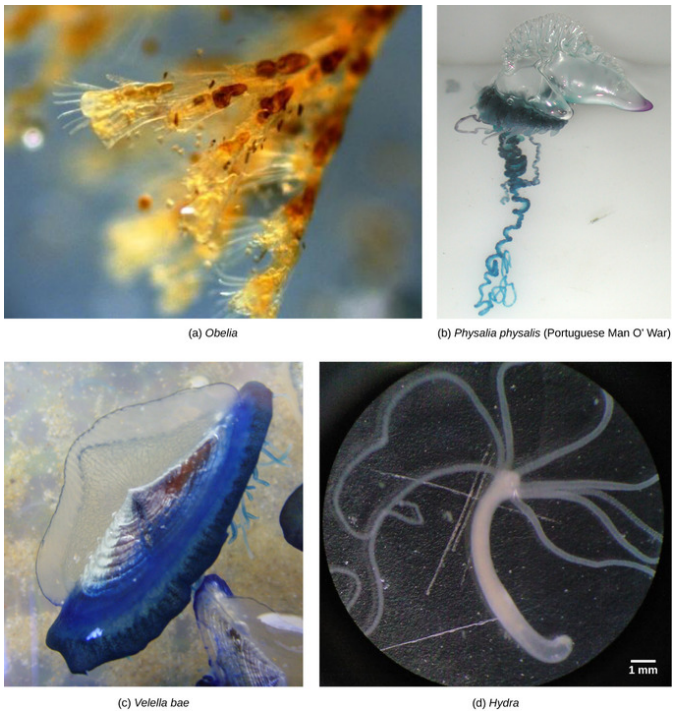


Figure 32.5.4.1: Hydrozoans: (a) *Obelia*, (b) *Physalia physalis*, known as the Portuguese Man O‘ War, (c) *Velella bae*, and (d) *Hydra* have different body shapes, but all belong to the family Hydrozoa.

The polyp form in these animals often shows a cylindrical morphology with a central gastrovascular cavity lined by the gastrodermis. The gastrodermis and epidermis have a simple layer of mesoglea sandwiched between them. A mouth opening, surrounded by tentacles, is present at the oral end of the animal. Many hydrozoans form colonies that are composed of a branched colony of specialized polyps that share a gastrovascular cavity, such as in the colonial hydroid *Obelia*. Colonies may also be free-floating and contain medusoid and polypoid individuals in the colony as in *Physalia* (the Portuguese Man O’ War) or *Velella* (By-the-wind sailor). Other species are solitary polyps (*Hydra*) or solitary medusae (*Gonionemus*). The true characteristic shared by all these diverse species is that their gonads for sexual reproduction are derived from epidermal tissue, whereas in all other cnidarians they are derived from gastrodermal tissue.

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Key Points

- Cubozoans differ from Scyphozoans in their arrangement of tentacles; they are also known for their box-shaped medusa.
- Out of all cnidarians, cubozoans are the most venomous.
- Hydrozoans are polymorphs, existing as solitary polyps, solitary medusae, or as colonies.
- Hydrozoans are unique from all other cnidarians in that their gonads are derived from epidermal tissue.

Key Terms

- **hydroid**: any of many colonial coelenterates that exist mainly as a polyp; a hydrozoan

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SECTION OVERVIEW

32.6: The Bilateria

Learning Objectives

- Describe the information needed to construct a phylogenetic tree of animals

Constructing an Animal Phylogenetic Tree

Evolutionary trees, or phylogeny, is the formal study of organisms and their evolutionary history with respect to each other. Phylogenetic trees are most-commonly used to depict the relationships that exist between species. In particular, they clarify whether certain traits are homologous (found in the common ancestor as a result of divergent evolution) or homoplasy (sometimes referred to as analogous: a character that is not found in a common ancestor, but whose function developed independently in two or more organisms through convergent evolution). Evolutionary trees are diagrams that show various biological species and their evolutionary relationships. They consist of branches that flow from lower forms of life to the higher forms of life.

Evolutionary trees differ from taxonomy which is an ordered division of organisms into categories based on a set of characteristics used to assess similarities and differences. Evolutionary trees involve biological classification and use morphology to show relationships. Phylogeny is evolutionary history shown by the relationships found when comparing polymeric molecules such as RNA, DNA, or proteins of various organisms. The evolutionary pathway is analyzed by the sequence similarity of these polymeric molecules. This is based on the assumption that the similarities of sequence result from having fewer evolutionary divergences than others. The evolutionary tree is constructed by aligning the sequences; the length of the branch is proportional to the amount of amino acid differences between the sequences.

Phylogenetic systematics informs the construction of phylogenetic trees based on shared characters. Comparing nucleic acids or other molecules to infer relationships is a valuable tool for tracing an organism's evolutionary history. The ability of molecular trees to encompass both short and long periods of time is hinged on the ability of genes to evolve at different rates, even in the same evolutionary lineage. For example, the DNA that codes for rRNA changes relatively slowly, so comparisons of DNA sequences in these genes are useful for investigating relationships between taxa that diverged a long time ago. Interestingly, 99% of the genes in humans and mice are detectably orthologous, and 50% of our genes are orthologous with those of yeast. The hemoglobin B genes in humans and in mice are orthologous. These genes serve similar functions, but their sequences have diverged since the time that humans and mice had a common ancestor.

Evolutionary pathways relating the members of a family of proteins may be deduced by examination of sequence similarity. This approach is based on the notion that sequences that are more similar to one another have had less evolutionary time to diverge than have sequences that are less similar. Evolutionary trees are used today for DNA hybridization, which determines the percentage difference of genetic material between two similar species. If there is a high resemblance of DNA between the two species, then the species are closely related. If only a small percentage is identical, then they are distantly related.

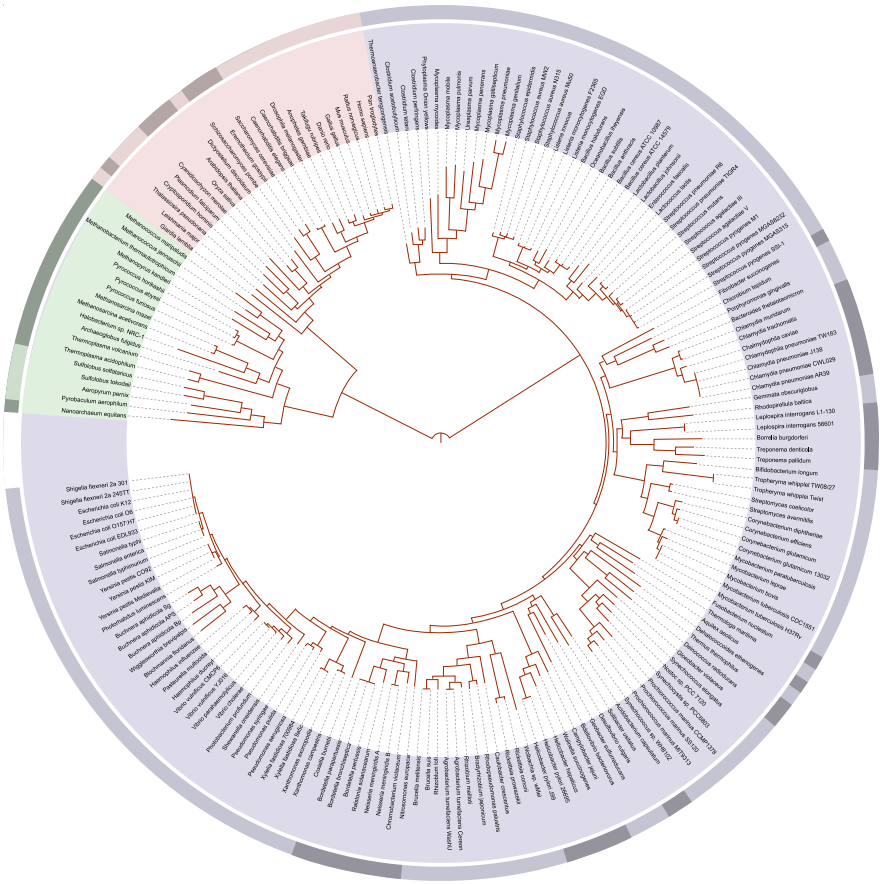


Figure **32.6.1**: Phylogenetic tree of life: A phylogenetic tree of life, showing the relationship between species whose genomes had been sequenced as of 2006. The very center represents the last universal ancestor of all life on earth. The different colors represent the three domains of life: pink represents eukaryota (animals, plants, and fungi); blue represents bacteria; and green represents archaea.

Animal Phyla

The current understanding of evolutionary relationships between animal, or Metazoa, phyla begins with the distinction between “true” animals with true differentiated tissues, called Eumetazoa, and animal phyla that do not have true differentiated tissues (such as the sponges), called Parazoa. Both Parazoa and Eumetazoa evolved from a common ancestral organism that resembles the modern-day protists called choanoflagellates. These protist cells strongly resemble sponge choanocyte cells.

Eumetazoa are subdivided into radially-symmetrical animals and bilaterally-symmetrical animals and are classified into clade Radiata or Bilateria, respectively. The cnidarians and ctenophores are animal phyla with true radial symmetry. All other Eumetazoa are members of the Bilateria clade. The bilaterally-symmetrical animals are further divided into deuterostomes (including chordates and echinoderms) and two distinct clades of protostomes (including ecdysozoans and lophotrochozoans). Ecdysozoa includes nematodes and arthropods; named for a commonly-found characteristic among the group: exoskeletal molting (termed ecdysis). Lophotrochozoa is named for two structural features, each common to certain phyla within the clade. Some lophotrochozoan phyla are characterized by a larval stage called trochophore larvae, and other phyla are characterized by the presence of a feeding structure called a lophophore.

Key Points

- Phylogenetic trees are constructed using various data derived from studies on homologous traits, analagous traits, and molecular evidence that can be used to establish relationships using polymeric molecules (DNA, RNA, and proteins).
- Evolutionary relationships between animal phyla, or Metazoa, are based on the the presence or absence of differentiated tissues, referred to as Eumetazoa or Parazoa, respectively.
- Eumetazoa can be further classified into categories that are based on whether they have radial or bilateral symmetry, referred to as Radiata or Bilateria, respectively.

Key Terms

- **orthologous**: having been separated by a speciation event
- **homoplasy**: a correspondence between the parts or organs of different species acquired as the result of parallel evolution or convergence

32.6.1: Molecular Analyses and Modern Phylogenetic Trees

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32.6.1: Molecular Analyses and Modern Phylogenetic Trees

Learning Objectives

- Distinguish between morphological and molecular data in creating phylogenetic trees of animals

Modern Advances in Phylogenetic Understanding Come from Molecular Analyses

The phylogenetic groupings are continually being debated and refined by evolutionary biologists. Each year, new evidence emerges that further alters the relationships described by a phylogenetic tree diagram. Previously, phylogenetic trees were constructed based on homologous and analogous morphology; however, with the advances in molecular biology, construction of phylogenetic trees is increasingly performed using data derived from molecular analyses.

Many evolutionary relationships in the modern tree have only recently been determined due to molecular evidence. Nucleic acid and protein analyses have informed the construction of the modern phylogenetic animal tree. These data come from a variety of molecular sources, such as mitochondrial DNA, nuclear DNA, ribosomal RNA (rRNA), and certain cellular proteins. Evolutionary trees can be made by the determination of sequence information of similar genes in different organisms. Sequences that are similar to each other frequently are considered to have less time to diverge, while less similar sequences have more evolutionary time to diverge. The evolutionary tree is created by aligning sequences and having each branch length proportional to the amino acid differences of the sequences. Furthermore, by assigning a constant mutation rate to a sequence and performing a sequence alignment, it is possible to calculate the approximate time when the sequence of interest diverged into monophyletic groups.

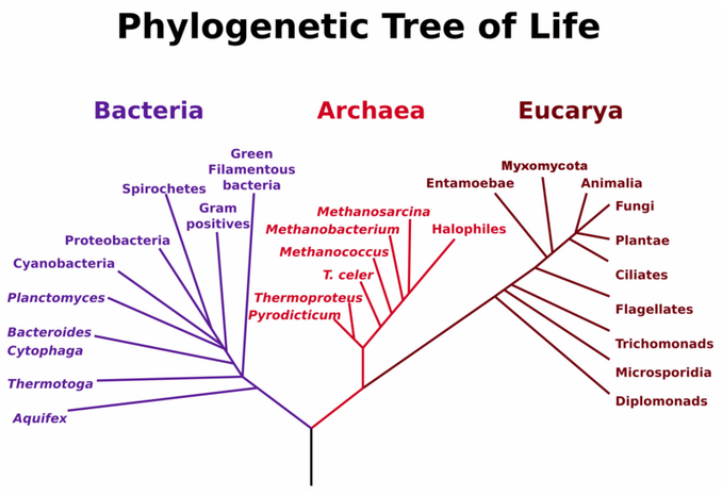


Figure **32.6.1.1**: Phlyogenetic tree of life: Advances in molecular biology and analysis of polymeric molecules such as DNA, RNA, and proteins have contributed to the development of phylogenetic trees.

Sequence alignments can be performed on a variety of sequences. For constructing an evolutionary tree from proteins, for example, the sequences are aligned and then compared. rRNA (ribosomal RNA) is typically used to compare organisms since rRNA has a slower mutation rate and is a better source for evolutionary tree construction. This is best supported by research of Dr. Carl Woese that was conducted in the late 1970s. Since the ribosomes are critical to the function of living organisms, they are not easily changed through the process of evolution. Taking advantage of this fact, Dr. Woese compared the minuscule differences in the sequences of ribosomes among a great array of bacteria and showed that they were not all related.

For example, a previously-classified group of animals called lophophorates, which included brachiopods and bryozoans, were long-thought to be primitive deuterostomes. Extensive molecular analysis using rRNA data found these animals to be protostomes, more closely related to annelids and mollusks. This discovery allowed for the distinction of the protostome clade: the lophotrochozoans. Molecular data have also shed light on some differences within the lophotrochozoan group. Some scientists believe that the phyla Platyhelminthes and Rotifera within this group should actually belong to their own group of protostomes termed Platyzoa.

Molecular research similar to the discoveries that brought about the distinction of the lophotrochozoan clade has also revealed a dramatic rearrangement of the relationships between mollusks, annelids, arthropods, and nematodes; a new ecdysozoan clade was

formed. Due to morphological similarities in their segmented body types, annelids and arthropods were once thought to be closely related. However, molecular evidence has revealed that arthropods are actually more closely related to nematodes, now comprising the ecdysozoan clade, and annelids are more closely related to mollusks, brachiopods, and other phyla in the lophotrochozoan clade. These two clades now make up the protostomes.

Another change to former phylogenetic groupings because of molecular analyses includes the emergence of an entirely new phylum of worm called Acoelomorpha. These acoel flatworms were long thought to belong to the phylum Platyhelminthes because of their similar "flatworm" morphology. However, molecular analyses revealed this to be a false relationship and originally suggested that acoels represented living species of some of the earliest divergent bilaterians. More recent research into the acoelomorphs has called this hypothesis into question and suggested a closer relationship with deuterostomes. The placement of this new phylum remains disputed, but scientists agree that with sufficient molecular data, their true phylogeny will be determined.

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Key Points

- The construction of phylogenetic trees is now based on similarities and differences within the molecular sources used for analysis which include DNA, RNA, and proteins.
- The ability to use molecular sources as a basis of phylogenetic tree construction has allowed for determination of previously-unknown evolutionary relationships between organisms.
- In addition to the establishment of new relationships within phylogenetic trees, the ability to use molecular sources for analysis has also created an emergence of new phlyums that were previously classified in larger groups.
- Besides identifying molecular similarities and differences between organisms, by assigning a constant mutation rate to a sequence and performing a sequence alignment, it is possible to determine when two organisms diverged from one another.

Key Terms

- **monophyletic**: of, pertaining to, or affecting a single phylum (or other taxon) of organisms

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CHAPTER OVERVIEW

33: Protostomes

33.1: The Clades of Protostomes

33.1.1: Superphylum Ecdysozoa

33.1.2: Superphylum Lophotrochozoa

33.1.3: Phylum Platyhelminthes

33.1.4: Phylum Rotifera

33.1.5: Phylum Nemertea

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SECTION OVERVIEW

33.1.1: Superphylum Ecdysozoa

Topic hierarchy

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33.1.2: Superphylum Lophotrochozoa

Learning Objectives

- Describe the phylogenetic position and basic features of lophotrochozoa

Lophotrochozoans

Animals belonging to superphylum Lophotrochozoa are protostomes: the blastopore (or the point of involution of the ectoderm or outer germ layer) becomes the mouth opening to the alimentary canal. This is called protostomy or “first mouth.” In protostomy, solid groups of cells split from the endoderm or inner germ layer to form a central mesodermal layer of cells. This layer multiplies into a band which then splits internally to form the coelom; this protostomic coelom is termed schizocoelom.

As lophotrochozoans, the organisms in this superphylum possess either lophophore or trochophore larvae. The exact relationships between the different phyla are not entirely certain. The lophophores include groups that are united by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth. Lophophorata include the flatworms and several other phyla, including the Bryozoa, Entoprocta, Phoronida, and Brachiopoda. These clades are upheld when RNA sequences are compared. Trochophore larvae are characterized by two bands of cilia around the body. Previously, these were treated together as the Trochozoa, together with the arthropods, which do not produce trochophore larvae, but were considered close relatives of the annelids because they are both segmented. However, they show a number of important differences. Arthropods are now placed separately among the Ecdysozoa. The Trochozoa include the Nemertea, Mollusca, Sipuncula, and Annelida.

The lophotrochozoans are triploblastic, possessing an embryonic mesoderm sandwiched between the ectoderm and endoderm found in the diploblastic cnidarians. These phyla are also bilaterally symmetrical: a longitudinal section will divide them into right and left sides that are symmetrical. They also show the beginning of cephalization: the evolution of a concentration of nervous tissues and sensory organs in the head of the organism, which is where it first encounters its environment.

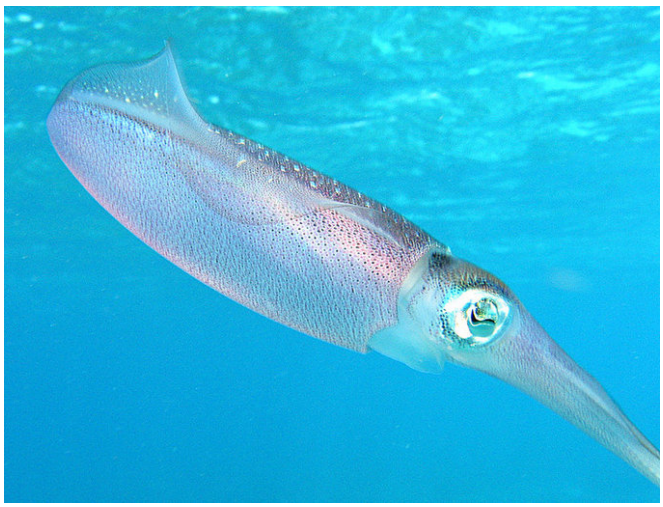


Figure **33.1.2.1**: Lophotrochozoans: The Caribbean Reef Squid or Sepioteuthis sepioidea is a complex lophotrochozoan. Species in this group have bilateral symmetry.

Key Points

- Lophotrochozoa have a blastopore, which is an involution of the ectoderm that forms a rudimentary mouth opening to the alimentary canal, a condition called protostomy or “first mouth”.
- The Lophotrochozoa are comprised of the trochozoans and the lophophorata, although the exact relationships between the different phyla are not clearly determined.
- Lophophores are characterized by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth; they include the flatworms and several other phyla whose relationships are upheld by genetic evidence.
- Trochophore larvae are distinguished from the lophophores by two bands of cilia around the body; they include the Nemertea, Mollusca, Sipuncula, and Annelida.

- The lophotrochozoans have a mesoderm layer positioned between the ectoderm and endoderm and are bilaterally symmetrical, which signals the beginning of cephalization, the concentration of nervous tissues and sensory organs in the head of the organism.

Key Terms

- **blastopore**: the opening into the archenteron
- **lophophore**: a feeding organ of brachiopods, bryozoans, and phoronids
- **cephalization**: an evolutionary trend in which the neural and sense organs become centralized at one end (the head) of an animal

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33.1.3: Phylum Platyhelminthes

Learning Objectives

- Differentiate among the classes of platyhelminthes

Phylum Platyhelminthes

Phylum Platyhelminthes is composed of the flatworms: acoelomate organisms that include many free-living and parasitic forms. Most of the flatworms are classified in the superphylum Lophotrochozoa, which also includes the mollusks and annelids. The Platyhelminthes consist of two lineages: the Catenulida and the Rhabditophora. The Catenulida, or “chain worms” is a small clade of just over 100 species. These worms typically reproduce asexually by budding. However, the offspring do not fully detach from the parents; therefore, they resemble a chain. The remaining flatworms discussed here are part of the Rhabditophora.

Many flatworms are parasitic, including important parasites of humans. Flatworms have three embryonic tissue layers that give rise to surfaces that cover tissues (from ectoderm), internal tissues (from mesoderm), and line the digestive system (from endoderm). The epidermal tissue is a single layer cells or a layer of fused cells (syncytium) that covers a layer of circular muscle above a layer of longitudinal muscle. The mesodermal tissues include mesenchymal cells that contain collagen and support secretory cells that secrete mucus and other materials at the surface. The flatworms are acoelomates: their bodies are solid between the outer surface and the cavity of the digestive system.

Physiological Processes of Flatworms

The free-living species of flatworms are predators or scavengers. Parasitic forms feed on the tissues of their hosts. Most flatworms have a gastrovascular cavity rather than a complete digestive system; in such animals, the “mouth” is also used to expel waste materials from the digestive system. Some species also have an anal opening. The gut may be a simple sac or highly branched. Digestion is extracellular, with digested materials taken in to the cells of the gut lining by phagocytosis. One group, the cestodes, lacks a digestive system. Flatworms have an excretory system with a network of tubules throughout the body with openings to the environment and nearby flame cells, whose cilia beat to direct waste fluids concentrated in the tubules out of the body. The system is responsible for the regulation of dissolved salts and the excretion of nitrogenous wastes. The nervous system consists of a pair of nerve cords running the length of the body with connections between them and a large ganglion or concentration of nerves at the anterior end of the worm, where there may also be a concentration of photosensory and chemosensory cells.

There is neither a circulatory nor respiratory system, with gas and nutrient exchange dependent on diffusion and cell-cell junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be “flat” worms. In addition, most flatworm species are monoecious; typically, fertilization is internal. Asexual reproduction is common in some groups.

Diversity of Flatworms

Platyhelminthes are traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda. The class Turbellaria includes mainly free-living, marine species, although some species live in freshwater or moist terrestrial environments. The ventral epidermis of turbellarians is ciliated which facilitates their locomotion. Some turbellarians are capable of remarkable feats of regeneration: they may regrow the entire body from a small fragment.



Figure **33.1.3.1**: Turbellaria: Pseudobiceros bedfordi (Bedford's Flatworm), a member of the Turbellaria, is a marine species which uses the epidermis of its belly for locomotion.

The monogeneans are ectoparasites, mostly of fish, with simple life cycles that consist of a free-swimming larva that attaches to a fish to begin transformation to the parasitic adult form. The worms may produce enzymes that digest the host tissues or simply graze on surface mucus and skin particles.

The trematodes, or flukes, are internal parasites of mollusks and many other groups, including humans. Trematodes have complex life cycles that involve a primary host in which sexual reproduction occurs and one or more secondary hosts in which asexual reproduction occurs. The primary host is almost always a mollusk. Trematodes are responsible for serious human diseases including schistosomiasis, a blood fluke.



Figure **33.1.3.1**: Trematodes: Botulus microporus is a trematode that lives only in the intestinal tract of Lancetfish, *Alepisaurus ferox*.

The cestodes, or tapeworms, are also internal parasites, mainly of vertebrates. Tapeworms live in the intestinal tract of the primary host, remaining fixed by using a sucker on the anterior end, or scolex, of the tapeworm body. The remainder of the tapeworm is composed of a long series of units called proglottids. Each may contain an excretory system with flame cells and both female and male reproductive structures. Tapeworms do not possess a digestive system; instead, they absorb nutrients from the food matter passing through them in the host's intestine.

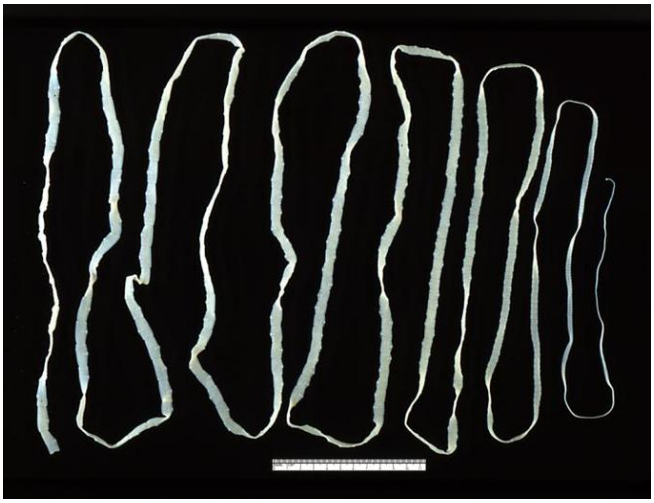


Figure **33.1.3.1**: Cestodes: Taenia saginata, also known as Taeniarhynchus saginata or the beef tapeworm, is a parasite of both cattle and humans. It displays the long series of proglottid subunits characteristic of the species.

Key Points

- The Platyhelminthes are acoelomate flatworms: their bodies are solid between the outer surface and the cavity of the digestive system.
- Most flatworms have a gastrovascular cavity rather than a complete digestive system; the same cavity used to bring in food is used to expel waste materials.
- Platyhelminthes are either predators or scavengers; many are parasites that feed on the tissues of their hosts.
- Flatworms posses a simple nervous system, no circulatory or respiratory system, and most produce both eggs and sperm, with internal fertilization.
- Platyhelminthes are divided into four classes: Turbellaria, free-living marine species; Monogenea, ectoparasites of fish; Trematoda, internal parasites of humans and other species; and Cestoda (tapeworms), which are internal parasites of many vertebrates.
- In flatworms, digested materials are taken into the cells of the gut lining by phagocytosis, rather than being processed internally.

Key Terms

- **acoelomate**: any animal without a coelom, or body cavity
- **ectoparasite**: a parasite that lives on the surface of a host organism
- **scolex**: the structure at the rear end of a tapeworm which, in the adult, has suckers and hooks by which it attaches itself to a host
- **proglottid**: any of the segments of a tapeworm; they contain both male and female reproductive organs

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33.1.4: Phylum Rotifera

Learning Objectives

- Identify the features of rotifers involved in movement and feeding

Phylum Rotifera

The rotifers are a microscopic (about 100 µm to 30 mm) group of mostly-aquatic organisms that get their name from the corona: a rotating, wheel-like structure that is covered with cilia at their anterior end. Although their taxonomy is currently in flux, one treatment places the rotifers in three classes: Bdelloidea, Monogononta, and Seisonidea. The classification of the group is currently under revision, however, as more phylogenetic evidence becomes available. It is possible that the “spiny headed worms” currently in phylum Acanthocephala will be incorporated into this group in the future.



Figure **33.1.4.1**: Rotifers: A bdelloid rotifer is a member of a class of rotifers found in fresh water and moist soil. The rotifer body consists of a head, a truck, and a foot. They eat by filtering food into the mouth by creating currents with the corona.

The rotifer body form consists of a head (which contains the corona), a trunk (which contains the organs), and the foot. Rotifers are typically free-swimming and truly planktonic organisms, but the toes or extensions of the foot can secrete a sticky material forming a holdfast to help them adhere to surfaces. The head contains sensory organs in the form of a bi-lobed brain and small eyespots near the corona.

The rotifers are filter feeders that will eat dead material, algae, and other microscopic living organisms. Therefore, they are very important components of aquatic food webs. Rotifers obtain food that is directed toward the mouth by the current created from the movement of the corona. The food particles enter the mouth and travel to the mastax (pharynx with jaw-like structures). Food passes by digestive and salivary glands into the stomach and then into the intestines. Digestive and excretory wastes are collected in a cloacal bladder before being released out the anus.

Rotifers are pseudocoelomates commonly found in fresh water and some salt water environments throughout the world. About 2,200 species of rotifers have been identified. Rotifers are dioecious organisms (having either male or female genitalia) and exhibit sexual dimorphism (males and females have different forms). Many species are parthenogenic and exhibit haplodiploidy, a method of gender determination in which a fertilized egg develops into a female and an unfertilized egg develops into a male. In many dioecious species, males are short-lived and smaller, with no digestive system and a single testis. Females can produce eggs that are capable of dormancy, which protects eggs during harsh environmental conditions.

Key Points

- The rotifer body form consists of a head (containing the sensory organs in the form of a bi-lobed brain and small eyespots near the corona), the trunk (containing organs), and the foot (which can hold fast).
- The foot of the rotifer secretes a sticky material to help it adhere to surfaces.

- Rotifers are filter feeders that generate a current using the corona to pass food into the mouth, which then passes by digestive and salivary glands into the stomach and intestines.
- Rotifers exhibit sexual dimorphism; the gender of many species is determined by whether the egg is fertilized (and develops into a female) or unfertilized (and develops into a male).

Key Terms

- **pseudocoelomate**: any invertebrate animal with a three-layered body and a pseudocoel
- **mastax**: the pharynx of a rotifer which usually contains four horny pieces that work to crush the food

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33.1.5: Phylum Nemertea

Learning Objectives

- Identify the key features of the Phylum Nemertea

Phylum Nemertea

The Nemertea are colloquially known as ribbon worms. Most species of phylum Nemertea are marine (predominantly benthic or bottom dwellers) with an estimated 900 species known. However, nemertini have been recorded in freshwater and terrestrial habitats as well. Most nemerteans are carnivores, feeding on worms, clams, and crustaceans. Some species are scavengers, while other nemertini species, such as *Malacobdella grossa*, have also evolved commensalistic relationships with some mollusks. Interestingly, nemerteans have almost no predators, two species are sold as fish bait, and some species have devastated commercial fishing of clams and crabs.

Morphology

Ribbon worms vary in size from 1 cm to several meters. They show bilateral symmetry and remarkable contractile properties. Because of their contractility, they can change their morphological presentation in response to environmental cues. Animals in phylum Nemertea also show a flattened morphology: they are flat from front to back, like a flattened tube. In addition, nemertea are soft, unsegmented animals.



Figure **33.1.5.1**: Morphology of Nemertea: A terrestrial Geonemertes, a Nemertean, displaying the flat, ribbon-like body of the organism that is unsegmented.

A unique characteristic of this phylum is the presence of a proboscis enclosed in a rhynchocoel. The proboscis serves to capture food and may be ornamented with barbs in some species. The rhynchocoel is a fluid-filled cavity that extends from the head to nearly two-thirds of the length of the gut in these animals. The proboscis may be extended or retracted by the retractor muscle attached to the wall of the rhynchocoel.

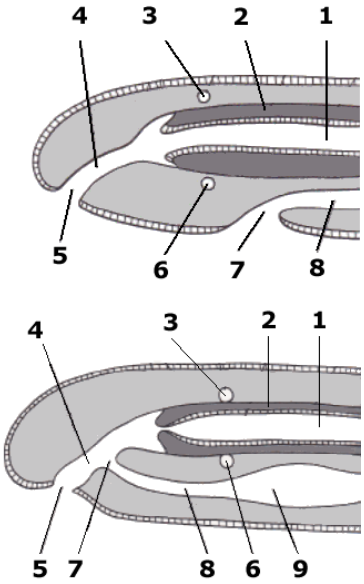


Figure **33.1.5.1**: Internal structures of the Nemertini: This image shows the internal structures of a basic nemertean, including the proboscis and the rhynchocoel: 1: Proboscis 2: Rhynchocoel 3: Dorsal commissure of brain 4: Rhynchodeum 5: Proboscis pore 6: Ventral commissure of brain 7: Mouth 8: Foregut 9: Stomach

Metabolism

The nemertini show a very well-developed digestive system. A mouth opening that is ventral to the rhynchocoel leads into the foregut, followed by the intestine. The intestine is present in the form of diverticular pouches which ends in a rectum that opens via an anus. Gonads are interspersed with the intestinal diverticular pouches, opening outwards via genital pores. A circulatory system consists of a closed loop of a pair of lateral blood vessels. The circulatory system is derived from the coelomic cavity of the embryo. Some animals may also have cross-connecting vessels in addition to lateral ones. Although these are called blood vessels, since they are of coelomic origin, the circulatory fluid is colorless. Some species bear hemoglobin as well as yellow or green pigments. The blood vessels are connected to the rhynchocoel. The flow of fluid in these vessels is facilitated by the contraction of muscles in the body wall. A pair of protonephridia, or primitive kidneys, is present in these animals to facilitate osmoregulation. Gaseous exchange occurs through the skin in the nemertini.

Nervous System

Nemertini have a ganglion or “brain” situated at the anterior end between the mouth and the foregut, surrounding the digestive system as well as the rhynchocoel. A ring of four nerve masses called “ganglia” comprises the brain in these animals. Paired longitudinal nerve cords emerge from the brain ganglia, extending to the posterior end. Ocelli or eyespots are present in pairs, in multiples of two in the anterior portion of the body. It is speculated that the eyespots originate from neural tissue and not from the epidermis.

Reproduction

Animals in phylum Nemertea show sexual dimorphism, although freshwater species may be hermaphroditic. Eggs and sperm are released into the water; fertilization occurs externally. The zygote develops into a special kind of nemertean larvae called a planuliform larva. In some nemertine species, another larva specific to the nemertinis, a pilidium, may develop inside the young worm from a series of imaginal discs. This larval form, characteristically shaped like a deerstalker cap, devours tissues from the young worm for survival before metamorphosing into the adult-like morphology.

Key Points

- The Nemertini are mostly bottom-dwelling marine organisms, although some are found in freshwater and terrestrial habitats.
- Most nemerteans are carnivores, some are scavengers, and others have evolved relationships with some mollusks that are benefit the Nemertean but do not harm the mollusk.

- Nemerteans vary greatly in size and are bilaterally symmetrical; they are unsegmented and resemble a flat tube which can change morphological presentation in response to environmental cues.
- Nemertini have a simple nervous system comprised of a ring of four nerve masses called “ganglia” at the anterior end between the mouth and the foregut from which paired longitudinal nerve cords emerge and extend to the posterior end.
- Nemertini are mostly sexually dimorphic, fertilizing eggs externally by releasing both eggs and sperm into the water; a larva may develop inside the resulting young worm and devour its tissues before metamorphosing into the adult.

Key Terms

- **protonephridia**: an invertebrate organ which occurs in pairs and removes metabolic wastes from an animal’s body
- **rhynchocoel**: a cavity which mostly runs above the midline and ends a little short of the rear of the body of a nemertean and extends or retracts the proboscis
- **proboscis**: an elongated tube from the head or connected to the mouth, of an animal

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33.1.6: Phylum Mollusca

Learning Objectives

- Describe the unique anatomical and morphological features of molluscs

Phylum Mollusca

Phylum Mollusca is the predominant phylum in marine environments. It is estimated that 23 percent of all known marine species are mollusks; there are around 85,000 described species, making them the second most diverse phylum of animals. The name “mollusca” signifies a soft body; the earliest descriptions of mollusks came from observations of unshelled cuttlefish. Mollusks are predominantly a marine group of animals; however, they are known to inhabit freshwater as well as terrestrial habitats. Mollusks display a wide range of morphologies in each class and subclass. They range from large predatory squids and octopus, some of which show a high degree of intelligence, to grazing forms with elaborately-sculpted and colored shells. In spite of their tremendous diversity, however, they also share a few key characteristics, including a muscular foot, a visceral mass containing internal organs, and a mantle that may or may not secrete a shell of calcium carbonate.



Figure **33.1.6.1**: Mollusk shells: Helix aspersa, a common land snail, has a calcium carbonate shell.

Mollusks have a muscular foot used for locomotion and anchorage that varies in shape and function, depending on the type of mollusk under study. In shelled mollusks, this foot is usually the same size as the opening of the shell. The foot is a retractable as well as an extendable organ. It is the ventral-most organ, whereas the mantle is the limiting dorsal organ. Mollusks are eucoelomate, but the cavity is restricted to a region around the heart in adult animals. The mantle cavity develops independently of the coelomic cavity.

The visceral mass is present above the foot in the visceral hump. This includes digestive, nervous, excretory, reproductive, and respiratory systems. Mollusk species that are exclusively aquatic have gills for respiration, whereas some terrestrial species have lungs for respiration. Additionally, a tongue-like organ called a radula, which bears chitinous tooth-like ornamentation, is present in many species, serving to shred or scrape food. The mantle (also known as the pallium) is the dorsal epidermis in mollusks; shelled mollusks are specialized to secrete a chitinous and hard calcareous shell.

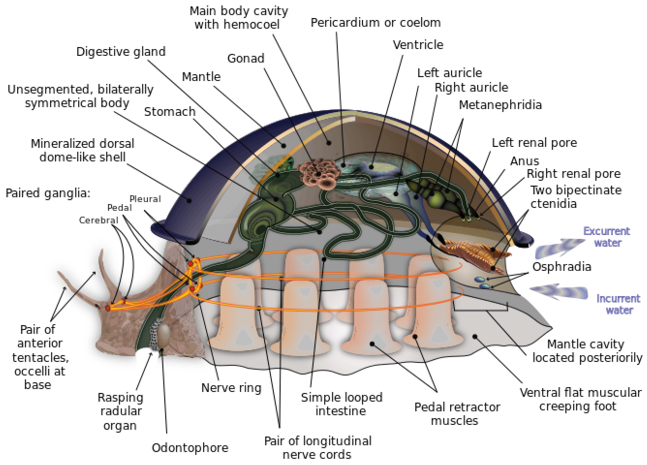


Figure **33.1.6.1**: A “generalized mollusk”: An anatomical diagram of a hypothetical ancestral mollusk, showing features common to many mollusk types.

Most mollusks are dioecious animals where fertilization occurs externally, although this is not the case in terrestrial mollusks, such as snails and slugs, or in cephalopods. In some mollusks, the zygote hatches and undergoes two larval stages, trochophore and veliger, before becoming a young adult; bivalves may exhibit a third larval stage, glochidia.

Key Points

- A mollusk’s muscular foot is used for locomotion and anchorage, varies in shape and function, and can both extend and retract.
- The visceral mass inside the mollusk includes digestive, nervous, excretory, reproductive, and respiratory systems.
- Most mollusks possess a radula, which is similar to a tongue with teeth-like projections, serving to shred or scrape food.
- The mantle is the dorsal epidermis in mollusks; in some mollusks it secretes a chitinous and hard calcareous shell.

Key Terms

- **visceral mass**: the soft, non-muscular metabolic region of the mollusc that contains the body organs
- **mantle**: the body wall of a mollusc, from which the shell is secreted
- **radula**: the rasping tongue of snails and most other mollusks

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33.1.7: Classification of Phylum Mollusca

Learning Objectives

- Differentiate among the classes in the phylum mollusca

Classes in Phylum Mollusca

Phylum Mollusca is a very diverse (85,000 species) group of mostly marine species, with a dramatic variety of form. This phylum can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda.

Class Aplacophora

Class Aplacophora ("bearing no plates") includes worm-like animals primarily found in benthic marine habitats. These animals lack a calcareous shell, but possess aragonite spicules on their epidermis. They have a rudimentary mantle cavity and lack eyes, tentacles, and nephridia (excretory organs).

Class Monoplacophora

Members of class Monoplacophora ("bearing one plate") posses a single, cap-like shell that encloses the body. The morphology of the shell and the underlying animal can vary from circular to ovate. A looped digestive system, multiple pairs of excretory organs, many gills, and a pair of gonads are present in these animals. The monoplacophorans were believed extinct and only known via fossil records until the discovery of Neopilina galathaea in 1952. Today, scientists have identified nearly two dozen extant species.

Class Polyplacophora

Animals in the class Polyplacophora ("bearing many plates") are commonly known as "chitons" and bear an armor-like, eight-plated dorsal shell. These animals have a broad, ventral foot that is adapted for suction to rocks and other substrates, and a mantle that extends beyond the shell in the form of a girdle. Calcareous spines may be present on the girdle to offer protection from predators. Chitons live worldwide, in cold water, warm water, and the tropics. Most chiton species inhabit intertidal or subtidal zones, and do not extend beyond the photic zone. Some species live quite high in the intertidal zone and are exposed to the air and light for long periods.



Figure **33.1.7.1**: Chiton morphology: The underside of the gumboot chiton, Cryptochiton stellari, showing the foot in the center, surrounded by the gills and mantle. The mouth is visible to the left in this image.

Class Bivalvia

Bivalvia is a class of marine and freshwater molluscs with laterally compressed bodies enclosed by a shell in two hinged parts. Bivalves include clams, oysters, mussels, scallops, and numerous other families of shells. The majority are filter feeders and have no head or radula. The gills have evolved into ctenidia, specialised organs for feeding and breathing. Most bivalves bury themselves in sediment on the seabed, while others lie on the sea floor or attach themselves to rocks or other hard surfaces.

The shell of a bivalve is composed of calcium carbonate, and consists of two, usually similar, parts called valves. These are joined together along one edge by a flexible ligament that, in conjunction with interlocking “teeth” on each of the valves, forms the hinge.



Figure **33.1.7.1**: Empty shell of a bivalve: The empty shell of the giant clam, Tridacna gigas. Note the pair of shells that are hinged together, a characteristic of members of the class Bivalvia.

Class Gastropoda

Animals in class Gastropoda (“stomach foot”) include well-known mollusks like snails, slugs, conchs, sea hares, and sea butterflies. Gastropoda includes shell-bearing species as well as species with a reduced shell. These animals are asymmetrical and usually present a coiled shell. Shells may be planospiral (like a garden hose wound up), commonly seen in garden snails, or conispiral (like a spiral staircase), commonly seen in marine conches.

The visceral mass in the shelled species displays torsion around the perpendicular axis on the center of the foot, which is the key characteristic of this group, along with a foot that is modified for crawling. Most gastropods bear a head with tentacles, eyes, and a style. A complex radula is used by the digestive system and aids in the ingestion of food. Eyes may be absent in some gastropods species. The mantle cavity encloses the ctenidia (singluar: ctenidium) as well as a pair of nephridia (singular: nephridium).



Figure **33.1.7.1**: Gastropod foot: Gastropods, such as this Roman snail, have a large foot that is modified for crawling.

Class Cephalopoda

Class Cephalopoda (“head foot” animals) includes octopuses, squids, cuttlefish, and nautilus. Cephalopods are a class of shell-bearing animals as well as mollusks with a reduced shell. They display vivid coloration, typically seen in squids and octopuses which is used for camouflage. All animals in this class are carnivorous predators and have beak-like jaws at the anterior end. All cephalopods show the presence of a very well-developed nervous system along with eyes, as well as a closed circulatory system. The foot is lobed and developed into tentacles and a funnel, which is used as the mode of locomotion. Locomotion in cephalopods is facilitated by ejecting a stream of water for propulsion (“jet” propulsion). Cephalopods, such as squids and octopuses, also produce sepia or a dark ink, which is squirted upon a predator to assist in a quick getaway. Suckers are present on the tentacles in

octopuses and squid. Ctenidia are enclosed in a large mantle cavity serviced by blood vessels, each with its own associated heart. The mantle has siphonophores that facilitate exchange of water.



Figure **33.1.7.1**: Cephalopods: Cephalopods (“head foot”) include this octopus, which ejects a stream of water from a funnel in its body to propel itself through the water.

A pair of nephridia is present within the mantle cavity. Sexual dimorphism is seen in this class of animals. Members of a species mate, then the female lays the eggs in a secluded and protected niche. Females of some species care for the eggs for an extended period of time and may end up dying during that time period. Reproduction in cephalopods is different from other mollusks in that the egg hatches to produce a juvenile adult without undergoing the trochophore and veliger larval stages.

Class Scaphopoda

Members of class Scaphopoda (“boat feet”) are known colloquially as “tusk shells” or “tooth shells,” as evident when examining Dentalium, one of the few remaining scaphopod genera. Scaphopods are usually buried in sand with the anterior opening exposed to water. These animals bear a single conical shell, which has both ends open. The head is rudimentary and protrudes out of the posterior end of the shell. These animals do not possess eyes, but they have a radula, as well as a foot modified into tentacles with a bulbous end, known as captaculae. Captaculae serve to catch and manipulate prey. Ctenidia are absent in these animals.



Figure **33.1.7.1**: The Scaphopods: The Scaphopods (“boat feet”) include the Antalis vulgaris, the shell of which is depicted here.

Key Points

- Mollusks can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda. These classes are distinguished by, among other criteria, the presence and types of shells they possess.
- Class Aplacophora includes worm-like animals with no shell and a rudimentary body structure.
- Members of class Monoplacophora have a single shell that encloses the body.
- Members of class Polyplacophora are better known as “chitons;” these molluscs have a large foot on the ventral side and a shell composed of eight hard plates on the dorsal side.

- Class Bivalvia consists of mollusks with two shells held together by a muscle; these include oysters, clams, and mussels.
- Members of class Gastropoda have an asymmetrical body plan and usually have a shell, which can be planospiral or conispiral. Their key characteristic is the torsion around the perpendicular axis on the center of the foot that is modified for crawling.
- Class Scaphopoda consists of mollusks with a single conical shell through which the head protrudes, and a foot modified into tentacles known as captaculae that are used to catch and manipulate prey.

Key Terms

- **ctenidium**: a respiratory system, in the form of a comb, in some molluscs
- **captacula**: the foot of a Scaphalopod, modified into tentacles for capturing prey
- **nephridium**: a tubular excretory organ in some invertebrates

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33.1.8: Phylum Annelida

Learning Objectives

- Describe the morphological and anatomical features of annelids

Phylum Annelida

Phylum Annelida contains the class Polychaeta (the polychaetes) and the class Oligochaeta (the earthworms, leeches, and their relatives). These animals are found in marine, terrestrial, and freshwater habitats, but a presence of water or humidity is a critical factor for their survival, especially in terrestrial habitats. The name of the phylum is derived from the Latin word annellus, which means a small ring. Animals in this phylum show parasitic and commensal symbioses with other species in their habitat. Approximately 16,500 species have been described in phylum Annelida. The phylum includes earthworms, polychaete worms, and leeches. Annelids show protostomic development in embryonic stages and are often called “segmented worms” due to their key characteristic of metamerism, or true segmentation.

Morphology

Annelids display bilateral symmetry and are worm-like in overall morphology. They have a segmented body plan where the internal and external morphological features are repeated in each body segment. Metamerism allows animals to become bigger by adding “compartments,” while making their movement more efficient. This metamerism is thought to arise from identical teloblast cells in the embryonic stage, which develop into identical mesodermal structures. The overall body can be divided into head, body, and pygidium (or tail). The clitellum is a reproductive structure that generates mucus that aids in sperm transfer and gives rise to a cocoon within which fertilization occurs; it appears as a fused band in the anterior third of the animal.



Figure **33.1.8.1**: Clitellum: The clitellum is the reproductive structure of an annelid. It creates mucus that aids in sperm transfer and gives rise to a cocoon within which fertilization occurs. It can be seen in this image as the enlarged band around the animal.

Anatomy

The epidermis is protected by an acellular, external cuticle, but this is much thinner than the cuticle found in the ecdysozoans and does not require periodic shedding for growth. Circular as well as longitudinal muscles are located interior to the epidermis. Chitinous hairlike extensions, anchored in the epidermis and projecting from the cuticle, called setae/chaetae are present in every segment. Annelids show the presence of a true coelom, derived from embryonic mesoderm and protostomy. Hence, they are the most advanced worms. A well-developed and complete digestive system is present in earthworms (oligochaetes) with a mouth, muscular pharynx, esophagus, crop, and gizzard being present. The gizzard leads to the intestine and ends in an anal opening. Each segment is limited by a membranous septum that divides the coelomic cavity into a series of compartments.

Annelids possess a closed circulatory system of dorsal and ventral blood vessels that run parallel to the alimentary canal as well as capillaries that service individual tissues. In addition, these vessels are connected by transverse loops in every segment. These animals lack a well-developed respiratory system; gas exchange occurs across the moist body surface. Excretion is facilitated by a pair of metanephridia (a type of primitive “kidney” that consists of a convoluted tubule and an open, ciliated funnel) that is present in every segment towards the ventral side. Annelids show well-developed nervous systems with a nerve ring of fused ganglia present around the pharynx. The nerve cord is ventral in position, bearing enlarged nodes or ganglia in each segment.

Annelids may be either monoecious, with permanent gonads (as in earthworms and leeches), or dioecious, with temporary or seasonal gonads that develop (as in polychaetes). However, cross-fertilization is preferred in hermaphroditic animals. These animals may also show simultaneous hermaphroditism, participating in simultaneous sperm exchange when they are aligned for copulation.

Earthworms are the most abundant members of the class Oligochaeta, distinguished by the presence of the clitellum as well as few, reduced chaetae (“oligo- = “few”; -chaetae = “hairs”). The number and size of chaetae are greatly diminished in Oligochaeta compared to the polychaetes (poly=many, chaetae = hairs). The many chetae of polychaetes are also arranged within fleshy, flat, paired appendages that protrude from each segment. These parapodia may be specialized for different functions in the polychates. A significant difference between leeches and other annelids is the development of suckers at the anterior and posterior ends and an absence of chaetae. Additionally, the segmentation of the body wall may not correspond to the internal segmentation of the coelomic cavity. This adaptation possibly helps the leeches to elongate when they ingest copious quantities of blood from host vertebrates.



Figure **33.1.8.1**: Leeches: Unlike earthworms, leeches lack chaetae and have suckers at both ends of the body.

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Key Points

- Annelids are often called “segmented worms” because they possess true segmentation of their bodies, with both internal and external morphological features repeated in each body segment.
- The clitellum is a structure on the anterior portion of the worm that generates mucus to aid in sperm transfer from one worm to another; it also forms a cocoon within which fertilization occurs.
- Most annelids have chitinous hairlike extensions in every segment called chaetae that are anchored in the epidermis, although the number and size of chaetae can vary in the different classes.
- Annelids possess a closed circulatory system, lack a well-developed respiratory system, but have well-developed nervous systems.
- Annelids can either have distinct male and female forms or be hermaphrodites (having both male and female reproductive organs). Earthworms are hermaphrodites and can self-fertilize, but prefer to cross-fertilize if possible.

Key Terms

- **clitellum**: a glandular swelling in the epidermis of some annelid worms; it secretes a viscous fluid in which the eggs are deposited
- **chaeta**: a chitinous bristle of an annelid worm
- **metamerism**: the segmentation of the body into similar discrete units

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SECTION OVERVIEW

33.2: Flatworms (Platyhelminthes)

Topic hierarchy

33.2.1: Superphylum Lophotrochozoa

33.2.2: Phylum Platyhelminthes

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33.2.1: Superphylum Lophotrochozoa

Learning Objectives

- Describe the phylogenetic position and basic features of lophotrochozoa

Lophotrochozoans

Animals belonging to superphylum Lophotrochozoa are protostomes: the blastopore (or the point of involution of the ectoderm or outer germ layer) becomes the mouth opening to the alimentary canal. This is called protostomy or “first mouth.” In protostomy, solid groups of cells split from the endoderm or inner germ layer to form a central mesodermal layer of cells. This layer multiplies into a band which then splits internally to form the coelom; this protostomic coelom is termed schizocoelom.

As lophotrochozoans, the organisms in this superphylum possess either lophophore or trochophore larvae. The exact relationships between the different phyla are not entirely certain. The lophophores include groups that are united by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth. Lophophorata include the flatworms and several other phyla, including the Bryozoa, Entoprocta, Phoronida, and Brachiopoda. These clades are upheld when RNA sequences are compared. Trochophore larvae are characterized by two bands of cilia around the body. Previously, these were treated together as the Trochozoa, together with the arthropods, which do not produce trochophore larvae, but were considered close relatives of the annelids because they are both segmented. However, they show a number of important differences. Arthropods are now placed separately among the Ecdysozoa. The Trochozoa include the Nemertea, Mollusca, Sipuncula, and Annelida.

The lophotrochozoans are triploblastic, possessing an embryonic mesoderm sandwiched between the ectoderm and endoderm found in the diploblastic cnidarians. These phyla are also bilaterally symmetrical: a longitudinal section will divide them into right and left sides that are symmetrical. They also show the beginning of cephalization: the evolution of a concentration of nervous tissues and sensory organs in the head of the organism, which is where it first encounters its environment.

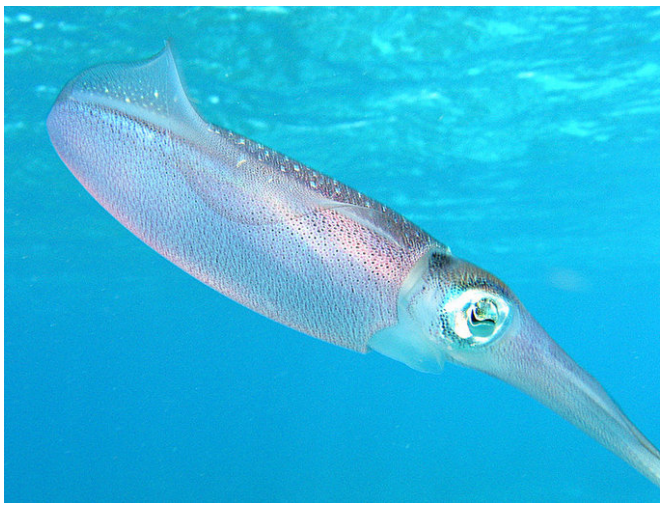


Figure **33.2.1.1**: Lophotrochozoans: The Caribbean Reef Squid or Sepioteuthis sepioidea is a complex lophotrochozoan. Species in this group have bilateral symmetry.

Key Points

- Lophotrochozoa have a blastopore, which is an involution of the ectoderm that forms a rudimentary mouth opening to the alimentary canal, a condition called protostomy or “first mouth”.
- The Lophotrochozoa are comprised of the trochozoans and the lophophorata, although the exact relationships between the different phyla are not clearly determined.
- Lophophores are characterized by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth; they include the flatworms and several other phyla whose relationships are upheld by genetic evidence.
- Trochophore larvae are distinguished from the lophophores by two bands of cilia around the body; they include the Nemertea, Mollusca, Sipuncula, and Annelida.

- The lophotrochozoans have a mesoderm layer positioned between the ectoderm and endoderm and are bilaterally symmetrical, which signals the beginning of cephalization, the concentration of nervous tissues and sensory organs in the head of the organism.

Key Terms

- **blastopore**: the opening into the archenteron
- **lophophore**: a feeding organ of brachiopods, bryozoans, and phoronids
- **cephalization**: an evolutionary trend in which the neural and sense organs become centralized at one end (the head) of an animal

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33.2.2: Phylum Platyhelminthes

Learning Objectives

- Differentiate among the classes of platyhelminthes

Phylum Platyhelminthes

Phylum Platyhelminthes is composed of the flatworms: acoelomate organisms that include many free-living and parasitic forms. Most of the flatworms are classified in the superphylum Lophotrochozoa, which also includes the mollusks and annelids. The Platyhelminthes consist of two lineages: the Catenulida and the Rhabditophora. The Catenulida, or “chain worms” is a small clade of just over 100 species. These worms typically reproduce asexually by budding. However, the offspring do not fully detach from the parents; therefore, they resemble a chain. The remaining flatworms discussed here are part of the Rhabditophora.

Many flatworms are parasitic, including important parasites of humans. Flatworms have three embryonic tissue layers that give rise to surfaces that cover tissues (from ectoderm), internal tissues (from mesoderm), and line the digestive system (from endoderm). The epidermal tissue is a single layer cells or a layer of fused cells (syncytium) that covers a layer of circular muscle above a layer of longitudinal muscle. The mesodermal tissues include mesenchymal cells that contain collagen and support secretory cells that secrete mucus and other materials at the surface. The flatworms are acoelomates: their bodies are solid between the outer surface and the cavity of the digestive system.

Physiological Processes of Flatworms

The free-living species of flatworms are predators or scavengers. Parasitic forms feed on the tissues of their hosts. Most flatworms have a gastrovascular cavity rather than a complete digestive system; in such animals, the “mouth” is also used to expel waste materials from the digestive system. Some species also have an anal opening. The gut may be a simple sac or highly branched. Digestion is extracellular, with digested materials taken in to the cells of the gut lining by phagocytosis. One group, the cestodes, lacks a digestive system. Flatworms have an excretory system with a network of tubules throughout the body with openings to the environment and nearby flame cells, whose cilia beat to direct waste fluids concentrated in the tubules out of the body. The system is responsible for the regulation of dissolved salts and the excretion of nitrogenous wastes. The nervous system consists of a pair of nerve cords running the length of the body with connections between them and a large ganglion or concentration of nerves at the anterior end of the worm, where there may also be a concentration of photosensory and chemosensory cells.

There is neither a circulatory nor respiratory system, with gas and nutrient exchange dependent on diffusion and cell-cell junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be “flat” worms. In addition, most flatworm species are monoecious; typically, fertilization is internal. Asexual reproduction is common in some groups.

Diversity of Flatworms

Platyhelminthes are traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda. The class Turbellaria includes mainly free-living, marine species, although some species live in freshwater or moist terrestrial environments. The ventral epidermis of turbellarians is ciliated which facilitates their locomotion. Some turbellarians are capable of remarkable feats of regeneration: they may regrow the entire body from a small fragment.



Figure **33.2.2.1**: Turbellaria: Pseudobiceros bedfordi (Bedford's Flatworm), a member of the Turbellaria, is a marine species which uses the epidermis of its belly for locomotion.

The monogeneans are ectoparasites, mostly of fish, with simple life cycles that consist of a free-swimming larva that attaches to a fish to begin transformation to the parasitic adult form. The worms may produce enzymes that digest the host tissues or simply graze on surface mucus and skin particles.

The trematodes, or flukes, are internal parasites of mollusks and many other groups, including humans. Trematodes have complex life cycles that involve a primary host in which sexual reproduction occurs and one or more secondary hosts in which asexual reproduction occurs. The primary host is almost always a mollusk. Trematodes are responsible for serious human diseases including schistosomiasis, a blood fluke.



Figure **33.2.2.1**: Trematodes: Botulus microporus is a trematode that lives only in the intestinal tract of Lancetfish, *Alepisaurus ferox*.

The cestodes, or tapeworms, are also internal parasites, mainly of vertebrates. Tapeworms live in the intestinal tract of the primary host, remaining fixed by using a sucker on the anterior end, or scolex, of the tapeworm body. The remainder of the tapeworm is composed of a long series of units called proglottids. Each may contain an excretory system with flame cells and both female and male reproductive structures. Tapeworms do not possess a digestive system; instead, they absorb nutrients from the food matter passing through them in the host's intestine.

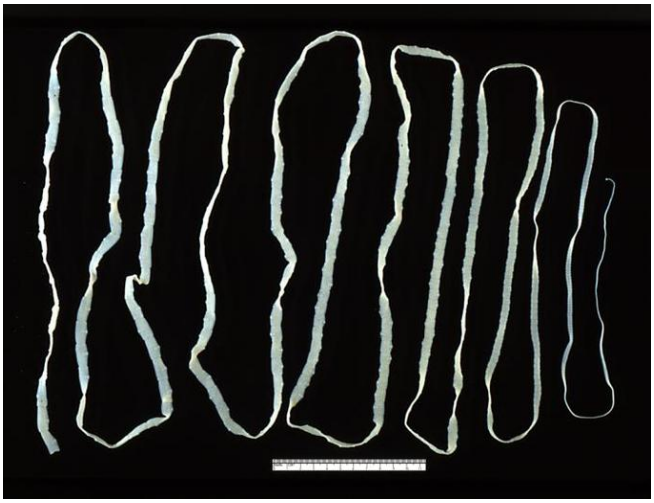


Figure **33.2.2.1**: Cestodes: Taenia saginata, also known as Taeniarhynchus saginata or the beef tapeworm, is a parasite of both cattle and humans. It displays the long series of proglottid subunits characteristic of the species.

Key Points

- The Platyhelminthes are acoelomate flatworms: their bodies are solid between the outer surface and the cavity of the digestive system.
- Most flatworms have a gastrovascular cavity rather than a complete digestive system; the same cavity used to bring in food is used to expel waste materials.
- Platyhelminthes are either predators or scavengers; many are parasites that feed on the tissues of their hosts.
- Flatworms posses a simple nervous system, no circulatory or respiratory system, and most produce both eggs and sperm, with internal fertilization.
- Platyhelminthes are divided into four classes: Turbellaria, free-living marine species; Monogenea, ectoparasites of fish; Trematoda, internal parasites of humans and other species; and Cestoda (tapeworms), which are internal parasites of many vertebrates.
- In flatworms, digested materials are taken into the cells of the gut lining by phagocytosis, rather than being processed internally.

Key Terms

- **acoelomate**: any animal without a coelom, or body cavity
- **ectoparasite**: a parasite that lives on the surface of a host organism
- **scolex**: the structure at the rear end of a tapeworm which, in the adult, has suckers and hooks by which it attaches itself to a host
- **proglottid**: any of the segments of a tapeworm; they contain both male and female reproductive organs

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SECTION OVERVIEW

33.3: Rotifers (Rotifera)

Topic hierarchy

33.3.1: Superphylum Lophotrochozoa

33.3.2: Phylum Rotifera

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33.3.1: Superphylum Lophotrochozoa

Learning Objectives

- Describe the phylogenetic position and basic features of lophotrochozoa

Lophotrochozoans

Animals belonging to superphylum Lophotrochozoa are protostomes: the blastopore (or the point of involution of the ectoderm or outer germ layer) becomes the mouth opening to the alimentary canal. This is called protostomy or “first mouth.” In protostomy, solid groups of cells split from the endoderm or inner germ layer to form a central mesodermal layer of cells. This layer multiplies into a band which then splits internally to form the coelom; this protostomic coelom is termed schizocoelom.

As lophotrochozoans, the organisms in this superphylum possess either lophophore or trochophore larvae. The exact relationships between the different phyla are not entirely certain. The lophophores include groups that are united by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth. Lophophorata include the flatworms and several other phyla, including the Bryozoa, Entoprocta, Phoronida, and Brachiopoda. These clades are upheld when RNA sequences are compared. Trochophore larvae are characterized by two bands of cilia around the body. Previously, these were treated together as the Trochozoa, together with the arthropods, which do not produce trochophore larvae, but were considered close relatives of the annelids because they are both segmented. However, they show a number of important differences. Arthropods are now placed separately among the Ecdysozoa. The Trochozoa include the Nemertea, Mollusca, Sipuncula, and Annelida.

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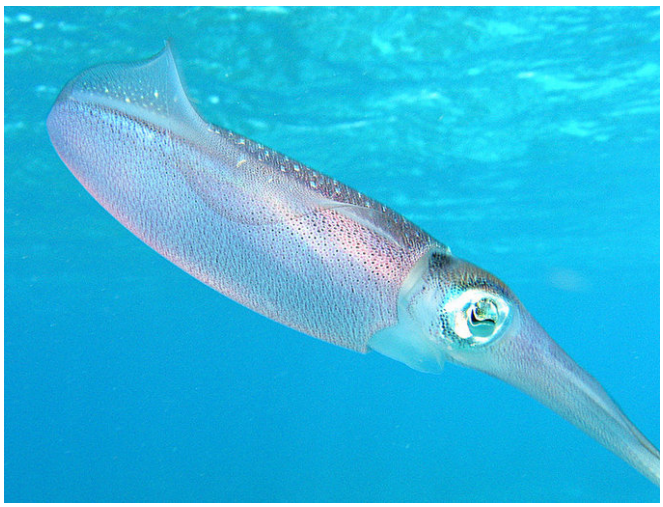


Figure **33.3.1.1**: Lophotrochozoans: The Caribbean Reef Squid or Sepioteuthis sepioidea is a complex lophotrochozoan. Species in this group have bilateral symmetry.

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- **cephalization**: an evolutionary trend in which the neural and sense organs become centralized at one end (the head) of an animal

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33.3.2: Phylum Rotifera

Learning Objectives

- Identify the features of rotifers involved in movement and feeding

Phylum Rotifera

The rotifers are a microscopic (about 100 µm to 30 mm) group of mostly-aquatic organisms that get their name from the corona: a rotating, wheel-like structure that is covered with cilia at their anterior end. Although their taxonomy is currently in flux, one treatment places the rotifers in three classes: Bdelloidea, Monogononta, and Seisonidea. The classification of the group is currently under revision, however, as more phylogenetic evidence becomes available. It is possible that the "spiny headed worms" currently in phylum Acanthocephala will be incorporated into this group in the future.



Figure **33.3.2.1**: Rotifers: A bdelloid rotifer is a member of a class of rotifers found in fresh water and moist soil. The rotifer body consists of a head, a truck, and a foot. They eat by filtering food into the mouth by creating currents with the corona.

The rotifer body form consists of a head (which contains the corona), a trunk (which contains the organs), and the foot. Rotifers are typically free-swimming and truly planktonic organisms, but the toes or extensions of the foot can secrete a sticky material forming a holdfast to help them adhere to surfaces. The head contains sensory organs in the form of a bi-lobed brain and small eyespots near the corona.

The rotifers are filter feeders that will eat dead material, algae, and other microscopic living organisms. Therefore, they are very important components of aquatic food webs. Rotifers obtain food that is directed toward the mouth by the current created from the movement of the corona. The food particles enter the mouth and travel to the mastax (pharynx with jaw-like structures). Food passes by digestive and salivary glands into the stomach and then into the intestines. Digestive and excretory wastes are collected in a cloacal bladder before being released out the anus.

Rotifers are pseudocoelomates commonly found in fresh water and some salt water environments throughout the world. About 2,200 species of rotifers have been identified. Rotifers are dioecious organisms (having either male or female genitalia) and exhibit sexual dimorphism (males and females have different forms). Many species are parthenogenic and exhibit haplodiploidy, a method of gender determination in which a fertilized egg develops into a female and an unfertilized egg develops into a male. In many dioecious species, males are short-lived and smaller, with no digestive system and a single testis. Females can produce eggs that are capable of dormancy, which protects eggs during harsh environmental conditions.

Key Points

- The rotifer body form consists of a head (containing the sensory organs in the form of a bi-lobed brain and small eyespots near the corona), the trunk (containing organs), and the foot (which can hold fast).
- The foot of the rotifer secretes a sticky material to help it adhere to surfaces.

- Rotifers are filter feeders that generate a current using the corona to pass food into the mouth, which then passes by digestive and salivary glands into the stomach and intestines.
- Rotifers exhibit sexual dimorphism; the gender of many species is determined by whether the egg is fertilized (and develops into a female) or unfertilized (and develops into a male).

Key Terms

- **pseudocoelomate**: any invertebrate animal with a three-layered body and a pseudocoel
- **mastax**: the pharynx of a rotifer which usually contains four horny pieces that work to crush the food

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SECTION OVERVIEW

33.4: Mollusks (Mollusca)

Topic hierarchy

33.4.1: Phylum Mollusca

33.4.2: Classification of Phylum Mollusca

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33.4.1: Phylum Mollusca

Learning Objectives

- Describe the unique anatomical and morphological features of molluscs

Phylum Mollusca

Phylum Mollusca is the predominant phylum in marine environments. It is estimated that 23 percent of all known marine species are mollusks; there are around 85,000 described species, making them the second most diverse phylum of animals. The name “mollusca” signifies a soft body; the earliest descriptions of mollusks came from observations of unshelled cuttlefish. Mollusks are predominantly a marine group of animals; however, they are known to inhabit freshwater as well as terrestrial habitats. Mollusks display a wide range of morphologies in each class and subclass. They range from large predatory squids and octopus, some of which show a high degree of intelligence, to grazing forms with elaborately-sculpted and colored shells. In spite of their tremendous diversity, however, they also share a few key characteristics, including a muscular foot, a visceral mass containing internal organs, and a mantle that may or may not secrete a shell of calcium carbonate.



Figure **33.4.1.1**: Mollusk shells: Helix aspersa, a common land snail, has a calcium carbonate shell.

Mollusks have a muscular foot used for locomotion and anchorage that varies in shape and function, depending on the type of mollusk under study. In shelled mollusks, this foot is usually the same size as the opening of the shell. The foot is a retractable as well as an extendable organ. It is the ventral-most organ, whereas the mantle is the limiting dorsal organ. Mollusks are eucoelomate, but the cavity is restricted to a region around the heart in adult animals. The mantle cavity develops independently of the coelomic cavity.

The visceral mass is present above the foot in the visceral hump. This includes digestive, nervous, excretory, reproductive, and respiratory systems. Mollusk species that are exclusively aquatic have gills for respiration, whereas some terrestrial species have lungs for respiration. Additionally, a tongue-like organ called a radula, which bears chitinous tooth-like ornamentation, is present in many species, serving to shred or scrape food. The mantle (also known as the pallium) is the dorsal epidermis in mollusks; shelled mollusks are specialized to secrete a chitinous and hard calcareous shell.

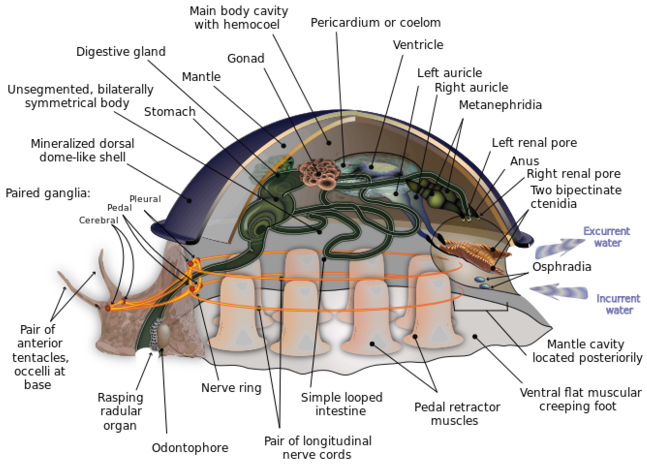


Figure **33.4.1.1**: A “generalized mollusk”: An anatomical diagram of a hypothetical ancestral mollusk, showing features common to many mollusk types.

Most mollusks are dioecious animals where fertilization occurs externally, although this is not the case in terrestrial mollusks, such as snails and slugs, or in cephalopods. In some mollusks, the zygote hatches and undergoes two larval stages, trochophore and veliger, before becoming a young adult; bivalves may exhibit a third larval stage, glochidia.

Key Points

- A mollusk’s muscular foot is used for locomotion and anchorage, varies in shape and function, and can both extend and retract.
- The visceral mass inside the mollusk includes digestive, nervous, excretory, reproductive, and respiratory systems.
- Most mollusks possess a radula, which is similar to a tongue with teeth-like projections, serving to shred or scrape food.
- The mantle is the dorsal epidermis in mollusks; in some mollusks it secretes a chitinous and hard calcareous shell.

Key Terms

- **visceral mass**: the soft, non-muscular metabolic region of the mollusc that contains the body organs
- **mantle**: the body wall of a mollusc, from which the shell is secreted
- **radula**: the rasping tongue of snails and most other mollusks

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33.4.2: Classification of Phylum Mollusca

Learning Objectives

- Differentiate among the classes in the phylum mollusca

Classes in Phylum Mollusca

Phylum Mollusca is a very diverse (85,000 species) group of mostly marine species, with a dramatic variety of form. This phylum can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda.

Class Aplacophora

Class Aplacophora ("bearing no plates") includes worm-like animals primarily found in benthic marine habitats. These animals lack a calcareous shell, but possess aragonite spicules on their epidermis. They have a rudimentary mantle cavity and lack eyes, tentacles, and nephridia (excretory organs).

Class Monoplacophora

Members of class Monoplacophora ("bearing one plate") posses a single, cap-like shell that encloses the body. The morphology of the shell and the underlying animal can vary from circular to ovate. A looped digestive system, multiple pairs of excretory organs, many gills, and a pair of gonads are present in these animals. The monoplacophorans were believed extinct and only known via fossil records until the discovery of Neopilina galathaea in 1952. Today, scientists have identified nearly two dozen extant species.

Class Polyplacophora

Animals in the class Polyplacophora ("bearing many plates") are commonly known as "chitons" and bear an armor-like, eight-plated dorsal shell. These animals have a broad, ventral foot that is adapted for suction to rocks and other substrates, and a mantle that extends beyond the shell in the form of a girdle. Calcareous spines may be present on the girdle to offer protection from predators. Chitons live worldwide, in cold water, warm water, and the tropics. Most chiton species inhabit intertidal or subtidal zones, and do not extend beyond the photic zone. Some species live quite high in the intertidal zone and are exposed to the air and light for long periods.



Figure **33.4.2.1**: Chiton morphology: The underside of the gumboot chiton, Cryptochiton stellari, showing the foot in the center, surrounded by the gills and mantle. The mouth is visible to the left in this image.

Class Bivalvia

Bivalvia is a class of marine and freshwater molluscs with laterally compressed bodies enclosed by a shell in two hinged parts. Bivalves include clams, oysters, mussels, scallops, and numerous other families of shells. The majority are filter feeders and have no head or radula. The gills have evolved into ctenidia, specialised organs for feeding and breathing. Most bivalves bury themselves in sediment on the seabed, while others lie on the sea floor or attach themselves to rocks or other hard surfaces.

The shell of a bivalve is composed of calcium carbonate, and consists of two, usually similar, parts called valves. These are joined together along one edge by a flexible ligament that, in conjunction with interlocking “teeth” on each of the valves, forms the hinge.



Figure **33.4.2.1**: Empty shell of a bivalve: The empty shell of the giant clam, Tridacna gigas. Note the pair of shells that are hinged together, a characteristic of members of the class Bivalvia.

Class Gastropoda

Animals in class Gastropoda (“stomach foot”) include well-known mollusks like snails, slugs, conchs, sea hares, and sea butterflies. Gastropoda includes shell-bearing species as well as species with a reduced shell. These animals are asymmetrical and usually present a coiled shell. Shells may be planospiral (like a garden hose wound up), commonly seen in garden snails, or conispiral (like a spiral staircase), commonly seen in marine conches.

The visceral mass in the shelled species displays torsion around the perpendicular axis on the center of the foot, which is the key characteristic of this group, along with a foot that is modified for crawling. Most gastropods bear a head with tentacles, eyes, and a style. A complex radula is used by the digestive system and aids in the ingestion of food. Eyes may be absent in some gastropods species. The mantle cavity encloses the ctenidia (singluar: ctenidium) as well as a pair of nephridia (singular: nephridium).



Figure **33.4.2.1**: Gastropod foot: Gastropods, such as this Roman snail, have a large foot that is modified for crawling.

Class Cephalopoda

Class Cephalopoda (“head foot” animals) includes octopuses, squids, cuttlefish, and nautilus. Cephalopods are a class of shell-bearing animals as well as mollusks with a reduced shell. They display vivid coloration, typically seen in squids and octopuses which is used for camouflage. All animals in this class are carnivorous predators and have beak-like jaws at the anterior end. All cephalopods show the presence of a very well-developed nervous system along with eyes, as well as a closed circulatory system. The foot is lobed and developed into tentacles and a funnel, which is used as the mode of locomotion. Locomotion in cephalopods is facilitated by ejecting a stream of water for propulsion (“jet” propulsion). Cephalopods, such as squids and octopuses, also produce sepia or a dark ink, which is squirted upon a predator to assist in a quick getaway. Suckers are present on the tentacles in

octopuses and squid. Ctenidia are enclosed in a large mantle cavity serviced by blood vessels, each with its own associated heart. The mantle has siphonophores that facilitate exchange of water.



Figure **33.4.2.1**: Cephalopods: Cephalopods (“head foot”) include this octopus, which ejects a stream of water from a funnel in its body to propel itself through the water.

A pair of nephridia is present within the mantle cavity. Sexual dimorphism is seen in this class of animals. Members of a species mate, then the female lays the eggs in a secluded and protected niche. Females of some species care for the eggs for an extended period of time and may end up dying during that time period. Reproduction in cephalopods is different from other mollusks in that the egg hatches to produce a juvenile adult without undergoing the trochophore and veliger larval stages.

Class Scaphopoda

Members of class Scaphopoda (“boat feet”) are known colloquially as “tusk shells” or “tooth shells,” as evident when examining Dentalium, one of the few remaining scaphopod genera. Scaphopods are usually buried in sand with the anterior opening exposed to water. These animals bear a single conical shell, which has both ends open. The head is rudimentary and protrudes out of the posterior end of the shell. These animals do not possess eyes, but they have a radula, as well as a foot modified into tentacles with a bulbous end, known as captaculae. Captaculae serve to catch and manipulate prey. Ctenidia are absent in these animals.



Figure **33.4.2.1**: The Scaphopods: The Scaphopods (“boat feet”) include the Antalis vulgaris, the shell of which is depicted here.

Key Points

- Mollusks can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda. These classes are distinguished by, among other criteria, the presence and types of shells they possess.
- Class Aplacophora includes worm-like animals with no shell and a rudimentary body structure.
- Members of class Monoplacophora have a single shell that encloses the body.
- Members of class Polyplacophora are better known as “chitons;” these molluscs have a large foot on the ventral side and a shell composed of eight hard plates on the dorsal side.

- Class Bivalvia consists of mollusks with two shells held together by a muscle; these include oysters, clams, and mussels.
- Members of class Gastropoda have an asymmetrical body plan and usually have a shell, which can be planospiral or conispiral. Their key characteristic is the torsion around the perpendicular axis on the center of the foot that is modified for crawling.
- Class Scaphopoda consists of mollusks with a single conical shell through which the head protrudes, and a foot modified into tentacles known as captaculae that are used to catch and manipulate prey.

Key Terms

- **ctenidium**: a respiratory system, in the form of a comb, in some molluscs
- **captacula**: the foot of a Scaphalopod, modified into tentacles for capturing prey
- **nephridium**: a tubular excretory organ in some invertebrates

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33.5: Ribbon Worms (Nemertea)

Learning Objectives

- Identify the key features of the Phylum Nemertea

Phylum Nemertea

The Nemertea are colloquially known as ribbon worms. Most species of phylum Nemertea are marine (predominantly benthic or bottom dwellers) with an estimated 900 species known. However, nemertini have been recorded in freshwater and terrestrial habitats as well. Most nemerteans are carnivores, feeding on worms, clams, and crustaceans. Some species are scavengers, while other nemertini species, such as *Malacobdella grossa*, have also evolved commensalistic relationships with some mollusks. Interestingly, nemerteans have almost no predators, two species are sold as fish bait, and some species have devastated commercial fishing of clams and crabs.

Morphology

Ribbon worms vary in size from 1 cm to several meters. They show bilateral symmetry and remarkable contractile properties. Because of their contractility, they can change their morphological presentation in response to environmental cues. Animals in phylum Nemertea also show a flattened morphology: they are flat from front to back, like a flattened tube. In addition, nemertea are soft, unsegmented animals.



Figure **33.5.1**: Morphology of Nemertea: A terrestrial Geonemertes, a Nemertean, displaying the flat, ribbon-like body of the organism that is unsegmented.

A unique characteristic of this phylum is the presence of a proboscis enclosed in a rhynchocoel. The proboscis serves to capture food and may be ornamented with barbs in some species. The rhynchocoel is a fluid-filled cavity that extends from the head to nearly two-thirds of the length of the gut in these animals. The proboscis may be extended or retracted by the retractor muscle attached to the wall of the rhynchocoel.

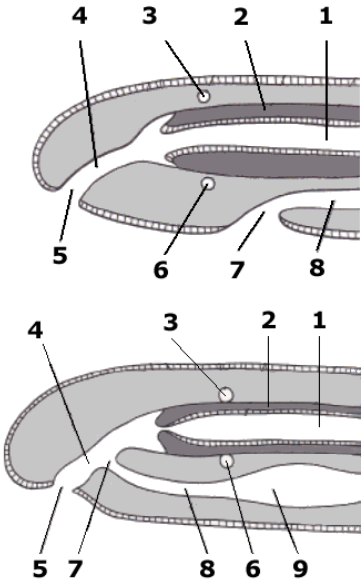


Figure **33.5.1**: Internal structures of the Nemertini: This image shows the internal structures of a basic nemertean, including the proboscis and the rhynchocoel: 1: Proboscis 2: Rhynchocoel 3: Dorsal commissure of brain 4: Rhynchodeum 5: Proboscis pore 6: Ventral commissure of brain 7: Mouth 8: Foregut 9: Stomach

Metabolism

The nemertini show a very well-developed digestive system. A mouth opening that is ventral to the rhynchocoel leads into the foregut, followed by the intestine. The intestine is present in the form of diverticular pouches which ends in a rectum that opens via an anus. Gonads are interspersed with the intestinal diverticular pouches, opening outwards via genital pores. A circulatory system consists of a closed loop of a pair of lateral blood vessels. The circulatory system is derived from the coelomic cavity of the embryo. Some animals may also have cross-connecting vessels in addition to lateral ones. Although these are called blood vessels, since they are of coelomic origin, the circulatory fluid is colorless. Some species bear hemoglobin as well as yellow or green pigments. The blood vessels are connected to the rhynchocoel. The flow of fluid in these vessels is facilitated by the contraction of muscles in the body wall. A pair of protonephridia, or primitive kidneys, is present in these animals to facilitate osmoregulation. Gaseous exchange occurs through the skin in the nemertini.

Nervous System

Nemertini have a ganglion or “brain” situated at the anterior end between the mouth and the foregut, surrounding the digestive system as well as the rhynchocoel. A ring of four nerve masses called “ganglia” comprises the brain in these animals. Paired longitudinal nerve cords emerge from the brain ganglia, extending to the posterior end. Ocelli or eyespots are present in pairs, in multiples of two in the anterior portion of the body. It is speculated that the eyespots originate from neural tissue and not from the epidermis.

Reproduction

Animals in phylum Nemertea show sexual dimorphism, although freshwater species may be hermaphroditic. Eggs and sperm are released into the water; fertilization occurs externally. The zygote develops into a special kind of nemertean larvae called a planuliform larva. In some nemertine species, another larva specific to the nemertinis, a pilidium, may develop inside the young worm from a series of imaginal discs. This larval form, characteristically shaped like a deerstalker cap, devours tissues from the young worm for survival before metamorphosing into the adult-like morphology.

Key Points

- The Nemertini are mostly bottom-dwelling marine organisms, although some are found in freshwater and terrestrial habitats.
- Most nemerteans are carnivores, some are scavengers, and others have evolved relationships with some mollusks that are benefit the Nemertean but do not harm the mollusk.

- Nemerteans vary greatly in size and are bilaterally symmetrical; they are unsegmented and resemble a flat tube which can change morphological presentation in response to environmental cues.
- Nemertini have a simple nervous system comprised of a ring of four nerve masses called “ganglia” at the anterior end between the mouth and the foregut from which paired longitudinal nerve cords emerge and extend to the posterior end.
- Nemertini are mostly sexually dimorphic, fertilizing eggs externally by releasing both eggs and sperm into the water; a larva may develop inside the resulting young worm and devour its tissues before metamorphosing into the adult.

Key Terms

- **protonephridia**: an invertebrate organ which occurs in pairs and removes metabolic wastes from an animal’s body
- **rhynchocoel**: a cavity which mostly runs above the midline and ends a little short of the rear of the body of a nemertean and extends or retracts the proboscis
- **proboscis**: an elongated tube from the head or connected to the mouth, of an animal

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33.6: Annelids (Annelida)

Learning Objectives

- Describe the morphological and anatomical features of annelids

Phylum Annelida

Phylum Annelida contains the class Polychaeta (the polychaetes) and the class Oligochaeta (the earthworms, leeches, and their relatives). These animals are found in marine, terrestrial, and freshwater habitats, but a presence of water or humidity is a critical factor for their survival, especially in terrestrial habitats. The name of the phylum is derived from the Latin word annellus, which means a small ring. Animals in this phylum show parasitic and commensal symbioses with other species in their habitat. Approximately 16,500 species have been described in phylum Annelida. The phylum includes earthworms, polychaete worms, and leeches. Annelids show protostomic development in embryonic stages and are often called “segmented worms” due to their key characteristic of metamerism, or true segmentation.

Morphology

Annelids display bilateral symmetry and are worm-like in overall morphology. They have a segmented body plan where the internal and external morphological features are repeated in each body segment. Metamerism allows animals to become bigger by adding “compartments,” while making their movement more efficient. This metamerism is thought to arise from identical teloblast cells in the embryonic stage, which develop into identical mesodermal structures. The overall body can be divided into head, body, and pygidium (or tail). The clitellum is a reproductive structure that generates mucus that aids in sperm transfer and gives rise to a cocoon within which fertilization occurs; it appears as a fused band in the anterior third of the animal.



Figure **33.6.1**: Clitellum: The clitellum is the reproductive structure of an annelid. It creates mucus that aids in sperm transfer and gives rise to a cocoon within which fertilization occurs. It can be seen in this image as the enlarged band around the animal.

Anatomy

The epidermis is protected by an acellular, external cuticle, but this is much thinner than the cuticle found in the ecdysozoans and does not require periodic shedding for growth. Circular as well as longitudinal muscles are located interior to the epidermis. Chitinous hairlike extensions, anchored in the epidermis and projecting from the cuticle, called setae/chaetae are present in every segment. Annelids show the presence of a true coelom, derived from embryonic mesoderm and protostomy. Hence, they are the most advanced worms. A well-developed and complete digestive system is present in earthworms (oligochaetes) with a mouth, muscular pharynx, esophagus, crop, and gizzard being present. The gizzard leads to the intestine and ends in an anal opening. Each segment is limited by a membranous septum that divides the coelomic cavity into a series of compartments.

Annelids possess a closed circulatory system of dorsal and ventral blood vessels that run parallel to the alimentary canal as well as capillaries that service individual tissues. In addition, these vessels are connected by transverse loops in every segment. These animals lack a well-developed respiratory system; gas exchange occurs across the moist body surface. Excretion is facilitated by a pair of metanephridia (a type of primitive “kidney” that consists of a convoluted tubule and an open, ciliated funnel) that is present in every segment towards the ventral side. Annelids show well-developed nervous systems with a nerve ring of fused ganglia present around the pharynx. The nerve cord is ventral in position, bearing enlarged nodes or ganglia in each segment.

Annelids may be either monoecious, with permanent gonads (as in earthworms and leeches), or dioecious, with temporary or seasonal gonads that develop (as in polychaetes). However, cross-fertilization is preferred in hermaphroditic animals. These animals may also show simultaneous hermaphroditism, participating in simultaneous sperm exchange when they are aligned for copulation.

Earthworms are the most abundant members of the class Oligochaeta, distinguished by the presence of the clitellum as well as few, reduced chaetae (“oligo- = “few”; -chaetae = “hairs”). The number and size of chaetae are greatly diminished in Oligochaeta compared to the polychaetes (poly=many, chaetae = hairs). The many chetae of polychaetes are also arranged within fleshy, flat, paired appendages that protrude from each segment. These parapodia may be specialized for different functions in the polychates. A significant difference between leeches and other annelids is the development of suckers at the anterior and posterior ends and an absence of chaetae. Additionally, the segmentation of the body wall may not correspond to the internal segmentation of the coelomic cavity. This adaptation possibly helps the leeches to elongate when they ingest copious quantities of blood from host vertebrates.



Figure **33.6.1**: Leeches: Unlike earthworms, leeches lack chaetae and have suckers at both ends of the body.

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Key Points

- Annelids are often called “segmented worms” because they possess true segmentation of their bodies, with both internal and external morphological features repeated in each body segment.
- The clitellum is a structure on the anterior portion of the worm that generates mucus to aid in sperm transfer from one worm to another; it also forms a cocoon within which fertilization occurs.
- Most annelids have chitinous hairlike extensions in every segment called chaetae that are anchored in the epidermis, although the number and size of chaetae can vary in the different classes.
- Annelids possess a closed circulatory system, lack a well-developed respiratory system, but have well-developed nervous systems.
- Annelids can either have distinct male and female forms or be hermaphrodites (having both male and female reproductive organs). Earthworms are hermaphrodites and can self-fertilize, but prefer to cross-fertilize if possible.

Key Terms

- **clitellum**: a glandular swelling in the epidermis of some annelid worms; it secretes a viscous fluid in which the eggs are deposited
- **chaeta**: a chitinous bristle of an annelid worm
- **metamerism**: the segmentation of the body into similar discrete units

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33.7: Bryozoans (Bryozoa) and Brachiopods (Brachiopoda)

Phylum Bryozoa

Bryozoa, also known as **Ectoprocta,** is a major invertebrate phylum, whose members, the **bryozoans,** are tiny, aquatic, and mostly sessile and colonial animals. Also known as **moss animals** or **sea mats,** the colonial species of bryozoans generally build collective stony skeletons of calcium carbonate that are superficially similar to coral.

Bryozoans have a distinctive feeding organ called a lophophore found only in two other animal phyla, Phoronida (phoronid worms) and Brachiopoda (lamp shells). Characterized by some as a "crown" of ciliated tentacles, the lophophore is essentially a tentacle-bearing ribbon or string that is an extension (either horseshoe-shaped or circular) surrounding the mouth.

Tiny as individuals, but clearly visible and significant in their large colonies, bryozoans play an important role in sediment stabilization and binding, as well as key roles in food chains, consuming microorganisms and in turn being prey for fish and other animals. Their bi-level functionality is apparent in the food chain where their harvesting of phytoplankton as a source of nutrition for their own maintenance, growth, and multiplication makes the nutrients from the phytoplankton available also to those fish and other animals that prey on the bryozoans. Additionally, while building their colonial structures in which they thrive, the byozoans serve the larger ecosystem by stabilizing sediments.

Bryozoans are found in marine, freshwater, and brackish environments. They generally prefer warm, tropical waters but are known to occur worldwide. There are about 5,000 living species, with several times that number of fossil forms known. Fossils are known from the early Ordovician period about 500 million years ago (mya).

Ecology

Although most species of Bryozoa live in marine environments, about 50 species inhabit freshwater. Some marine colonies have been found at 8,200 meters below the surface, but most bryozoans inhabit shallower water (Waggoner and Collins 1999).

Bryozoans attach to a variety of solid substrates, including rocks, shells, wood, sand grains, and blades of kelp, although some colonies form on sediment (Waggoner and Collins 1999). Bryozoan colonies also encrust pipes and ships, becoming a nuisance. Freshwater bryozoans may attach to tree roots and aquatic plants.

Most extant (living) bryozoans are typically immobile, sessile, and colonial. Nonetheless, whether there are one or a few exceptions, bryozoans are characteristically colony-forming animals. Many millions of individuals can form one colony. The colonies range from millimeters to meters in size, but the individuals that make up the colonies are tiny, usually less than a millimeter long. In each colony, different individuals assume different functions. Some individuals (the autozooids) gather up the food for the colony, while others (the heterozooids) depend on them for food and contribute to the colony in other ways. Some individuals (the kenozooids) are devoted to strengthening the colony and still others (the vibracula) to cleaning the colony.

Bryozoans are suspension feeders, preying on phytoplankton, including diatoms and unicellular algae and being preyed upon by fish and sea urchins (Waggoner and Collins, 1999).

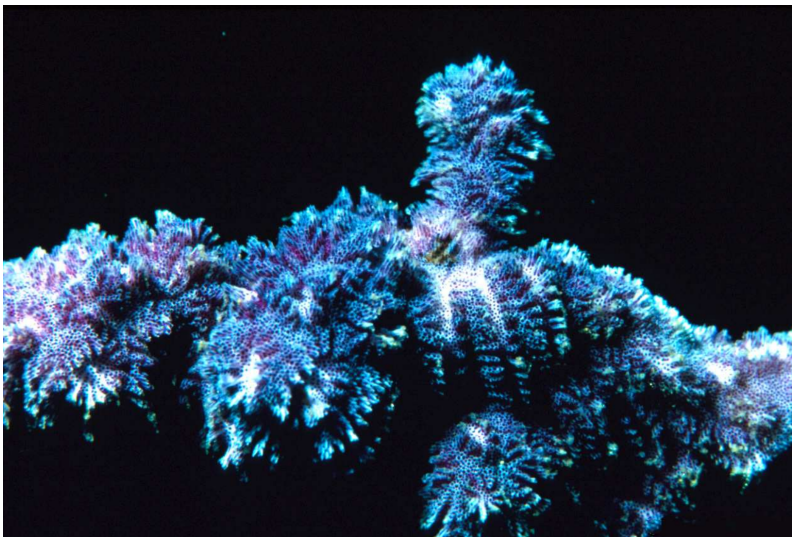


Figure **33.7.1**: *Costazia costazi*, a coralline bryozoan.. (CC-BY Wikipedia Katya Swarts)

Bryozoan "skeletons" are a collective production growing in a variety of shapes and patterns: Mound-shaped, lacy fans, branching twigs, and even corkscrew-shaped. Their "skeletons" have numerous tiny openings, each of which is the home of a minute animal called a *zooid*.

Each bryozoan zooid has a coelomate body (having a true body cavity) with a looped alimentary canal or gut, opening at the mouth and terminating at the anus.

Bryozoans feed with a specialized structure called a lophophore, which looks like a "crown" of tentacles and has been more precisely characterized as essentially a tentacle-bearing ribbon or string in the shape of a horseshoe or closed ring surrounding the mouth (Smithsonian 2007; Luria et al. 1981). Bryozoans have no defined respiratory or circulatory systems due to their small size. They do, however, have a hydrostatic skeletal system and a simple nervous system.

The tentacles of the bryozoans are ciliated, and the beating of the cilia creates a powerful current of water that drives water, together with entrained food particles (mainly phytoplankton), toward the mouth. The digestive system has a U-shaped gut, and comprises a pharynx, which passes into the esophagus, followed by the stomach. The stomach has three parts: the cardia, the caecum, and the pylorus. The pylorus leads to an intestine and a short rectum terminating at the anus, which opens outside the lophophore. In some groups among the bryozoa, notably some members of the bryozoan order ctenostome, a specialized gizzard may be formed from the proximal part of the cardia.

The gut and lophophore, which comprise most of the organs and tissues of an individual zooid, are also the principal components of what is called the "polypide." Cyclical degeneration and regeneration of the polypide is characteristic of marine bryozoans. After the final cycle of polypide degeneration and regeneration, the skeletal aperture of the feeding zooid may become sealed by the secretion of a terminal diaphragm. In many bryozoan colonies, only the zooids within a few generations of the growing edge are in an actively feeding state; older, more proximal zooids (for example, in the interiors of bushy colonies) are usually dormant. Gaseous exchange occurs across the entire surface of the body, but particularly through the tentacles of the lophophore.

Bryozoans can reproduce both sexually and asexually. All freshwater bryozoans, as far as is known, are hermaphroditic (meaning they are both male and female), and most marine bryozoans as well (Smithsonian 2007). They may produce sperm and eggs at the same time (simultanenous hermaphrodites), or the male sexual organs may mature before the female organs (protandric hermaphrodites).

Asexual reproduction occurs by budding off new zooids as the colony grows, and is the main way by which a colony expands in size. If a piece of a bryozoan colony breaks off, the piece can continue to grow and will form a new colony. A colony formed in this way is composed entirely of clones (genetically identical individuals) of the first animal, which is called the *ancestrula*.

Distinguishing features of Bryozoans, and **B**rachiopods

Bryozoans, and brachiopods strain food out of the water by means of a lophophore, a "crown" of hollow tentacles. Bryozoans form colonies consisting of clones called zooids. Brachiopods, generally thought to be closely related to bryozoans and phoronids, are distinguished by having shells rather like those of bivalves. All three of these phyla have a coelom, an internal cavity lined by mesothelium. Some encrusting bryozoan colonies with mineralized exoseletons look very like small corals. However, bryozoan colonies are founded by an ancestrula, which is round rather than shaped like a normal zooid of that species.

Phylum Brachiopoda

Brachiopods are shelled, filter-feeding marine organisms (Figure **33.7.2**) that inhabit the seafloor and come in various shapes and sizes. They have been around since the Cambrian with incredible diversity during the Paleozoic Era

(Figure **33.7.3**). Brachiopods are still around today, but their diversity is greatly diminished.



Figure **33.7.2** – Examples of brachiopods. Image credit: Digital Atlas of Ancient Life, CC BY-NC-SA.

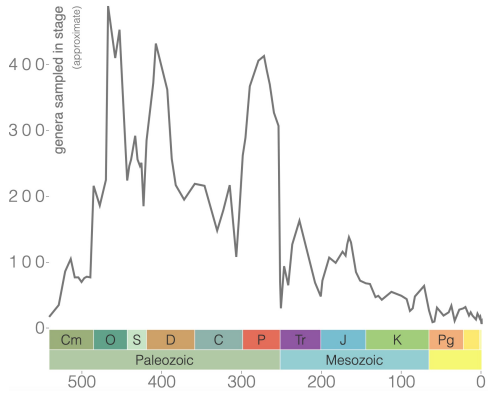


Figure **33.7.3** – Diversity of Brachiopoda genera. Image credit: Paleobiology Database, CC BY.

Superficially, brachiopods may look like bivalves, but the two are not related. One of the biggest differences between brachiopods and bivalves lies in their symmetry. Both have bilateral symmetry, but the plane of symmetry in brachiopods is vertical rather than horizontal (Figure **33.7.3**). This means that the left half of a brachiopod is a mirror image to the right half. In bivalves, the plane of symmetry is horizontal, and the upper half is a mirror image of the lower half.



Figure **33.7.4** – Differences in symmetries between a brachiopod (left) and a bivalve (right). Image credit: Jaleigh Q. Pier, CC BY-SA.

Brachiopod shells have two valves that are distinct in both size and shape (Figure **33.7.5**). The brachial valve is usually the smaller of the two valves and has a ridge, or fold, down the middle of the valve. The pedicle valve is usually larger than the brachial valve and has a valley down the middle. It also has a hole through which the pedicle passes. The pedicle is a fleshy, stalk-like feature which some groups use to attach themselves to hard rocky seafloor. It is rarely preserved, but brachiopod shells will often have a pedicle opening preserved along the hinge-line that varies in shape from rounded to triangular.

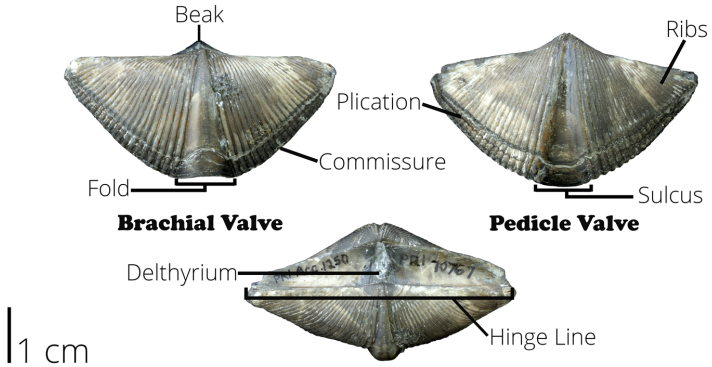


Figure **33.7.5** – Brachiopod morphology. Image credit: Jaleigh Q. Pier, CC BY-SA.

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33.8: Roundworms (Nematoda)

Learning Objectives

- Describe the features of animals classified in phylum Nematoda

Phylum Nematoda

The Nematoda, similar to most other animal phyla, are triploblastic, possessing an embryonic mesoderm that is sandwiched between the ectoderm and endoderm. They are also bilaterally symmetrical: a longitudinal section will divide them into right and left sides that are symmetrical. Furthermore, the nematodes, or roundworms, possess a pseudocoelom and have both free-living and parasitic forms.

Both the nematodes and arthropods belong to the superphylum Ecdysozoa that is believed to be a clade consisting of all evolutionary descendants from one common ancestor. The name derives from the word ecdysis, which refers to the shedding, or molting, of the exoskeleton. The phyla in this group have a hard cuticle covering their bodies, which must be periodically shed and replaced for them to increase in size.

Phylum Nematoda includes more than 28,000 species with an estimated 16,000 being parasitic in nature. Nematodes are present in all habitats.

Morphology

In contrast with cnidarians, nematodes show a tubular morphology and circular cross-section. These animals are pseudocoelomates; they have a complete digestive system with a distinct mouth and anus. This is in contrast with the cnidarians where only one opening is present (an incomplete digestive system).

The cuticle of Nematodes is rich in collagen and a carbohydrate-protein polymer called chitin. It forms an external “skeleton” outside the epidermis. The cuticle also lines many of the organs internally, including the pharynx and rectum. The epidermis can be either a single layer of cells or a syncytium, which is a multinucleated cell formed from the fusion of uninucleated cells.

The overall morphology of these worms is cylindrical, while the head is radially symmetrical. A mouth opening is present at the anterior end with three or six lips. Teeth occur in some species in the form of cuticle extensions. Some nematodes may present other external modifications such as rings, head shields, or warts. Rings, however, do not reflect true internal body segmentation. The mouth leads to a muscular pharynx and intestine, which leads to a rectum and anal opening at the posterior end. In addition, the muscles of nematodes differ from those of most animals; they have a longitudinal layer only, which accounts for the whip-like motion of their movement.



Figure **33.8.1**: Nematode shape: Scanning electron micrograph of soybean cyst nematode and its egg. Nematodes are cylindrical in shape, often looking like thin hairs. They possess an exoskeleton that prevents them from drying out. It must be shed (a process called ecdysis) in order for them to grow.

Excretory System

In nematodes, specialized excretory systems are not well developed. Nitrogenous wastes may be lost by diffusion through the entire body or into the pseudocoelom (body cavity), where they are removed by specialized cells. Regulation of water and salt content of the body is achieved by renette glands, present under the pharynx in marine nematodes.

Nervous system

Most nematodes possess four longitudinal nerve cords that run along the length of the body in dorsal, ventral, and lateral positions. The ventral nerve cord is better developed than the dorsal or lateral cords. All nerve cords fuse at the anterior end, around the pharynx, to form head ganglia, or the “brain” of the worm (taking the form of a ring around the pharynx), as well as at the posterior end to form the tail ganglia. In *C. elegans*, the nervous system accounts for nearly one-third of the total number of cells in the animal.

Reproduction

Nematodes employ a variety of reproductive strategies that range from monoecious to dioecious to parthenogenic, depending upon the species under consideration. *C. elegans* is a monoecious species, having development of ova contained in a uterus as well as sperm contained in the spermatheca. The uterus has an external opening known as the vulva. The female genital pore is near the middle of the body, whereas the male’s is at the tip. Specialized structures at the tail of the male keep him in place while he deposits sperm with copulatory spicules. Fertilization is internal with embryonic development beginning very soon after fertilization. The embryo is released from the vulva during the gastrulation stage. The embryonic development stage lasts for 14 hours; development then continues through four successive larval stages with ecdysis between each stage (L1, L2, L3, and L4) ultimately leading to the development of a young male or female adult worm. Adverse environmental conditions such as overcrowding and lack of food can result in the formation of an intermediate larval stage known as the dauer larva.

Key Points

- Nematodes are in the same phylogenetic grouping as the arthropods because of the presence of an external cuticle that protects the animal and keeps it from drying out.
- There are an estimated 28,000 species of nematodes, with approximately 16,000 of them being parasitic.
- Nematodes are tubular in shape and are considered pseudocoelomates because of they do not possess a true coelom.
- Nematodes do not have a well-developed excretory system, but do have a complete digestive system.
- Nematodes possess the ability to shed their exoskeleton in order to grow, a process called ecdysis.

Key Terms

- **exoskeleton**: a hard outer structure that provides both structure and protection to creatures such as insects, Crustacea, and Nematoda

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33.9: Arthropods (Arthropoda)

Learning Objectives

- Describe the morphology of arthropoda

Phylum Arthropoda

The name “arthropoda” means “jointed legs” (in the Greek, “arthros” means “joint” and “podos” means “leg”); it aptly describes the enormous number of invertebrates included in this phylum. Arthropods dominate the animal kingdom with an estimated 85 percent of known species included in this phylum; many arthropods are as yet undocumented. The principal characteristics of all the animals in this phylum are functional segmentation of the body and presence of jointed appendages. Arthropods also show the presence of an exoskeleton made principally of chitin, which is a waterproof, tough polysaccharide. Phylum Arthropoda is the largest phylum in the animal world; insects form the single largest class within this phylum. Arthropods are eucoelomate, protostomic organisms.

Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. This phylum is further classified into five subphyla: Trilobitomorpha (trilobites, all extinct), Hexapoda (insects and relatives), Myriapoda (millipedes, centipedes, and relatives), Crustaceans (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Chelicerata (horseshoe crabs, arachnids, scorpions, and daddy longlegs). Trilobites are an extinct group of arthropods found chiefly in the pre-Cambrian Era that are probably most closely related to the Chelicerata. These are identified based on fossil records.



Figure **33.9.1**: Trilobite fossil: *Acadoparadoxides*, possibly *A. briareus*, a large trilobite from about 500 million years ago from Morocco, North Africa (Middle Cambrian)

Morphology

A unique feature of animals in the arthropod phylum is the presence of a segmented body and fusion of sets of segments that give rise to functional body regions called tagma. Tagma may be in the form of a head, thorax, and abdomen, or a cephalothorax and abdomen, or a head and trunk. A central cavity, called the hemocoel (or blood cavity), is present; the open circulatory system is regulated by a tubular, or single-chambered, heart. Respiratory systems vary depending on the group of arthropod. Insects and myriapods use a series of tubes (tracheae) that branch through the body, open to the outside through openings called spiracles, and perform gas exchange directly between the cells and air in the tracheae. Other organisms use variants of gills and lungs. Aquatic crustaceans utilize gills, terrestrial chelicerates employ book lungs, and aquatic chelicerates use book gills. The book lungs of arachnids (scorpions, spiders, ticks, and mites) contain a vertical stack of hemocoel wall tissue that somewhat resembles the pages of a book. Between each of the “pages” of tissue is an air space. This allows both sides of the tissue to be in contact with the air at all times, greatly increasing the efficiency of gas exchange. The gills of crustaceans are filamentous structures that exchange gases with the surrounding water.



Figure **33.9.1**: Book gills: The ventral side of a horseshoe crab showing the book gills located near the telson (tail). These gills flap back and forth bringing oxygen to the blood.

Groups of arthropods also differ in the organs used for excretion. Crustaceans possess green glands while insects use Malpighian tubules, which work in conjunction with the hindgut to reabsorb water while ridding the body of nitrogenous waste. The cuticle is the covering of an arthropod. It is made up of two layers: the epicuticle, which is a thin, waxy, water-resistant outer layer containing no chitin; and the chitinous procuticle, which is beneath the epicuticle. Chitin is a tough, flexible polysaccharide. In order to grow, the arthropod must shed the exoskeleton during a process called ecdysis ("to strip off"); this is a cumbersome method of growth. During this time, the animal is vulnerable to predation.

Key Points

- Arthropods include the Hexapoda (insects), the Crustacea (lobsters, crabs, and shrimp), the Chelicerata (the spiders and scorpions), and the Myriapoda (the centipedes and millipedes).
- Arthropods have a segmented body plan that contains fused segments divided into regions called tagma.
- Arthropods have an open circulatory system and can use book gills, book lungs, or tracheal tubes for respiration.

Key Terms

- **tagma**: a specialized grouping of arthropodan segments, such as the head, the thorax, and the abdomen with a common function
- **malpighian tubule**: a tubule that extends from the alimentary canal to the exterior of the organism, excreting water and wastes in the form of solid nitrogenous compounds
- **spiracle**: a pore or opening used (especially by spiders and some fish) for breathing

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33.9.1: Subphyla of Arthropoda

Learning Objectives

- Differentiate among the subphylums hexapoda, myriapoda, crustacea, and chelicerata

Representatives of Phylum Arthropoda

Subphylum Hexapoda

The name Hexapoda denotes the presence of six legs (three pairs) in these animals, which differentiates them from the number of pairs present in other arthropods. Hexapods are characterized by the presence of a head, thorax, and abdomen, constituting three tagma. The thorax bears the wings as well as six legs in three pairs. Many of the common insects we encounter on a daily basis, including ants, cockroaches, butterflies, and flies, are examples of Hexapoda.

Among the hexapods, the insects are the largest class in terms of species diversity as well as biomass in terrestrial habitats). Typically, the head bears one pair of sensory antennae, mandibles as mouthparts, a pair of compound eyes, and some ocelli (simple eyes), along with numerous sensory hairs. The thorax bears three pairs of legs (one pair per segment) and two pairs of wings, with one pair each on the second and third thoracic segments. The abdomen usually has eleven segments and bears reproductive apertures. Hexapoda includes insects that are winged (like fruit flies) and wingless (like fleas).



Figure **33.9.1.1**: Insect showing wings and body segments: *Protaetia fieberi* in flight posture. Hexapods are characterized by having three distinct tagma, or body segments. This beetle is just one of over one million different species of insects that inhabit the Earth.

Subphylum Myriapoda

Subphylum Myriapoda includes arthropods with numerous legs. Although the name is hyperbolic in suggesting that myriad legs are present in these invertebrates, the number of legs may vary from 10 to 750. This subphylum includes 13,000 species; the most commonly-found examples are millipedes and centipedes. All myriapods are terrestrial animals, prefering a humid environment.

Myriapods are typically found in moist soils, decaying biological material, and leaf litter. Centipedes, such as *Scutigera coleoptrata*,are classified as chilopods. These animals bear one pair of legs per segment, mandibles as mouthparts, and are somewhat dorsoventrally flattened. The legs in the first segment are modified to form forcipules (poison claws) that deliver venom to prey such as spiders and cockroaches, as centipedes are predatory. Millipedes bear two pairs of legs per diplosegment, a feature that results from embryonic fusion of adjacent pairs of body segments, are usually rounder in cross-section, and are herbivores or detritivores. Millipedes have visibly more numbers of legs as compared to centipedes, although they do not bear a thousand legs.



Figure **33.9.1.1**: House centipede: The house centipede (*Scutigera coleoptrata*) is one of the 13,000 species of Myriapoda. They bear one pair of legs per segment and can inject venom. The Myriapods contain the millipedes and centipedes.

Subphylum Crustacea

Crustaceans are the most dominant aquatic arthropods since the total number of marine crustacean species stands at 67,000. However, there are also freshwater and terrestrial crustacean species. Krill, shrimp, lobsters, crabs, and crayfish are all examples of crustaceans. Terrestrial species like the wood lice (*Armadillidium* spp.) (also called pill bugs, rolly pollies, potato bugs, or isopods) are also crustaceans, although the number of non-aquatic species in this subphylum is relatively low.



Figure **33.9.1.1**: Mediterranean green Crab: This crab (*Carcinus aestuarii*) is one of the 67,000 species of crustaceans inhabiting the world's oceans. Most crustaceans are decapods, having ten legs.

Crustaceans possess two pairs of antennae, mandibles as mouthparts, and biramous ("two branched") appendages: their legs are formed in two parts, as distinct from the uniramous ("one branched") myriapods and hexapods.

Unlike that of the Hexapoda, the head and thorax of most crustaceans is fused to form a cephalothorax, which is covered by a plate called the carapace, thus producing a body structure of two tagma. Crustaceans have a chitinous exoskeleton that is shed by molting whenever the animal increases in size. The exoskeletons of many species are also infused with calcium carbonate, which makes them even stronger than in other arthropods. Crustaceans have an open circulatory system where blood is pumped into the hemocoel by the dorsally-located heart. Hemocyanin and hemoglobin are the respiratory pigments present in these animals.

Subphylum Chelicerata

This subphylum includes animals such as spiders, scorpions, horseshoe crabs, and sea spiders and is predominantly terrestrial, although some marine species also exist. An estimated 77,000 species, found in almost all habitats, are included in subphylum Chelicerata.

The body of chelicerates may be divided into two parts: prosoma and opisthosoma, which are basically the equivalents of cephalothorax (usually smaller) and abdomen (usually larger). A "head" tagmum is not usually discernible. The phylum derives its name from the first pair of appendages, the chelicerae, which are specialized claw-like or fang-like mouthparts. These animals do not possess antennae. The second pair of appendages is known as pedipalps. In some species, such as sea spiders, an additional pair of appendages, called ovigers, is present between the chelicerae and pedipalps.

Chelicerae are used primarily for feeding, but in spiders, these are often modified into fangs that inject venom into their prey before feeding. Members of this subphylum have an open circulatory system with a heart that pumps blood into the hemocoel. Aquatic species have gills, whereas terrestrial species have either trachea or book lungs for gaseous exchange.



Figure **33.9.1.1**: Chelicera of spiders: This photo shows the chelicera of a spider being held open with a stick. Some chelicerae, such as those found in spiders, are hollow and contain (or are connected to) venom glands which are used to inject venom into prey or a (perceived) threat.

The nervous system in chelicerates consists of a brain and two ventral nerve cords. These animals use external as well as internal fertilization strategies for reproduction, depending upon the species and its habitat. Parental care for the young ranges from absolutely none to relatively-prolonged care.

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Key Points

- The Hexapoda include insects; the Crustacea include lobster, crabs, and shrimp; the Myriapoda include centipedes and millipedes; and the Chelicerata include spiders, scorpions.
- The Hexapoda are the largest grouping of Arthropods, containing the more than one million species of insects, having representatives with six legs and one pair of antennae.
- The Myriapoda are terrestrial, prefering humid environments; they have between 10 and 750 legs.
- The Crustacea are primarily aquatic arthropods, but also include terrestrial forms, which have a cephalothorax covered by a carapace.
- The Chelicerata, which includes the spiders, horseshoe crabs, and scorpions, have mouth parts that are fang-like and used for capturing prey.

Key Terms

- **cephalothorax**: the fused head and thorax of spiders and crustaceans
- **forcipule**: a modified pincer-like foreleg in centipedes, capable of injecting venom

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CHAPTER OVERVIEW

34: Deuterostomes

34.1: Echinoderms
34.2: Chordates
34.3: Nonvertebrate Chordates
34.4: Vertebrate Chordates
34.5: Fishes
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34.1: Echinoderms

Skills to Develop

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates

The phyla Echinodermata and Chordata (the phylum in which humans are placed) both belong to the superphylum Deuterostomia. Recall that protostome and deuterostomes differ in certain aspects of their embryonic development, and they are named based on which opening of the digestive cavity develops first. The word deuterostome comes from the Greek word meaning “mouth second,” indicating that the anus is the first to develop. There are a series of other developmental characteristics that differ between protostomes and deuterostomes, including the mode of formation of the coelom and the early cell division of the embryo. In deuterostomes, internal pockets of the endodermal lining called the archenteron fuse to form the coelom. The endodermal lining of the archenteron (or the primitive gut) forms membrane protrusions that bud off and become the mesodermal layer. These buds, known as coelomic pouches, fuse to form the coelomic cavity, as they eventually separate from the endodermal layer. The resultant coelom is termed an enterocoelom. The archenteron develops into the alimentary canal, and a mouth opening is formed by invagination of ectoderm at the pole opposite the blastopore of the gastrula. The blastopore forms the anus of the alimentary system in the juvenile and adult forms. The fates of embryonic cells in deuterostomes can be altered if they are experimentally moved to a different location in the embryo due to indeterminant cleavage in early embryogenesis.

Phylum Echinodermata

Echinodermata are so named owing to their spiny skin (from the Greek “echinos” meaning “spiny” and “dermos” meaning “skin”), and this phylum is a collection of about 7,000 described living species. Echinodermata are exclusively marine organisms. Sea stars (Figure **34.1.1**), sea cucumbers, sea urchins, sand dollars, and brittle stars are all examples of echinoderms. To date, no freshwater or terrestrial echinoderms are known.

Morphology and Anatomy

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles, although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells and may possess pigment cells, giving vivid colors to these animals, as well as cells laden with toxins. Gonads are present in each arm. In echinoderms like sea stars, every arm bears two rows of tube feet on the oral side. These tube feet help in attachment to the substratum. These animals possess a true coelom that is modified into a unique circulatory system called a water vascular system. An interesting feature of these animals is their power to regenerate, even when over 75 percent of their body mass is lost.

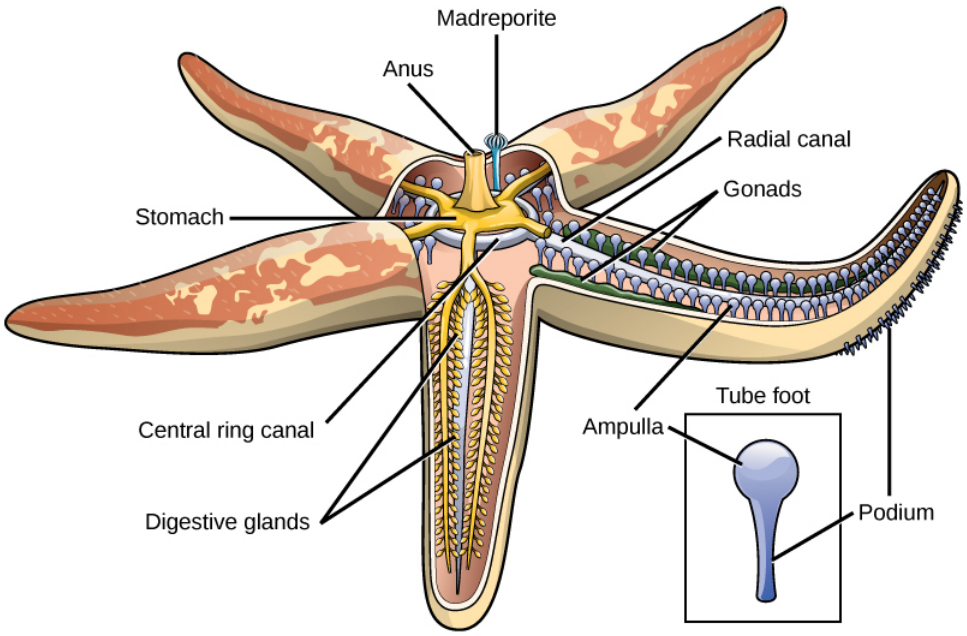


Figure **34.1.1**: This diagram shows the anatomy of a sea star.

Water Vascular System

Echinoderms possess a unique ambulacral or water vascular system, consisting of a central ring canal and radial canals that extend along each arm. Water circulates through these structures and facilitates gaseous exchange as well as nutrition, predation, and locomotion. The water vascular system also projects from holes in the skeleton in the form of tube feet. These tube feet can expand or contract based on the volume of water present in the system of that arm. By using hydrostatic pressure, the animal can either protrude or retract the tube feet. Water enters the madreporite on the aboral side of the echinoderm. From there, it passes into the stone canal, which moves water into the ring canal. The ring canal connects the radial canals (there are five in a pentaradial animal), and the radial canals move water into the ampullae, which have tube feet through which the water moves. By moving water through the unique water vascular system, the echinoderm can move and force open mollusk shells during feeding.

Nervous System

The nervous system in these animals is a relatively simple structure with a nerve ring at the center and five radial nerves extending outward along the arms. Structures analogous to a brain or derived from fusion of ganglia are not present in these animals.

Excretory System

Podocytes, cells specialized for ultrafiltration of bodily fluids, are present near the center of echinoderms. These podocytes are connected by an internal system of canals to an opening called the madreporite.

Reproduction

Echinoderms are sexually dimorphic and release their eggs and sperm cells into water; fertilization is external. In some species, the larvae divide asexually and multiply before they reach sexual maturity. Echinoderms may also reproduce asexually, as well as regenerate body parts lost in trauma.

Classes of Echinoderms

This phylum is divided into five extant classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies or feather stars), and Holothuroidea (sea cucumbers) (Figure **34.1.2**).

The most well-known echinoderms are members of class Asteroidea, or sea stars. They come in a large variety of shapes, colors, and sizes, with more than 1,800 species known so far. The key characteristic of sea stars that distinguishes them from other echinoderm classes includes thick arms (ambulacra) that extend from a central disk where organs penetrate into the arms. Sea stars use their tube feet not only for gripping surfaces but also for grasping prey. Sea stars have two stomachs, one of which can protrude

through their mouths and secrete digestive juices into or onto prey, even before ingestion. This process can essentially liquefy the prey and make digestion easier.

Brittle stars belong to the class Ophiuroidea. Unlike sea stars, which have plump arms, brittle stars have long, thin arms that are sharply demarcated from the central disk. Brittle stars move by lashing out their arms or wrapping them around objects and pulling themselves forward. Sea urchins and sand dollars are examples of Echinoidea. These echinoderms do not have arms, but are hemispherical or flattened with five rows of tube feet that help them in slow movement; tube feet are extruded through pores of a continuous internal shell called a test. Sea lilies and feather stars are examples of Crinoidea. Both of these species are suspension feeders. Sea cucumbers of class Holothuroidea are extended in the oral-aboral axis and have five rows of tube feet. These are the only echinoderms that demonstrate "functional" bilateral symmetry as adults, because the uniquely extended oral-aboral axis compels the animal to lie horizontally rather than stand vertically.

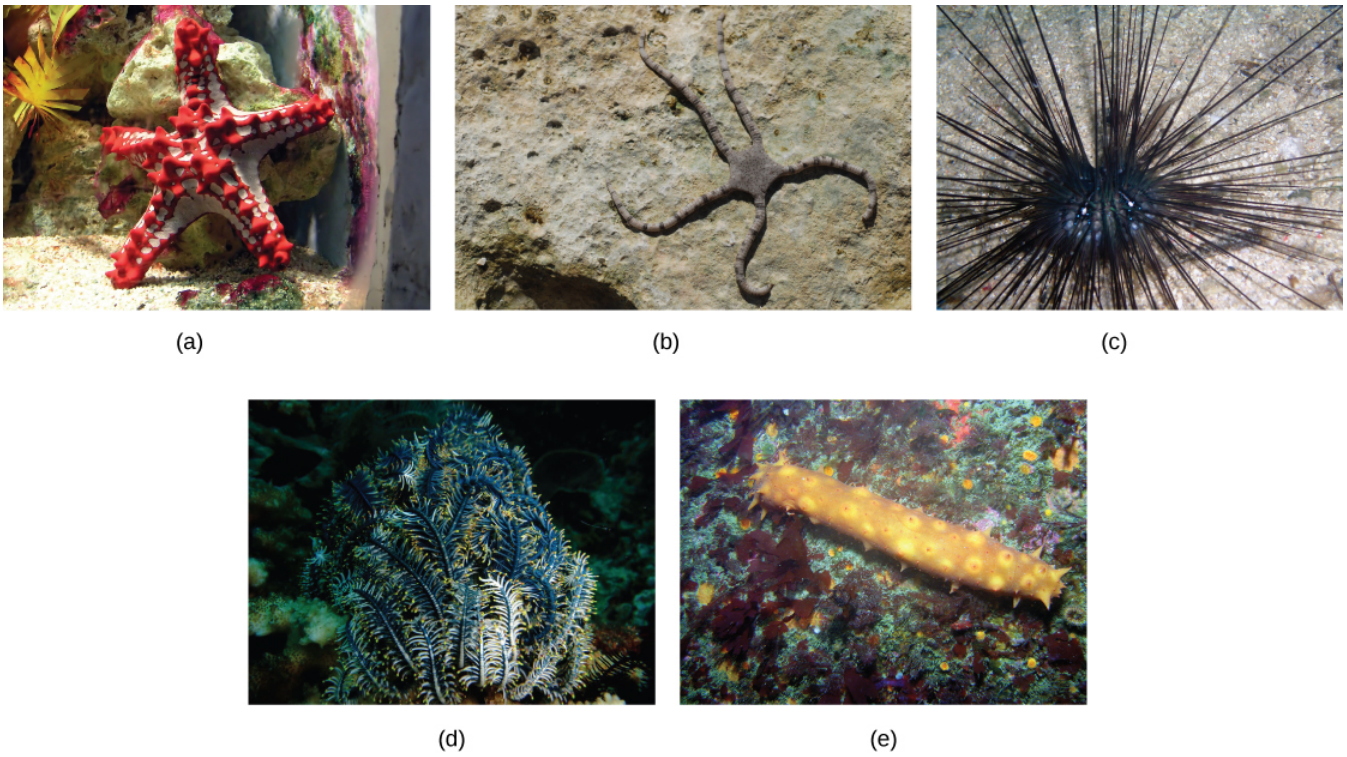


Figure **34.1.2**: Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (e) sea cucumbers, representing class Holothuroidea. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed Bierman)

Phylum Chordata

Animals in the phylum Chordata share four key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. In some groups, some of these traits are present only during embryonic development. In addition to containing vertebrate classes, the phylum Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets). Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

Summary

Echinoderms are deuterostomic marine organisms. This phylum of animals bears a calcareous endoskeleton composed of ossicles. These animals also have spiny skin. Echinoderms possess water-based circulatory systems. A pore termed the madreporite is the point of entry and exit for water into the water vascular system. Osmoregulation is carried out by specialized cells known as podocytes.

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

Glossary

archenteron
primitive gut cavity within the gastrula that opens outwards via the blastopore

Chordata
phylum of animals distinguished by their possession of a notochord, a dorsal, hollow nerve cord, pharyngeal slits, and a post-anal tail at some point in their development

Echinodermata
phylum of deuterostomes with spiny skin; exclusively marine organisms

enterocoelom
coelom formed by fusion of coelomic pouches budded from the endodermal lining of the archenteron

madreporite
pore for regulating entry and exit of water into the water vascular system

water vascular system
system in echinoderms where water is the circulatory fluid

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34.2: Chordates

Skills to Develop

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates

The phyla Echinodermata and Chordata (the phylum in which humans are placed) both belong to the superphylum Deuterostomia. Recall that protostome and deuterostomes differ in certain aspects of their embryonic development, and they are named based on which opening of the digestive cavity develops first. The word deuterostome comes from the Greek word meaning “mouth second,” indicating that the anus is the first to develop. There are a series of other developmental characteristics that differ between protostomes and deuterostomes, including the mode of formation of the coelom and the early cell division of the embryo. In deuterostomes, internal pockets of the endodermal lining called the archenteron fuse to form the coelom. The endodermal lining of the archenteron (or the primitive gut) forms membrane protrusions that bud off and become the mesodermal layer. These buds, known as coelomic pouches, fuse to form the coelomic cavity, as they eventually separate from the endodermal layer. The resultant coelom is termed an enterocoelom. The archenteron develops into the alimentary canal, and a mouth opening is formed by invagination of ectoderm at the pole opposite the blastopore of the gastrula. The blastopore forms the anus of the alimentary system in the juvenile and adult forms. The fates of embryonic cells in deuterostomes can be altered if they are experimentally moved to a different location in the embryo due to indeterminant cleavage in early embryogenesis.

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Morphology and Anatomy

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles, although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells and may possess pigment cells, giving vivid colors to these animals, as well as cells laden with toxins. Gonads are present in each arm. In echinoderms like sea stars, every arm bears two rows of tube feet on the oral side. These tube feet help in attachment to the substratum. These animals possess a true coelom that is modified into a unique circulatory system called a water vascular system. An interesting feature of these animals is their power to regenerate, even when over 75 percent of their body mass is lost.

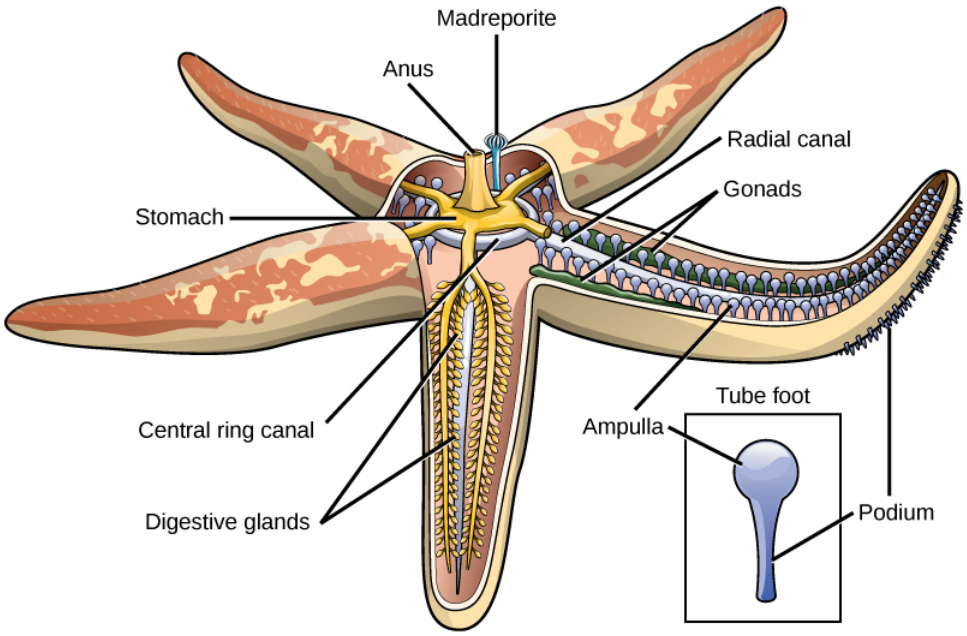


Figure **34.2.1**: This diagram shows the anatomy of a sea star.

Water Vascular System

Echinoderms possess a unique ambulacral or water vascular system, consisting of a central ring canal and radial canals that extend along each arm. Water circulates through these structures and facilitates gaseous exchange as well as nutrition, predation, and locomotion. The water vascular system also projects from holes in the skeleton in the form of tube feet. These tube feet can expand or contract based on the volume of water present in the system of that arm. By using hydrostatic pressure, the animal can either protrude or retract the tube feet. Water enters the madreporite on the aboral side of the echinoderm. From there, it passes into the stone canal, which moves water into the ring canal. The ring canal connects the radial canals (there are five in a pentaradial animal), and the radial canals move water into the ampullae, which have tube feet through which the water moves. By moving water through the unique water vascular system, the echinoderm can move and force open mollusk shells during feeding.

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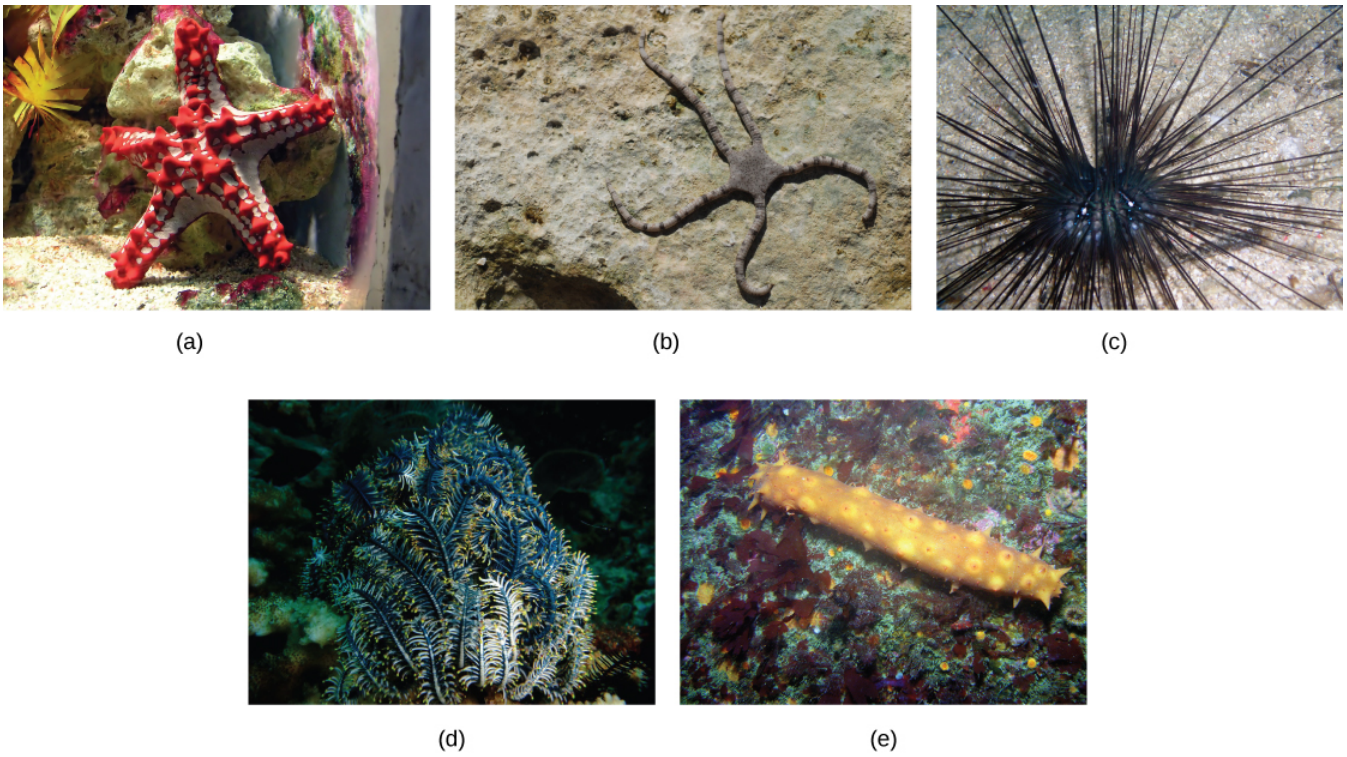


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34.3: Nonvertebrate Chordates

Skills to Develop

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates

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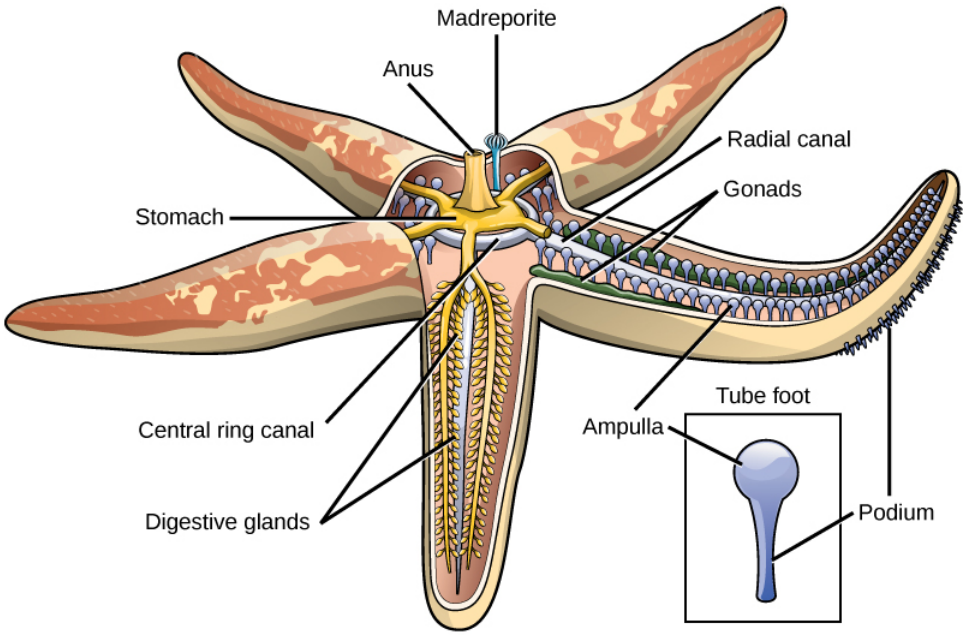


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through their mouths and secrete digestive juices into or onto prey, even before ingestion. This process can essentially liquefy the prey and make digestion easier.

Brittle stars belong to the class Ophiuroidea. Unlike sea stars, which have plump arms, brittle stars have long, thin arms that are sharply demarcated from the central disk. Brittle stars move by lashing out their arms or wrapping them around objects and pulling themselves forward. Sea urchins and sand dollars are examples of Echinoidea. These echinoderms do not have arms, but are hemispherical or flattened with five rows of tube feet that help them in slow movement; tube feet are extruded through pores of a continuous internal shell called a test. Sea lilies and feather stars are examples of Crinoidea. Both of these species are suspension feeders. Sea cucumbers of class Holothuroidea are extended in the oral-aboral axis and have five rows of tube feet. These are the only echinoderms that demonstrate "functional" bilateral symmetry as adults, because the uniquely extended oral-aboral axis compels the animal to lie horizontally rather than stand vertically.

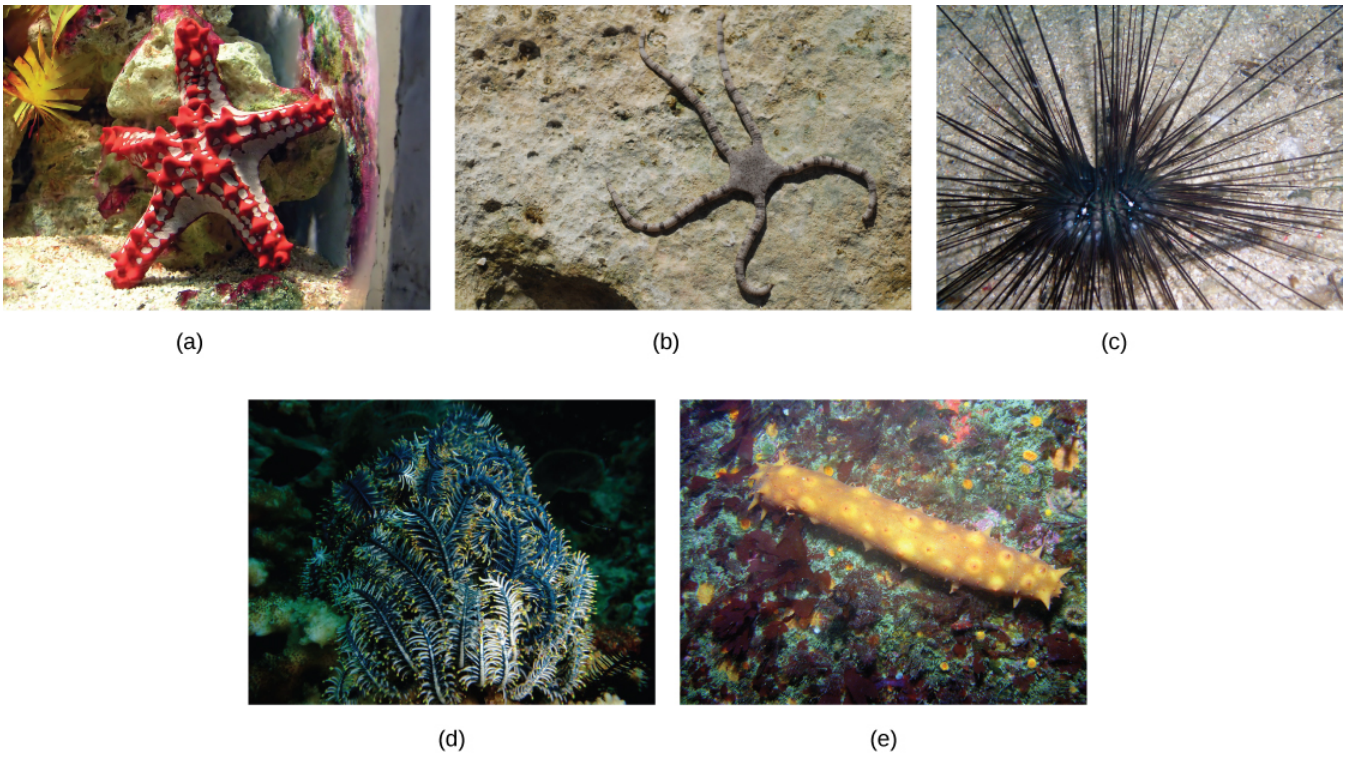


Figure **34.3.2**: Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (e) sea cucumbers, representing class Holothuroidea. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed Bierman)

Phylum Chordata

Animals in the phylum Chordata share four key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. In some groups, some of these traits are present only during embryonic development. In addition to containing vertebrate classes, the phylum Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets). Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

Summary

Echinoderms are deuterostomic marine organisms. This phylum of animals bears a calcareous endoskeleton composed of ossicles. These animals also have spiny skin. Echinoderms possess water-based circulatory systems. A pore termed the madreporite is the point of entry and exit for water into the water vascular system. Osmoregulation is carried out by specialized cells known as podocytes.

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

Glossary

archenteron
primitive gut cavity within the gastrula that opens outwards via the blastopore

Chordata
phylum of animals distinguished by their possession of a notochord, a dorsal, hollow nerve cord, pharyngeal slits, and a post-anal tail at some point in their development

Echinodermata
phylum of deuterostomes with spiny skin; exclusively marine organisms

enterocoelom
coelom formed by fusion of coelomic pouches budded from the endodermal lining of the archenteron

madreporite
pore for regulating entry and exit of water into the water vascular system

water vascular system
system in echinoderms where water is the circulatory fluid

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- **28.5: Superphylum Deuterostomia** by OpenStax is licensed CC BY 4.0.

34.4: Vertebrate Chordates

Skills to Develop

- Describe the distinguishing characteristics of chordates
- Identify the derived character of craniates that sets them apart from other chordates
- Describe the developmental fate of the notochord in vertebrates

Vertebrates are members of the kingdom Animalia and the phylum Chordata (Figure **34.4.1**). Recall that animals that possess bilateral symmetry can be divided into two groups—protostomes and deuterostomes—based on their patterns of embryonic development. The deuterostomes, whose name translates as "second mouth," consist of two phyla: Chordata and Echinodermata. Echinoderms are invertebrate marine animals that have pentaradial symmetry and a spiny body covering, a group that includes sea stars, sea urchins, and sea cucumbers. The most conspicuous and familiar members of Chordata are vertebrates, but this phylum also includes two groups of invertebrate chordates.

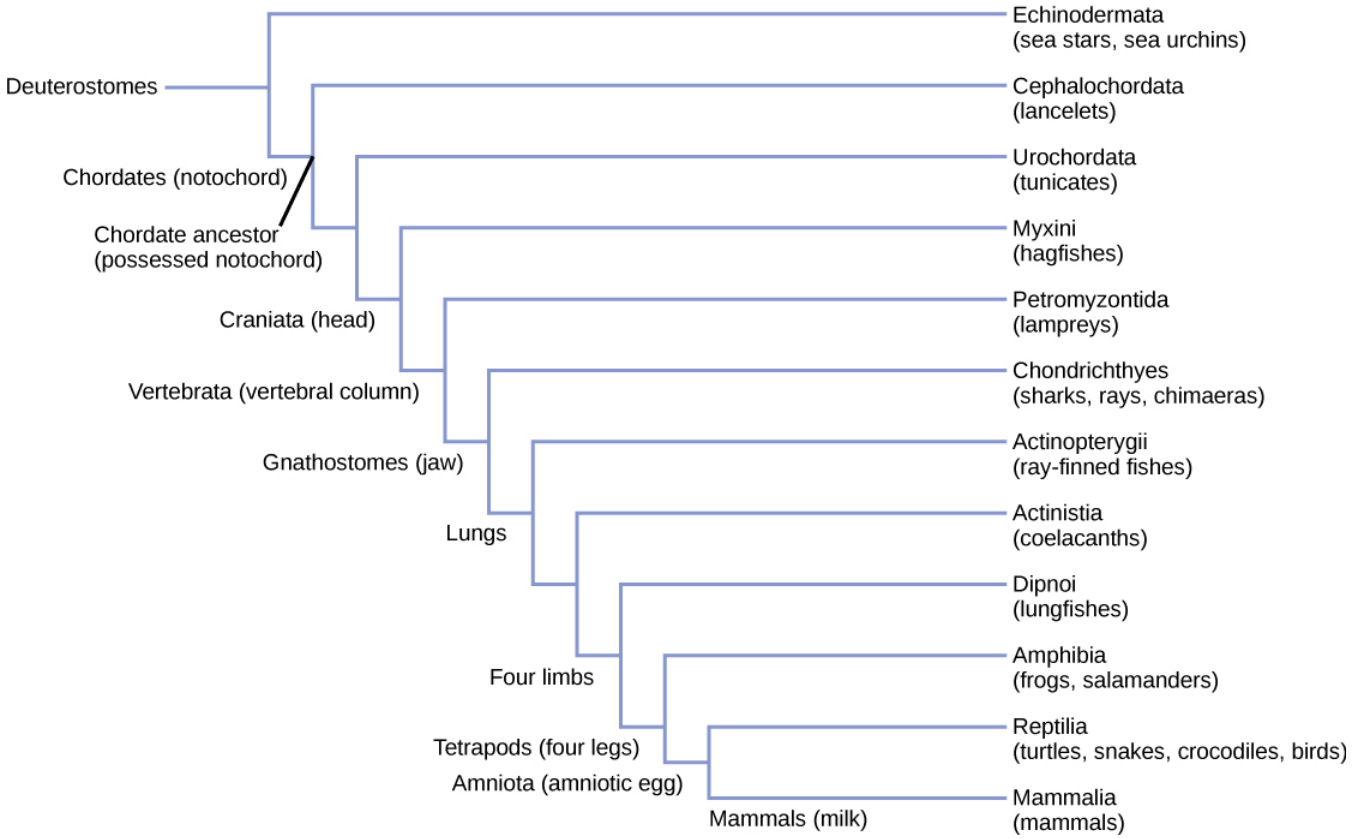


Figure **34.4.1**: All chordates are deuterostomes possessing a notochord.

Characteristics of Chordata

Animals in the phylum Chordata share four key features that appear at some stage during their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail (Figure **34.4.2**). In some groups, some of these are present only during embryonic development.

The chordates are named for the notochord, which is a flexible, rod-shaped structure that is found in the embryonic stage of all chordates and in the adult stage of some chordate species. It is located between the digestive tube and the nerve cord, and provides skeletal support through the length of the body. In some chordates, the notochord acts as the primary axial support of the body throughout the animal's lifetime. In vertebrates, the notochord is present during embryonic development, at which time it induces

the development of the neural tube and serves as a support for the developing embryonic body. The notochord, however, is not found in the postnatal stage of vertebrates; at this point, it has been replaced by the vertebral column (that is, the spine).

Art Connection

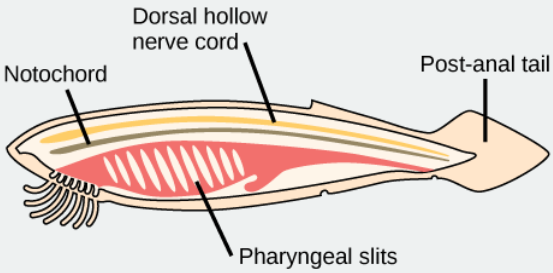


Figure 34.4.2: In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

Which of the following statements about common features of chordates is true?

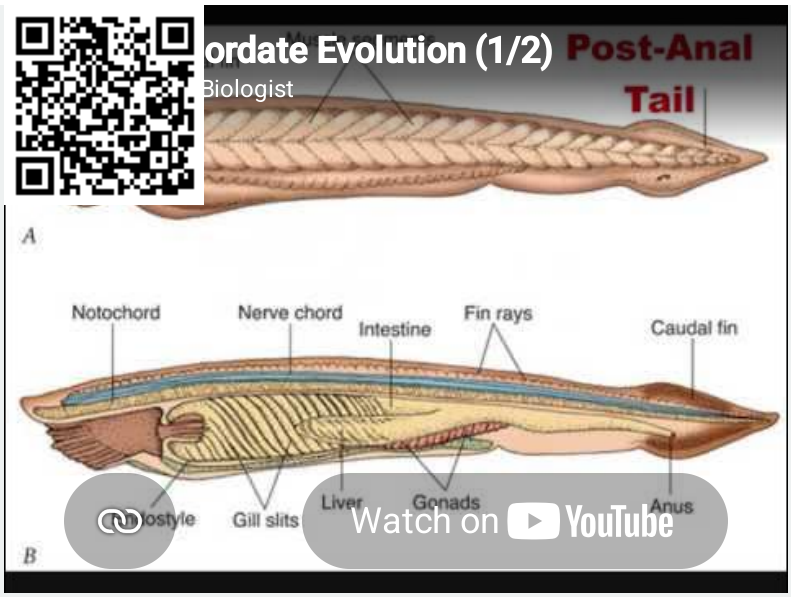
A. The dorsal hollow nerve cord is part of the chordate central nervous system.
B. In vertebrate fishes, the pharyngeal slits become the gills.
C. Humans are not chordates because humans do not have a tail.
D. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

The dorsal hollow nerve cord derives from ectoderm that rolls into a hollow tube during development. In chordates, it is located dorsal to the notochord. In contrast, other animal phyla are characterized by solid nerve cords that are located either ventrally or laterally. The nerve cord found in most chordate embryos develops into the brain and spinal cord, which compose the central nervous system.

Pharyngeal slits are openings in the pharynx (the region just posterior to the mouth) that extend to the outside environment. In organisms that live in aquatic environments, pharyngeal slits allow for the exit of water that enters the mouth during feeding. Some invertebrate chordates use the pharyngeal slits to filter food out of the water that enters the mouth. In vertebrate fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, into jaw supports. In tetrapods, the slits are modified into components of the ear and tonsils. Tetrapod literally means “four-footed,” which refers to the phylogenetic history of various groups that evolved accordingly, even though some now possess fewer than two pairs of walking appendages. Tetrapods include amphibians, reptiles, birds, and mammals.

The post-anal tail is a posterior elongation of the body, extending beyond the anus. The tail contains skeletal elements and muscles, which provide a source of locomotion in aquatic species, such as fishes. In some terrestrial vertebrates, the tail also helps with balance, courting, and signaling when danger is near. In humans, the post-anal tail is vestigial, that is, reduced in size and nonfunctional.

Link to Learning



Click for a video discussing the evolution of chordates and five characteristics that they share.

Chordates and the Evolution of Vertebrates

Chordata also contains two clades of invertebrates: Urochordata and Cephalochordata. Members of these groups also possess the four distinctive features of chordates at some point during their development.

Urochordata

Members of Urochordata are also known as tunicates (Figure **34.4.3**). The name tunicate derives from the cellulose-like carbohydrate material, called the tunic, which covers the outer body of tunicates. Although adult tunicates are classified as chordates, they do not have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits. The larval form, however, possesses all four structures. Most tunicates are hermaphrodites. Tunicate larvae hatch from eggs inside the adult tunicate's body. After hatching, a tunicate larva swims for a few days until it finds a suitable surface on which it can attach, usually in a dark or shaded location. It then attaches via the head to the surface and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear.

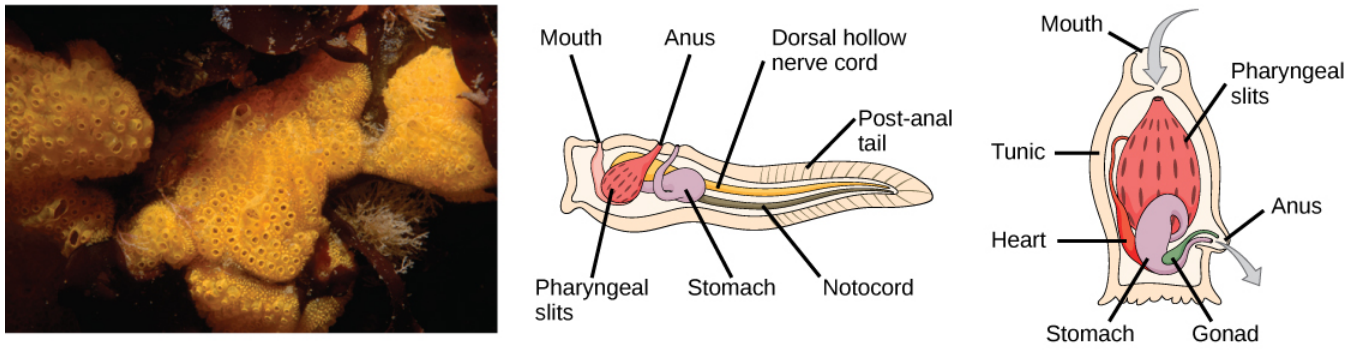


Figure **34.4.3**: (a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. (c) In the adult stage, the notochord, nerve cord, and tail disappear. (credit: modification of work by Dann Blackwood, USGS)

Most tunicates live a sessile existence on the ocean floor and are suspension feeders. The primary foods of tunicates are plankton and detritus. Seawater enters the tunicate's body through its incurrent siphon. Suspended material is filtered out of this water by a mucous net (pharyngeal slits) and is passed into the intestine via the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water. Tunicates are found in shallow ocean waters around the world.

Cephalochordata

Members of Cephalochordata possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage (Figure **34.4.4**). The notochord extends into the head, which gives the subphylum its name. Extinct members of this subphylum include *Pikaia*, which is the oldest known cephalochordate. *Pikaia* fossils were recovered from the Burgess shales of Canada and dated to the middle of the Cambrian age, making them more than 500 million years old.

Extant members of Cephalochordata are the lancelets, named for their blade-like shape. Lancelets are only a few centimeters long and are usually found buried in sand at the bottom of warm temperate and tropical seas. Like tunicates, they are suspension feeders.

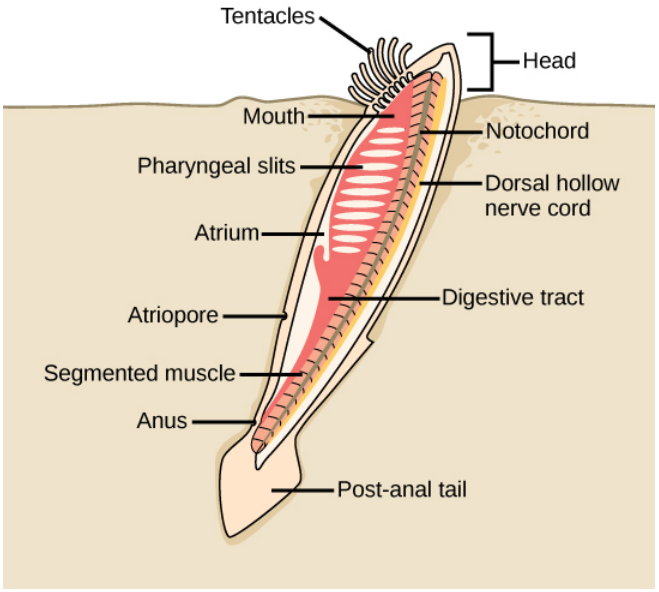


Figure **34.4.4**: The lancelet, like all cephalochordates, has a head. Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Water from the mouth enters the pharyngeal slits, which filter out food particles. The filtered water then collects in the atrium and exits through the atriopore.

Craniata and Vertebrata

A cranium is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones (Figure **34.4.5**). Most bilaterally symmetrical animals have a head; of these, those that have a cranium compose the clade Craniata. Craniata includes the hagfishes (Myxini), which have a cranium but lack a backbone, and all of the organisms called “vertebrates.”

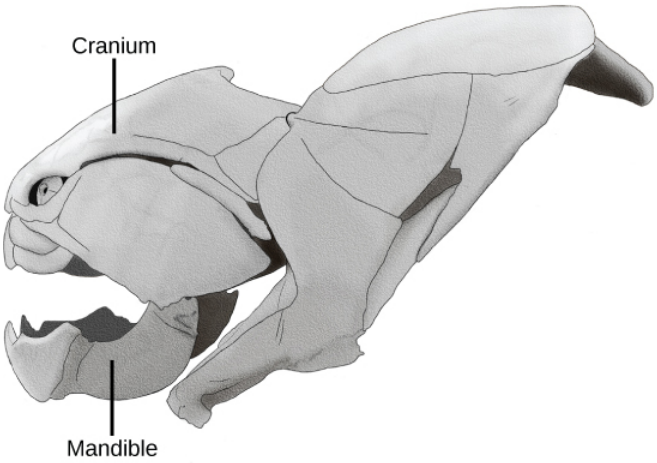


Figure **34.4.5**: Craniata, including this fish (*Dunkleosteus* sp.), are characterized by the presence of a cranium, mandible, and other facial bones. (credit: “Steveoc 86”/Wikimedia Commons)

Vertebrates are members of the clade Vertebrata. Vertebrates display the four characteristic features of the chordates; however, members of this group also share derived characteristics that distinguish them from invertebrate chordates. Vertebrata is named for

the vertebral column, composed of vertebrae, a series of separate bones joined together as a backbone (Figure **34.4.6**). In adult vertebrates, the vertebral column replaces the notochord, which is only seen in the embryonic stage.

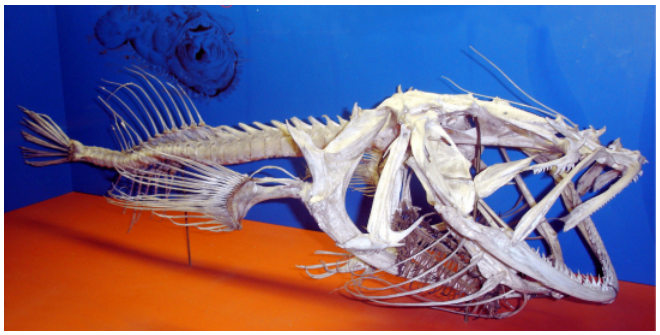


Figure **34.4.6**: Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium. (credit: Ernest V. More; taken at Smithsonian Museum of Natural History, Washington, D.C.)

Based on molecular analysis, vertebrates appear to be more closely related to lancelets (cephalochordates) than to tunicates (urochordates) among the invertebrate chordates. This evidence suggests that the cephalochordates diverged from Urochordata and the vertebrates subsequently diverged from the cephalochordates. This hypothesis is further supported by the discovery of a fossil in China from the genus *Haikouella*. This organism seems to be an intermediate form between cephalochordates and vertebrates. The *Haikouella* fossils are about 530 million years old and appear similar to modern lancelets. These organisms had a brain and eyes, as do vertebrates, but lack the skull found in craniates.[1] This evidence suggests that vertebrates arose during the Cambrian explosion. Recall that the "Cambrian explosion" is the name given to a relatively brief span of time during the Cambrian period during which many animal groups appeared and rapidly diversified. Most modern animal phyla originated during the Cambrian explosion.

Vertebrates are the largest group of chordates, with more than 62,000 living species. Vertebrates are grouped based on anatomical and physiological traits. More than one classification and naming scheme is used for these animals. Here we will consider the traditional groups Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia, which constitute classes in the subphylum Vertebrata. Many modern authors classify birds within Reptilia, which correctly reflects their evolutionary heritage. We consider them separately only for convenience. Further, we will consider hagfishes and lampreys together as jawless fishes, the agnathans, although emerging classification schemes separate them into chordate jawless fishes (the hagfishes) and vertebrate jawless fishes (the lampreys).

Animals that possess jaws are known as gnathostomes, which means "jawed mouth." Gnathostomes include fishes and tetrapods—amphibians, reptiles, birds, and mammals. Tetrapods can be further divided into two groups: amphibians and amniotes. Amniotes are animals whose eggs are adapted for terrestrial living, and this group includes mammals, reptiles, and birds. Amniotic embryos, developing in either an externally shed egg or an egg carried by the female, are provided with a water-retaining environment and are protected by amniotic membranes.

Summary

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms. Vertebrata is named for the vertebral column, which is a feature of almost all members of this clade.

Art Connections

Figure **34.4.2**: Which of the following statements about common features of chordates is true?

A. The dorsal hollow nerve cord is part of the chordate central nervous system.
B. In vertebrate fishes, the pharyngeal slits become the gills.
C. Humans are not chordates because humans do not have a tail.

D. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

Answer

A

Footnotes

1. 1 Chen, J. Y., Huang, D. Y., and Li, C. W., “An early Cambrian craniate-like chordate,” *Nature* 402 (1999): 518–522, doi:10.1038/990080.

Glossary

Cephalochordata
chordate clade whose members possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage

Chordata
phylum of animals distinguished by their possession of a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail at some point during their development

Craniata
clade composed of chordates that possess a cranium; includes Vertebrata together with hagfishes

cranium
bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones

dorsal hollow nerve cord
hollow, tubular structure derived from ectoderm, which is located dorsal to the notochord in chordates

lancelet
member of Cephalochordata; named for its blade-like shape

notochord
flexible, rod-shaped support structure that is found in the embryonic stage of all chordates and in the adult stage of some chordates

pharyngeal slit
opening in the pharynx

post-anal tail
muscular, posterior elongation of the body extending beyond the anus in chordates

tetrapod
phylogenetic reference to an organism with a four-footed evolutionary history; includes amphibians, reptiles, birds, and mammals

tunicate
sessile chordate that is a member of Urochordata

Urochordata
clade composed of tunicates

vertebral column
series of separate bones joined together as a backbone

Vertebrata

members of the phylum Chordata that possess a backbone

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34.5: Fishes

Skills to Develop

- Describe the difference between jawless and jawed fishes
- Discuss the distinguishing features of sharks and rays compared to other modern fishes

Modern fishes include an estimated 31,000 species. Fishes were the earliest vertebrates, with jawless species being the earliest and jawed species evolving later. They are active feeders, rather than sessile, suspension feeders. Jawless fishes—the hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, distinguishing them from the invertebrate chordates.

Jawless Fishes

Jawless fishes are craniates that represent an ancient vertebrate lineage that arose over one half-billion years ago. In the past, the hagfishes and lampreys were classified together as agnathans. Today, hagfishes and lampreys are recognized as separate clades, primarily because lampreys are true vertebrates, whereas hagfishes are not. A defining feature is the lack of paired lateral appendages (fins). Some of the earliest jawless fishes were the ostracoderms (which translates to “shell-skin”). Ostracoderms were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

Myxini: Hagfishes

The clade Myxini includes at least 20 species of hagfishes. Hagfishes are eel-like scavengers that live on the ocean floor and feed on dead invertebrates, other fishes, and marine mammals (Figure **34.5.1**). Hagfishes are entirely marine and are found in oceans around the world, except for the polar regions. A unique feature of these animals is the slime glands beneath the skin that release mucus through surface pores. This mucus allows the hagfish to escape from the grip of predators. Hagfish can also twist their bodies in a knot to feed and sometimes eat carcasses from the inside out.

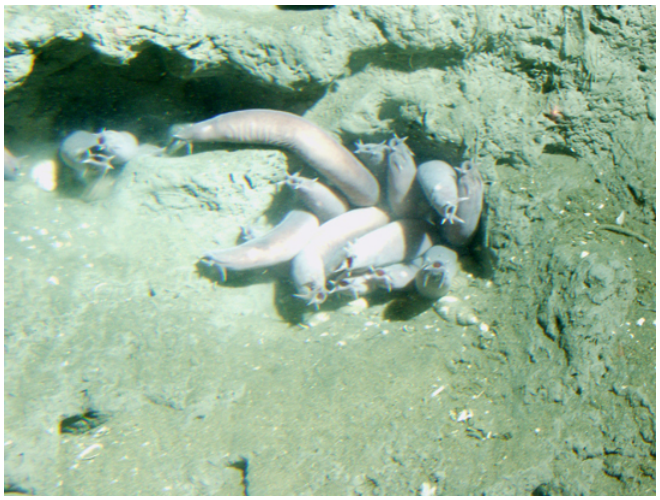


Figure **34.5.1**: Pacific hagfish are scavengers that live on the ocean floor. (credit: Linda Snook, NOAA/CBNMS)

The skeleton of a hagfish is composed of cartilage, which includes a cartilaginous notochord that runs the length of the body. This notochord provides support to the hagfish’s body. Hagfishes do not replace the notochord with a vertebral column during development, as do true vertebrates.

Petromyzontidae: Lampreys

The clade Petromyzontidae includes approximately 35–40 or more species of lampreys. Lampreys are similar to hagfishes in size and shape; however, lampreys possess some vertebral elements. Lampreys lack paired appendages and bone, as do the hagfishes. As adults, lampreys are characterized by a toothed, funnel-like sucking mouth. Many species have a parasitic stage of their life cycle during which they are ectoparasites of fishes (Figure **34.5.2**).



Figure **34.5.2**: These parasitic sea lampreys attach to their lake trout host by suction and use their rough tongues to rasp away flesh in order to feed on the trout's blood. (credit: USGS)

Lampreys live primarily in coastal and fresh waters, and have a worldwide distribution, except for in the tropics and polar regions. Some species are marine, but all species spawn in fresh water. Eggs are fertilized externally, and the larvae distinctly differ from the adult form, spending 3 to 15 years as suspension feeders. Once they attain sexual maturity, the adults reproduce and die within days.

Lampreys possess a notochord as adults; however, this notochord is surrounded by a cartilaginous structure called an arcualia, which may resemble an evolutionarily early form of the vertebral column.

Gnathostomes: Jawed Fishes

Gnathostomes or "jaw-mouths" are vertebrates that possess jaws. One of the most significant developments in early vertebrate evolution was the development of the jaw, which is a hinged structure attached to the cranium that allows an animal to grasp and tear its food. The evolution of jaws allowed early gnathostomes to exploit food resources that were unavailable to jawless fishes.

Early gnathostomes also possessed two sets of paired fins, allowing the fishes to maneuver accurately. Pectoral fins are typically located on the anterior body, and pelvic fins on the posterior. Evolution of the jaw and paired fins permitted gnathostomes to expand from the sedentary suspension feeding of jawless fishes to become mobile predators. The ability of gnathostomes to exploit new nutrient sources likely is one reason that they replaced most jawless fishes during the Devonian period. Two early groups of gnathostomes were the acanthodians and placoderms (Figure **34.5.3**), which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes.



Figure **34.5.3**: *Dunkleosteous* was an enormous placoderm from the Devonian period, 380–360 million years ago. It measured up to 10 meters in length and weighed up to 3.6 tons. (credit: Nobu Tamura)

Chondrichthyes: Cartilaginous Fishes

The clade Chondrichthyes is diverse, consisting of sharks (Figure **34.5.4**), rays, and skates, together with sawfishes and a few dozen species of fishes called *chimaeras*, or "ghost" sharks." Chondrichthyes are jawed fishes that possess paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the early or middle Devonian. They are thought to be descended from the placoderms, which had skeletons made of bone; thus, the cartilaginous skeleton of Chondrichthyes is a later development. Parts of shark skeleton are strengthened by granules of calcium carbonate, but this is not the same as bone.

Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for a part or all of their lives. Most sharks are carnivores that feed on live prey, either swallowing it whole or using their jaws and teeth to tear it into smaller pieces. Shark teeth likely evolved from the jagged scales that cover their skin, called placoid scales. Some species of sharks and rays are suspension feeders that feed on plankton.

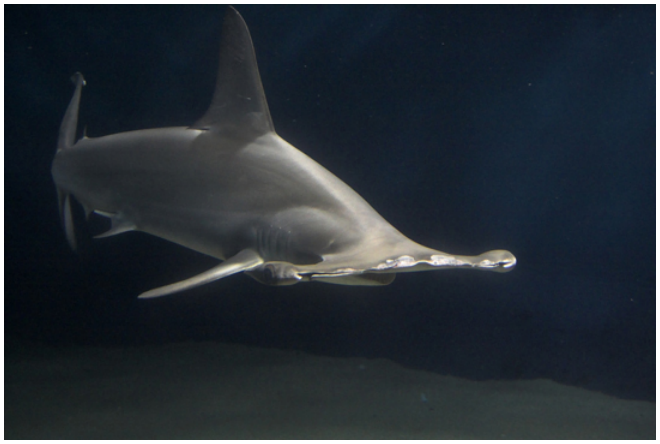


Figure **34.5.4**: Hammerhead sharks tend to school during the day and hunt prey at night. (credit: Masashi Sugawara)

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and electroreception, with the latter perhaps the most sensitive of any animal. Organs called ampullae of Lorenzini allow sharks to detect the electromagnetic fields that are produced by all living things, including their prey. Electroreception has only been observed in aquatic or amphibious animals. Sharks, together with most fishes and aquatic and larval amphibians, also have a sense organ called the lateral line, which is used to detect movement and vibration in the surrounding water, and is often considered homologous to "hearing" in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of a fish's body.

Sharks reproduce sexually, and eggs are fertilized internally. Most species are ovoviviparous: The fertilized egg is retained in the oviduct of the mother's body and the embryo is nourished by the egg yolk. The eggs hatch in the uterus, and young are born alive and fully functional. Some species of sharks are oviparous: They lay eggs that hatch outside of the mother's body. Embryos are protected by a shark egg case or "mermaid's purse" (Figure **34.5.5**) that has the consistency of leather. The shark egg case has tentacles that snag in seaweed and give the newborn shark cover. A few species of sharks are viviparous: The young develop within the mother's body and she gives live birth.

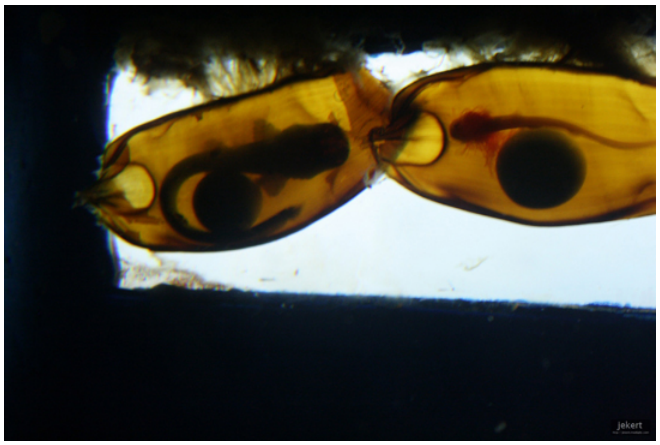


Figure **34.5.5**: Shark embryos are clearly visible through these transparent egg cases. The round structure is the yolk that nourishes the growing embryo. (credit: Jek Bacarisas)

Rays and skates comprise more than 500 species and are closely related to sharks. They can be distinguished from sharks by their flattened bodies, pectoral fins that are enlarged and fused to the head, and gill slits on their ventral surface (Figure **34.5.6**). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.



Figure **34.5.6**: This stingray blends into the sandy bottom of the ocean floor. (credit: "Sailn1"/Flickr)

Osteichthyes: Bony Fishes

Members of the clade Osteichthyes, also called bony fishes, are characterized by a bony skeleton. The vast majority of present-day fishes belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fishes have an ossified skeleton with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. This characteristic has only reversed in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered by overlapping scales, and glands in the skin secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fishes have a lateral line system that detects vibrations in water.

All bony fishes use gills to breathe. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Many bony fishes also have a swim bladder, a gas-filled organ that helps to control the buoyancy of the fish. Bony fishes are further divided into two extant clades: Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes).

Actinopterygii, the ray-finned fishes, include many familiar fishes—tuna, bass, trout, and salmon (Figure **34.5.7**), among others. Ray-finned fishes are named for their fins that are webs of skin supported by bony spines called rays. In contrast, the fins of Sarcopterygii are fleshy and lobed, supported by bone (Figure **34.5.7**). Living members of this clade include the less-familiar lungfishes and coelacanths.

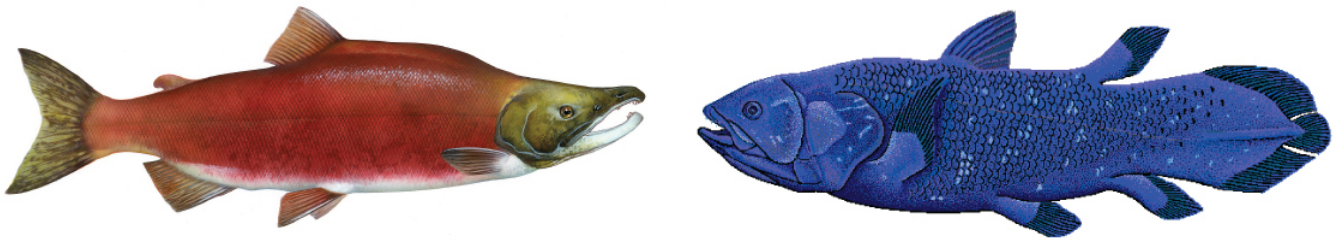


Figure **34.5.7**: The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish, was thought to have gone extinct in the Late Cretaceous period, 100 million years ago, until one was discovered in 1938 near the Comoros Islands between Africa and Madagascar. (credit a: modification of work by Timothy Knepp, USFWS; credit b: modification of work by Robbie Cada)

Summary

The earliest vertebrates that diverged from the invertebrate chordates were the jawless fishes. Fishes with jaws (gnathostomes) evolved later. Jaws allowed early gnathostomes to exploit new food sources. Agnathans include the hagfishes and lampreys. Hagfishes are eel-like scavengers that feed on dead invertebrates and other fishes. Lampreys are characterized by a toothed, funnel-like sucking mouth, and most species are parasitic on other fishes. Gnathostomes include the cartilaginous fishes and the bony fishes, as well as all other tetrapods. Cartilaginous fishes include sharks, rays, skates, and ghost sharks. Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for part or all of their lives. The vast majority of present-day fishes belong to the clade Osteichthyes, which consists of approximately 30,000 species. Bony fishes can be divided into two clades: Actinopterygii (ray-finned fishes, virtually all extant species) and Sarcopterygii (lobe-finned fishes, comprising fewer than 10 extant species but which are the ancestors of tetrapods).

Glossary

Actinopterygii
ray-finned fishes

ampulla of Lorenzini
sensory organ that allows sharks to detect electromagnetic fields produced by living things

Chondrichthyes
jawed fish with paired fins and a skeleton made of cartilage

gnathostome
jawed fish

hagfish
eel-like jawless fish that live on the ocean floor and are scavengers

lamprey
jawless fish characterized by a toothed, funnel-like, sucking mouth

lateral line
sense organ that runs the length of a fish's body; used to detect vibration in the water

Myxini

hagfishes

Osteichthyes
bony fish

ostracoderm
one of the earliest jawless fish covered in bone

Petromyzontidae
clade of lampreys

Sarcopterygii
lobe-finned fish

swim bladder
in fishes, a gas filled organ that helps to control the buoyancy of the fish

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34.6: Amphibians

Skills to Develop

- Describe the important difference between the life cycle of amphibians and the life cycles of other vertebrates
- Distinguish between the characteristics of Urodela, Anura, and Apoda
- Describe the evolutionary history of amphibians

Amphibians are vertebrate tetrapods. Amphibia includes frogs, salamanders, and caecilians. The term amphibian loosely translates from the Greek as “dual life,” which is a reference to the metamorphosis that many frogs and salamanders undergo and their mixture of aquatic and terrestrial environments in their life cycle. Amphibians evolved during the Devonian period and were the earliest terrestrial tetrapods.

Link to Learning

Watch this series of Animal Planet videos on tetrapod evolution:

1: The evolution from fish to earliest tetrapod

2: Fish to Earliest Tetrapod

3: The discovery of coelacanth and *Acanthostega* fossils

4: The number of fingers on “legs”

Characteristics of Amphibians

As tetrapods, most amphibians are characterized by four well-developed limbs. Some species of salamanders and all caecilians are functionally limbless; their limbs are vestigial. An important characteristic of extant amphibians is a moist, permeable skin that is achieved via mucus glands that keep the skin moist; thus, exchange of oxygen and carbon dioxide with the environment can take place through it (cutaneous respiration). Additional characteristics of amphibians include pedicellate teeth—teeth in which the root and crown are calcified, separated by a zone of noncalcified tissue—and a papilla amphibiorum and papilla basilaris, structures of the inner ear that are sensitive to frequencies below and above 10,00 hertz, respectively. Amphibians also have an auricular operculum, which is an extra bone in the ear that transmits sounds to the inner ear. All extant adult amphibians are carnivorous, and some terrestrial amphibians have a sticky tongue that is used to capture prey.

Evolution of Amphibians

The fossil record provides evidence of the first tetrapods: now-extinct amphibian species dating to nearly 400 million years ago. Evolution of tetrapods from fishes represented a significant change in body plan from one suited to organisms that respired and swam in water, to organisms that breathed air and moved onto land; these changes occurred over a span of 50 million years during the Devonian period. One of the earliest known tetrapods is from the genus *Acanthostega*. *Acanthostega* was aquatic; fossils show that it had gills similar to fishes. However, it also had four limbs, with the skeletal structure of limbs found in present-day tetrapods, including amphibians. Therefore, it is thought that *Acanthostega* lived in shallow waters and was an intermediate form between lobe-finned fishes and early, fully terrestrial tetrapods. What preceded *Acanthostega*?

In 2006, researchers published news of their discovery of a fossil of a “tetrapod-like fish,” *Tiktaalik roseae*, which seems to be an intermediate form between fishes having fins and tetrapods having limbs (Figure **34.6.1**). *Tiktaalik* likely lived in a shallow water

environment about 375 million years ago.[1]

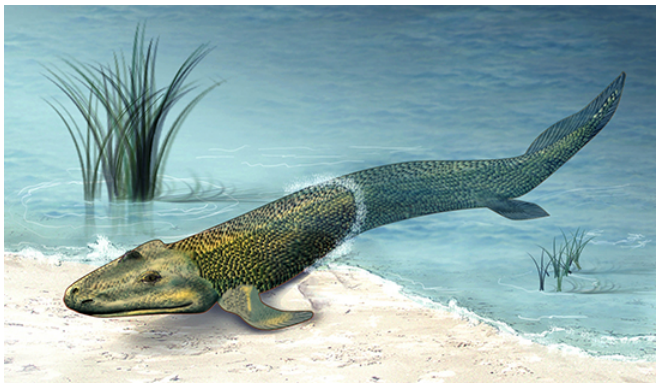


Figure **34.6.1**: The recent fossil discovery of *Tiktaalik roseae* suggests evidence for an animal intermediate to finned fish and legged tetrapods. (credit: Zina Deretsky, National Science Foundation)

The early tetrapods that moved onto land had access to new nutrient sources and relatively few predators. This led to the widespread distribution of tetrapods during the early Carboniferous period, a period sometimes called the "age of the amphibians."

Modern Amphibians

Amphibia comprises an estimated 6,770 extant species that inhabit tropical and temperate regions around the world. Amphibians can be divided into three clades: Urodela ("tailed-ones"), the salamanders; Anura ("tail-less ones"), the frogs; and Apoda ("legless ones"), the caecilians.

Urodela: Salamanders

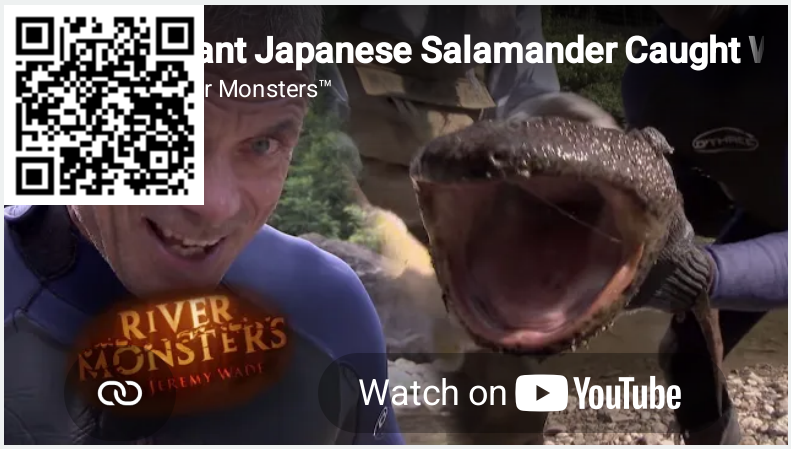
Salamanders are amphibians that belong to the order Urodela. Living salamanders (Figure **34.6.1**) include approximately 620 species, some of which are aquatic, other terrestrial, and some that live on land only as adults. Adult salamanders usually have a generalized tetrapod body plan with four limbs and a tail. They move by bending their bodies from side to side, called lateral undulation, in a fish-like manner while "walking" their arms and legs fore and aft. It is thought that their gait is similar to that used by early tetrapods. Respiration differs among different species. The majority of salamanders are lungless, and respiration occurs through the skin or through external gills. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs.

Unlike frogs, virtually all salamanders rely on internal fertilization of the eggs. The only male amphibians that possess copulatory structures are the caecilians, so fertilization among salamanders typically involves an elaborate and often prolonged courtship. Such a courtship allows the successful transfer of sperm from male to female via a spermatophore. Development in many of the most highly evolved salamanders, which are fully terrestrial, occurs during a prolonged egg stage, with the eggs guarded by the mother. During this time, the gilled larval stage is found only within the egg capsule, with the gills being resorbed, and metamorphosis being completed, before hatching. Hatchlings thus resemble tiny adults.



Figure **34.6.2**: Most salamanders have legs and a tail, but respiration varies among species. (credit: Valentina Storti)

Link to Learning



View River Monsters: Fish With Arms and Hands? to see a video about an unusually large salamander species.

Anura: Frogs

Frogs are amphibians that belong to the order Anura (Figure **34.6.3**). Anurans are among the most diverse groups of vertebrates, with approximately 5,965 species that occur on all of the continents except Antarctica. Anurans have a body plan that is more specialized for movement. Adult frogs use their hind limbs to jump on land. Frogs have a number of modifications that allow them to avoid predators, including skin that acts as camouflage. Many species of frogs and salamanders also release defensive chemicals from glands in the skin that are poisonous to predators.



Figure **34.6.3**: The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source.

Frog eggs are fertilized externally, and like other amphibians, frogs generally lay their eggs in moist environments. A moist environment is required as eggs lack a shell and thus dehydrate quickly in dry environments. Frogs demonstrate a great diversity of parental behaviors, with some species laying many eggs and exhibiting little parental care, to species that carry eggs and tadpoles on their hind legs or backs. The life cycle of frogs, as other amphibians, consists of two distinct stages: the larval stage followed by metamorphosis to an adult stage. The larval stage of a frog, the tadpole, is often a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, and lack limbs. At the end of the tadpole stage, frogs undergo metamorphosis into the adult form (Figure **34.6.4**). During this stage, the gills, tail, and lateral line system disappear, and four limbs develop. The jaws become larger and are suited for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop. These changes during metamorphosis allow the larvae to move onto land in the adult stage.



Figure **34.6.4**: A juvenile frog metamorphoses into a frog. Here, the frog has started to develop limbs, but its tadpole tail is still evident.

Apoda: Caecilians

An estimated 185 species comprise caecilians, a group of amphibians that belong to the order Apoda. Although they are vertebrates, a complete lack of limbs leads to their resemblance to earthworms in appearance. They are adapted for a soil-burrowing or aquatic lifestyle, and they are nearly blind. These animals are found in the tropics of South America, Africa, and Southern Asia. They have vestigial limbs, evidence that they evolved from a legged ancestor.

Evolution Connection: The Paleozoic Era and the Evolution of Vertebrates

The climate and geography of Earth was vastly different during the Paleozoic Era, when vertebrates arose, as compared to today. The Paleozoic spanned from approximately 542 to 251 million years ago. The landmasses on Earth were very different from those of today. Laurentia and Gondwana were continents located near the equator that subsumed much of the current day landmasses in a different configuration (Figure **34.6.5**). At this time, sea levels were very high, probably at a level that hasn't been reached since. As the Paleozoic progressed, glaciations created a cool global climate, but conditions warmed near the end of the first half of the Paleozoic. During the latter half of the Paleozoic, the landmasses began moving together, with the initial formation of a large northern block called Laurasia. This contained parts of what is now North America, along with Greenland, parts of Europe, and Siberia. Eventually, a single supercontinent, called Pangaea, was formed, starting in the latter third of the Paleozoic. Glaciations then began to affect Pangaea's climate, affecting the distribution of vertebrate life.

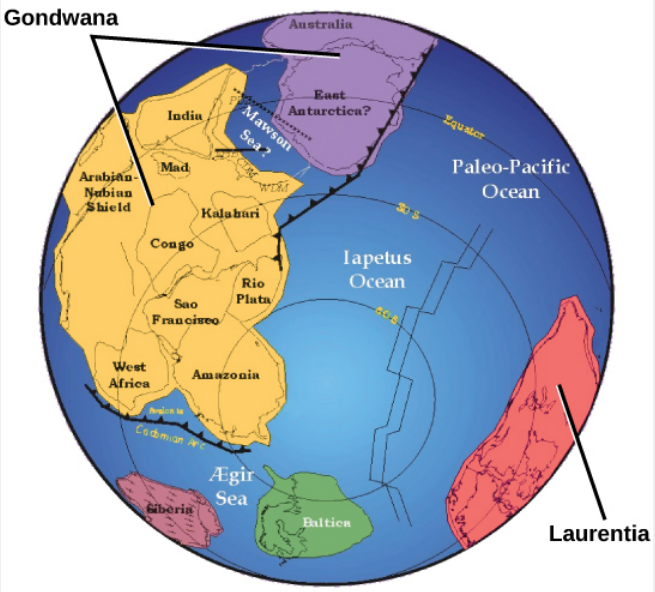
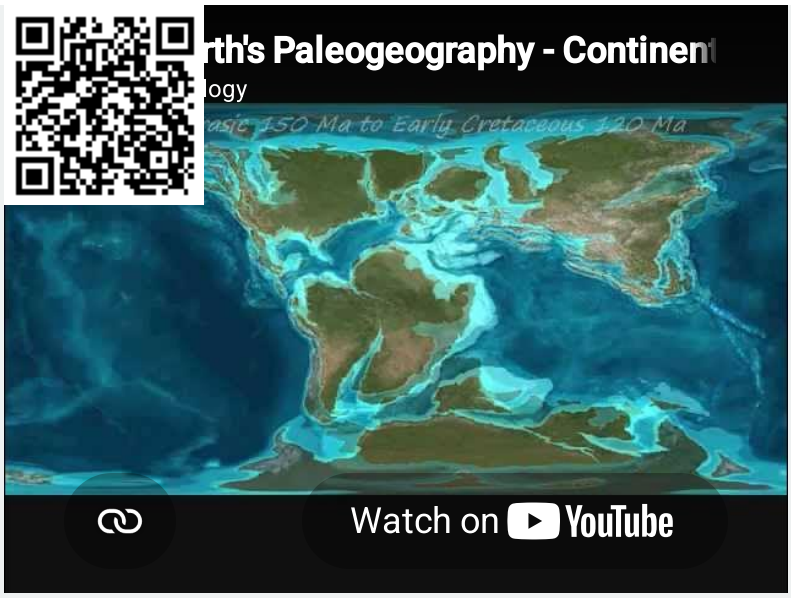


Figure **34.6.5**: During the Paleozoic Era, around 550 million years ago, the continent Gondwana formed. Both Gondwana and the continent Laurentia were located near the equator.

During the early Paleozoic, the amount of carbon dioxide in the atmosphere was much greater than it is today. This may have begun to change later, as land plants became more common. As the roots of land plants began to infiltrate rock and soil began to form, carbon dioxide was drawn out of the atmosphere and became trapped in the rock. This reduced the levels of carbon dioxide and increased the levels of oxygen in the atmosphere, so that by the end of the Paleozoic, atmospheric conditions were similar to those of today.

As plants became more common through the latter half of the Paleozoic, microclimates began to emerge and ecosystems began to change. As plants and ecosystems continued to grow and become more complex, vertebrates moved from the water to land. The presence of shoreline vegetation may have contributed to the movement of vertebrates onto land. One hypothesis suggests that the fins of aquatic vertebrates were used to maneuver through this vegetation, providing a precursor to the movement of fins on land and the development of limbs. The late Paleozoic was a time of diversification of vertebrates, as amniotes emerged and became two different lines that gave rise, on one hand, to mammals, and, on the other hand, to reptiles and birds. Many marine vertebrates became extinct near the end of the Devonian period, which ended about 360 million years ago, and both marine and terrestrial vertebrates were decimated by a mass extinction in the early Permian period about 250 million years ago.

Link to Learning



View Earth's Paleogeography: Continental Movements Through Time to see changes in Earth as life evolved.

Summary

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians are limbless. The most important characteristic of extant amphibians is a moist, permeable skin used for cutaneous respiration. The fossil record provides evidence of amphibian species, now extinct, that arose over 400 million years ago as the first tetrapods. Amphibia can be divided into three clades: salamanders (Urodela), frogs (Anura), and caecilians (Apoda). The life cycle of frogs, like the majority of amphibians, consists of two distinct stages: the larval stage and metamorphosis to an adult stage. Some species in all orders bypass a free-living larval stage.

Footnotes

1. 1 Daeschler, E. B., Shubin, N. H., and Jenkins, F. J. "A Devonian tetrapod-like fish and the evolution of the tetrapod body plan," *Nature* 440 (2006): 757–763, doi:10.1038/nature04639, http://www.nature.com/nature/journal/v440/n7085/abs/nature04639.html.

Glossary

Acanthostega
one of the earliest known tetrapods

Amphibia
frogs, salamanders, and caecilians

Anura
frogs

Apoda
caecilians

caecilian
legless amphibian that belongs to the clade Apoda

cutaneous respiration
gas exchange through the skin

frog

tail-less amphibian that belongs to the clade Anura

salamander

tailed amphibian that belongs to the clade Urodela

tadpole

larval stage of a frog

Urodela

salamanders

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34.7: Reptiles

Skills to Develop

- Describe the main characteristics of amniotes
- Explain the difference between anapsids, synapsids, and diapsids, and give an example of each
- Identify the characteristics of reptiles
- Discuss the evolution of reptiles

The amniotes —reptiles, birds, and mammals—are distinguished from amphibians by their terrestrially adapted egg, which is protected by amniotic membranes. The evolution of amniotic membranes meant that the embryos of amniotes were provided with their own aquatic environment, which led to less dependence on water for development and thus allowed the amniotes to branch out into drier environments. This was a significant development that distinguished them from amphibians, which were restricted to moist environments due their shell-less eggs. Although the shells of various amniotic species vary significantly, they all allow retention of water. The shells of bird eggs are composed of calcium carbonate and are hard, but fragile. The shells of reptile eggs are leathery and require a moist environment. Most mammals do not lay eggs (except for monotremes). Instead, the embryo grows within the mother's body; however, even with this internal gestation, amniotic membranes are still present.

Characteristics of Amniotes

The amniotic egg is the key characteristic of amniotes. In amniotes that lay eggs, the shell of the egg provides protection for the developing embryo while being permeable enough to allow for the exchange of carbon dioxide and oxygen. The albumin, or egg white, provides the embryo with water and protein, whereas the fattier egg yolk is the energy supply for the embryo, as is the case with the eggs of many other animals, such as amphibians. However, the eggs of amniotes contain three additional extra-embryonic membranes: the chorion, amnion, and allantois (Figure **34.7.1**). Extra-embryonic membranes are membranes present in amniotic eggs that are not a part of the body of the developing embryo. While the inner amniotic membrane surrounds the embryo itself, the chorion surrounds the embryo and yolk sac. The chorion facilitates exchange of oxygen and carbon dioxide between the embryo and the egg's external environment. The amnion protects the embryo from mechanical shock and supports hydration. The allantois stores nitrogenous wastes produced by the embryo and also facilitates respiration. In mammals, membranes that are homologous to the extra-embryonic membranes in eggs are present in the placenta.

Art Connection

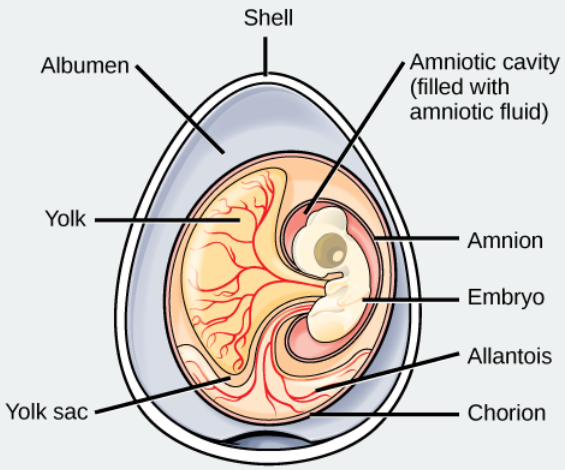


Figure **34.7.1**: The key features of an amniotic egg are shown.

Which of the following statements about the parts of an egg are false?

A. The allantois stores nitrogenous waste and facilitates respiration.
B. The chorion facilitates gas exchange.
C. The yolk provides food for the growing embryo.

D. The amniotic cavity is filled with albumen.

Additional derived characteristics of amniotes include waterproof skin, due to the presence of lipids, and costal (rib) ventilation of the lungs.

Evolution of Amniotes

The first amniotes evolved from amphibian ancestors approximately 340 million years ago during the Carboniferous period. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids and sauropsids. Synapsids include all mammals, including extinct mammalian species. Synapsids also include therapsids, which were mammal-like reptiles from which mammals evolved. Sauropsids include reptiles and birds, and can be further divided into anapsids and diapsids. The key differences between the synapsids, anapsids, and diapsids are the structures of the skull and the number of temporal fenestrae behind each eye (Figure **34.7.2**). Temporal fenestrae are post-orbital openings in the skull that allow muscles to expand and lengthen. Anapsids have no temporal fenestrae, synapsids have one, and diapsids have two. Anapsids include extinct organisms and may, based on anatomy, include turtles. However, this is still controversial, and turtles are sometimes classified as diapsids based on molecular evidence. The diapsids include birds and all other living and extinct reptiles.

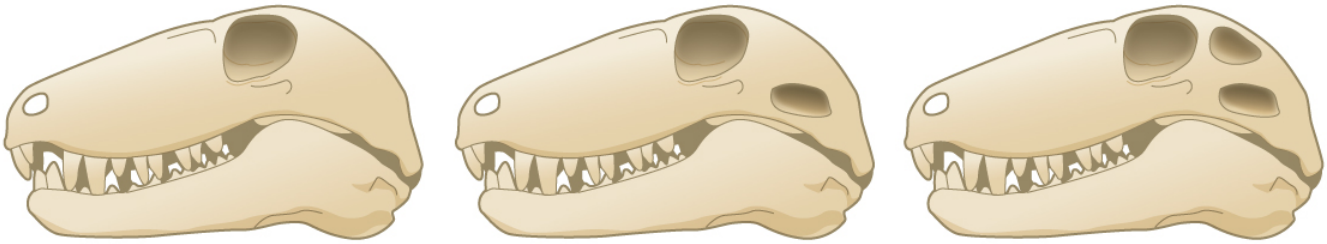


Figure **34.7.2**: Compare the skulls and temporal fenestrae of anapsids, synapsids, and diapsids. Anapsids have no openings, synapsids have one opening, and diapsids have two openings.

The diapsids diverged into two groups, the Archosauromorpha (“ancient lizard form”) and the Lepidosauromorpha (“scaly lizard form”) during the Mesozoic period (Figure **34.7.3**). The lepidosaurs include modern lizards, snakes, and tuataras. The archosaurs include modern crocodiles and alligators, and the extinct pterosaurs (“winged lizard”) and dinosaurs (“terrible lizard”). Clade Dinosauria includes birds, which evolved from a branch of dinosaurs.

Art Connection

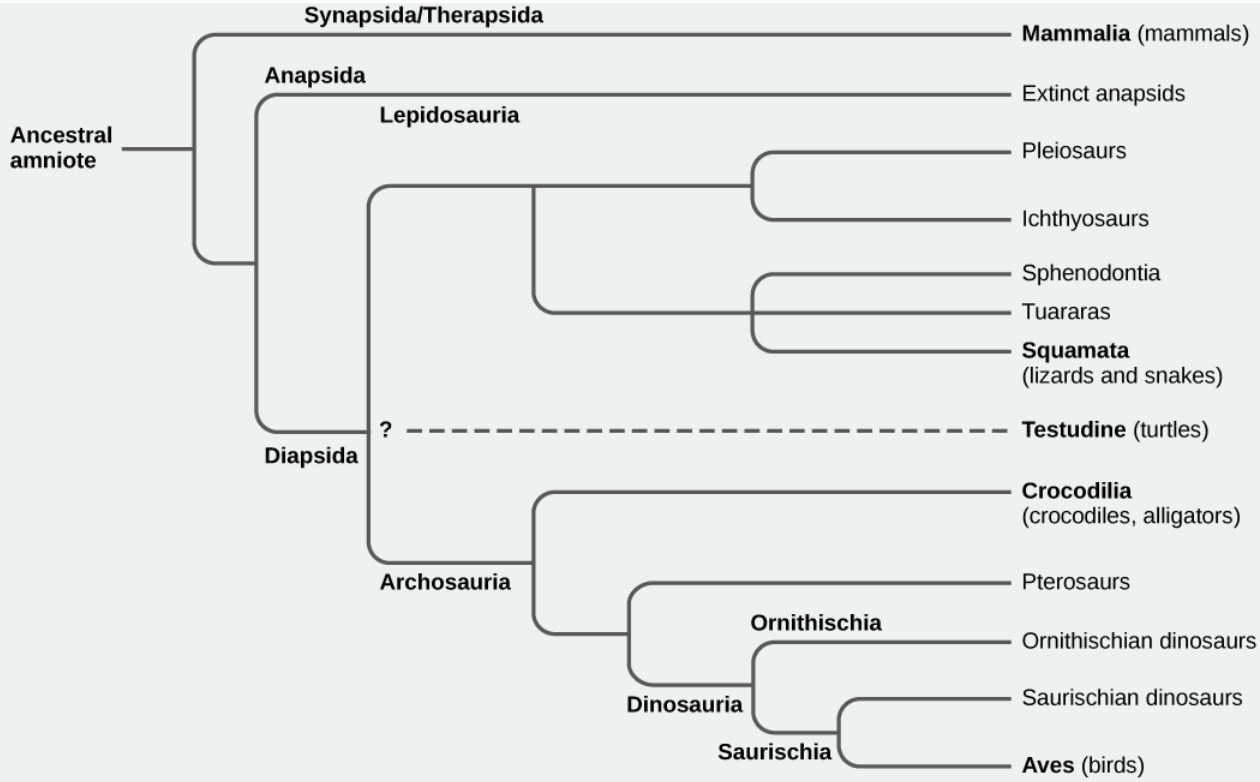


Figure **34.7.3**: This chart shows the evolution of amniotes. The placement of Testudines (turtles) is currently still debated.

Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

In the past, the most common division of amniotes has been into the classes Mammalia, Reptilia, and Aves. Birds are descended, however, from dinosaurs, so this classical scheme results in groups that are not true clades. We will consider birds as a group distinct from reptiles for the purpose of this discussion with the understanding that this does not completely reflect phylogenetic history and relationships.

Characteristics of Reptiles

Reptiles are tetrapods. Limbless reptiles—snakes and other squamates—have vestigial limbs and, like caecilians, are classified as tetrapods because they are descended from four-limbed ancestors. Reptiles lay eggs enclosed in shells on land. Even aquatic reptiles return to the land to lay eggs. They usually reproduce sexually with internal fertilization. Some species display ovoviviparity, with the eggs remaining in the mother's body until they are ready to hatch. Other species are viviparous, with the offspring born alive.

One of the key adaptations that permitted reptiles to live on land was the development of their scaly skin, containing the protein keratin and waxy lipids, which reduced water loss from the skin. This occlusive skin means that reptiles cannot use their skin for respiration, like amphibians, and thus all breathe with lungs.

Reptiles are ectotherms, animals whose main source of body heat comes from the environment. This is in contrast to endotherms, which use heat produced by metabolism to regulate body temperature. In addition to being ectothermic, reptiles are categorized as poikilotherms, or animals whose body temperatures vary rather than remain stable. Reptiles have behavioral adaptations to help regulate body temperature, such as basking in sunny places to warm up and finding shady spots or going underground to cool down. The advantage of ectothermy is that metabolic energy from food is not required to heat the body; therefore, reptiles can survive on about 10 percent of the calories required by a similarly sized endotherm. In cold weather, some reptiles such as the garter snake brumate. Brumation is similar to hibernation in that the animal becomes less active and can go for long periods without eating, but differs from hibernation in that brumating reptiles are not asleep or living off fat reserves. Rather, their metabolism is slowed in response to cold temperatures, and the animal is very sluggish.

Evolution of Reptiles

Reptiles originated approximately 300 million years ago during the Carboniferous period. One of the oldest known amniotes is Casineria, which had both amphibian and reptilian characteristics. One of the earliest undisputed reptiles was Hylonomus. Soon after the first amniotes appeared, they diverged into three groups—synapsids, anapsids, and diapsids—during the Permian period. The Permian period also saw a second major divergence of diapsid reptiles into archosaurs (predecessors of crocodilians and dinosaurs) and lepidosaurs (predecessors of snakes and lizards). These groups remained inconspicuous until the Triassic period, when the archosaurs became the dominant terrestrial group due to the extinction of large-bodied anapsids and synapsids during the Permian-Triassic extinction. About 250 million years ago, archosaurs radiated into the dinosaurs and the pterosaurs.

Although they are sometimes mistakenly called dinosaurs, the pterosaurs were distinct from true dinosaurs (Figure **34.7.4**). Pterosaurs had a number of adaptations that allowed for flight, including hollow bones (birds also exhibit hollow bones, a case of convergent evolution). Their wings were formed by membranes of skin that attached to the long, fourth finger of each arm and extended along the body to the legs.



Figure **34.7.4**: Pterosaurs, which existed from the late Triassic to the Cretaceous period (210 to 65.5 million years ago), possessed wings but are not believed to have been capable of powered flight. Instead, they may have been able to soar after launching from cliffs. (credit: Mark Witton, Darren Naish)

The dinosaurs were a diverse group of terrestrial reptiles with more than 1,000 species identified to date. Paleontologists continue to discover new species of dinosaurs. Some dinosaurs were quadrupeds (Figure **34.7.5**); others were bipeds. Some were carnivorous, whereas others were herbivorous. Dinosaurs laid eggs, and a number of nests containing fossilized eggs have been found. It is not known whether dinosaurs were endotherms or ectotherms. However, given that modern birds are endothermic, the dinosaurs that served as ancestors to birds likely were endothermic as well. Some fossil evidence exists for dinosaurian parental care, and comparative biology supports this hypothesis since the archosaur birds and crocodilians display parental care.

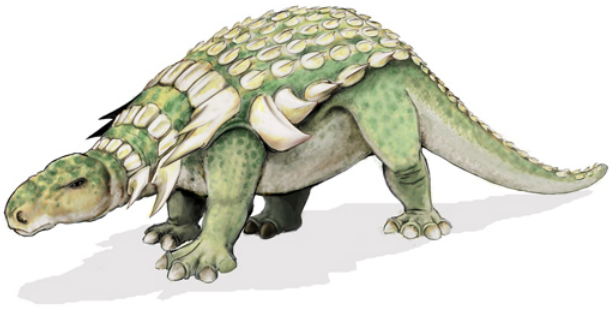


Figure **34.7.5**: *Edmontonia* was an armored dinosaur that lived in the late Cretaceous period, 145.5 to 65.6 million years ago. (credit: Mariana Ruiz Villareal)

Dinosaurs dominated the Mesozoic Era, which was known as the “age of reptiles.” The dominance of dinosaurs lasted until the end of the Cretaceous, the last period of the Mesozoic Era. The Cretaceous-Tertiary extinction resulted in the loss of most of the large-bodied animals of the Mesozoic Era. Birds are the only living descendants of one of the major clades of dinosaurs.

Link to Learning

Visit this site to see a video discussing the hypothesis that an asteroid caused the Cretaceous-Triassic (KT) extinction.

Modern Reptiles

Class Reptilia includes many diverse species that are classified into four living clades. These are the 25 species of Crocodilia, 2 species of Sphenodontia, approximately 9,200 Squamata species, and the Testudines, with about 325 species.

Crocodilia

Crocodilia (“small lizard”) arose with a distinct lineage by the middle Triassic; extant species include alligators, crocodiles, and caimans. Crocodilians (Figure **34.7.6**) live throughout the tropics and subtropics of Africa, South America, Southern Florida, Asia, and Australia. They are found in freshwater, saltwater, and brackish habitats, such as rivers and lakes, and spend most of their time in water. Some species are able to move on land due to their semi-erect posture.



Figure **34.7.6**: Crocodilians, such as this Siamese crocodile (*Crocodylus siamensis*), provide parental care for their offspring. (credit: Keshav Mukund Kandhadai)

Sphenodontia

Sphenodontia (“wedge tooth”) arose in the Mesozoic era and includes only one living genus, *Tuatara*, comprising two species that are found in New Zealand (Figure **34.7.7**). Tuataras measure up to 80 centimeters and weigh about 1 kilogram. Although quite lizard-like in gross appearance, several unique features of the skull and jaws clearly define them and distinguish the group from the squamates.



Figure **34.7.7**: This tuatara from New Zealand may resemble a lizard but belongs to a distinct lineage, the Sphenodontidae family. (credit: Sid Mosdell)

Squamata

Squamata ("scaly") arose in the late Permian, and extant species include lizards and snakes. Both are found on all continents except Antarctica. Lizards and snakes are most closely related to tuataras, both groups having evolved from a lepidosaurian ancestor. Squamata is the largest extant clade of reptiles (Figure **34.7.8**). Most lizards differ from snakes by having four limbs, although these have been variously lost or significantly reduced in at least 60 lineages. Snakes lack eyelids and external ears, which are present in lizards. Lizard species range in size from chameleons and geckos, which are a few centimeters in length, to the Komodo dragon, which is about 3 meters in length. Most lizards are carnivorous, but some large species, such as iguanas, are herbivores.



Figure **34.7.8**: This Jackson's chameleon (*Trioceros jacksonii*) blends in with its surroundings.

Snakes are thought to have descended from either burrowing lizards or aquatic lizards over 100 million years ago (Figure **34.7.9**). Snakes comprise about 3,000 species and are found on every continent except Antarctica. They range in size from 10 centimeter-long thread snakes to 10 meter-long pythons and anacondas. All snakes are carnivorous and eat small animals, birds, eggs, fish, and insects. The snake body form is so specialized that, in its general morphology, a "snake is a snake." Their specializations all point to snakes having evolved to feed on relatively large prey (even though some current species have reversed this trend). Although variations exist, most snakes have a skull that is very flexible, involving eight rotational joints. They also differ from other squamates by having mandibles (lower jaws) without either bony or ligamentous attachment anteriorly. Having this connection via skin and muscle allows for great expansion of the gape and independent motion of the two sides—both advantages in swallowing big items.



Figure **34.7.9**: The garter snake belongs to the genus *Thamnophis*, the most widely distributed reptile genus in North America. (credit: Steve Jurvetson)

Testudines

Turtles are members of the clade Testudines (“having a shell”) (Figure **34.7.10**). Turtles are characterized by a bony or cartilaginous shell. The shell consists of the ventral surface called the plastron and the dorsal surface called the carapace, which develops from the ribs. The plastron is made of scutes or plates; the scutes can be used to differentiate species of turtles. The two clades of turtles are most easily recognized by how they retract their necks. The dominant group, which includes all North American species, retracts its neck in a vertical S-curve. Turtles in the less speciose clade retract the neck with a horizontal curve.

Turtles arose approximately 200 million years ago, predating crocodiles, lizards, and snakes. Similar to other reptiles, turtles are ectotherms. They lay eggs on land, although many species live in or near water. None exhibit parental care. Turtles range in size from the speckled padloper tortoise at 8 centimeters (3.1 inches) to the leatherback sea turtle at 200 centimeters (over 6 feet). The term “turtle” is sometimes used to describe only those species of Testudines that live in the sea, with the terms “tortoise” and “terrapin” used to refer to species that live on land and in fresh water, respectively.



Figure **34.7.10**: The African spurred tortoise (*Geochelone sulcata*) lives at the southern edge of the Sahara Desert. It is the third largest tortoise in the world. (credit: Jim Bowen)

Summary

The amniotes are distinguished from amphibians by the presence of a terrestrially adapted egg protected by amniotic membranes. The amniotes include reptiles, birds, and mammals. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids (mammals) and sauropsids. Sauropsids can be further divided into anapsids (turtles) and

diapsids (birds and reptiles). Reptiles are tetrapods either having four limbs or descending from such. Limbless reptiles (snakes) are classified as tetrapods, as they are descended from four-limbed organisms. One of the key adaptations that permitted reptiles to live on land was the development of scaly skin containing the protein keratin, which prevented water loss from the skin. Reptilia includes four living clades: Crocodilia (crocodiles and alligators), Sphenodontia (tuataras), Squamata (lizards and snakes), and Testudines (turtles).

Art Connections

Figure **34.7.1**: Which of the following statements about the parts of an egg are false?

A. The allantois stores nitrogenous waste and facilitates respiration.
B. The chorion facilitates gas exchange.
C. The yolk provides food for the growing embryo.
D. The amniotic cavity is filled with albumen.

Answer

D

Figure **34.7.3**: Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

Answer

The ancestor of modern Testudines may at one time have had a second opening in the skull, but over time this might have been lost.

Glossary

amniote
animal that produces a terrestrially adapted egg protected by amniotic membranes

allantois
membrane of the egg that stores nitrogenous wastes produced by the embryo; also facilitates respiration

amnion
membrane of the egg that protects the embryo from mechanical shock and prevents dehydration

anapsid
animal having no temporal fenestrae in the cranium

archosaur
modern crocodilian or bird, or an extinct pterosaur or dinosaur

brumation
period of much reduced metabolism and torpor that occurs in any ectotherm in cold weather

Casineria
one of the oldest known amniotes; had both amphibian and reptilian characteristics

chorion
membrane of the egg that surrounds the embryo and yolk sac

Crocodilia

crocodiles and alligators

diapsid
animal having two temporal fenestrae in the cranium

Hylonomus
one of the earliest reptiles

lepidosaur
modern lizards, snakes, and tuataras

sauropsid
reptile or bird

Sphenodontia
clade of tuataras

Squamata
clade of lizards and snakes

synapsid
mammal having one temporal fenestra

temporal fenestra
non-orbital opening in the skull that may allow muscles to expand and lengthen

Testudines
order of turtles

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34.8: Birds

Skills to Develop

- Describe the evolutionary history of birds
- Describe the derived characteristics in birds that facilitate flight

The most obvious characteristic that sets birds apart from other modern vertebrates is the presence of feathers, which are modified scales. While vertebrates like bats fly without feathers, birds rely on feathers and wings, along with other modifications of body structure and physiology, for flight.

Characteristics of Birds

Birds are endothermic, and because they fly, they require large amounts of energy, necessitating a high metabolic rate. Like mammals, which are also endothermic, birds have an insulating covering that keeps heat in the body: feathers. Specialized feathers called down feathers are especially insulating, trapping air in spaces between each feather to decrease the rate of heat loss. Certain parts of a bird's body are covered in down feathers, and the base of other feathers have a downy portion, whereas newly hatched birds are covered in down.

Feathers not only act as insulation but also allow for flight, enabling the lift and thrust necessary to become airborne. The feathers on a wing are flexible, so the collective feathers move and separate as air moves through them, reducing the drag on the wing. Flight feathers are asymmetrical, which affects airflow over them and provides some of the lifting and thrusting force required for flight (Figure **34.8.1**). Two types of flight feathers are found on the wings, primary feathers and secondary feathers. Primary feathers are located at the tip of the wing and provide thrust. Secondary feathers are located closer to the body, attach to the forearm portion of the wing and provide lift. Contour feathers are the feathers found on the body, and they help reduce drag produced by wind resistance during flight. They create a smooth, aerodynamic surface so that air moves smoothly over the bird's body, allowing for efficient flight.

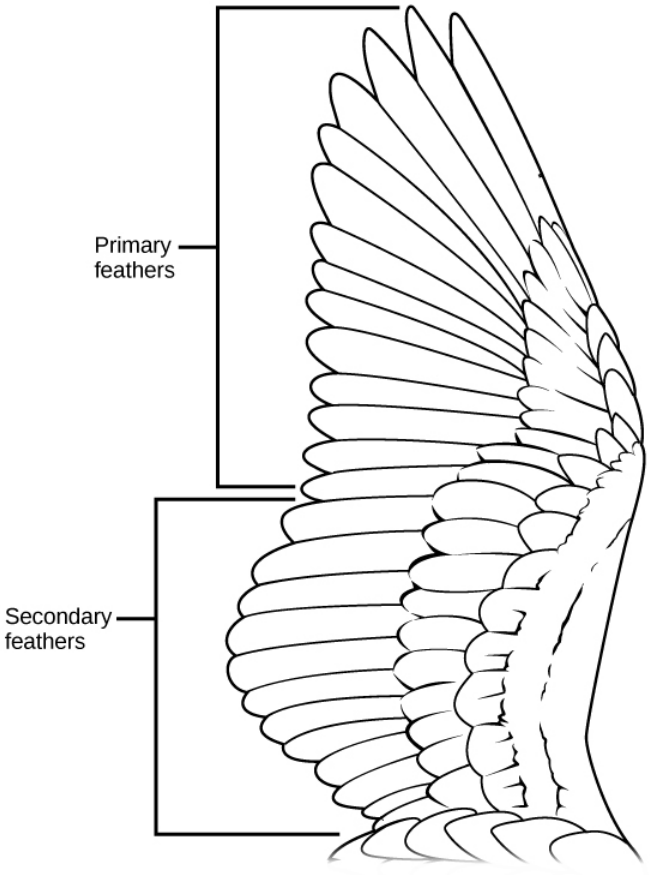


Figure **34.8.1**: Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift.

Flapping of the entire wing occurs primarily through the actions of the chest muscles, the pectoralis and the supracoracoideus. These muscles are highly developed in birds and account for a higher percentage of body mass than in most mammals. These attach to a blade-shaped keel, like that of a boat, located on the sternum. The sternum of birds is larger than that of other vertebrates, which accommodates the large muscles required to generate enough upward force to generate lift with the flapping of the wings. Another skeletal modification found in most birds is the fusion of the two clavicles (collarbones), forming the furcula or wishbone. The furcula is flexible enough to bend and provide support to the shoulder girdle during flapping.

An important requirement of flight is a low body weight. As body weight increases, the muscle output required for flying increases. The largest living bird is the ostrich, and while it is much smaller than the largest mammals, it is flightless. For birds that do fly, reduction in body weight makes flight easier. Several modifications are found in birds to reduce body weight, including pneumatization of bones. Pneumatic bones are bones that are hollow, rather than filled with tissue (Figure **34.8.2**). They contain air spaces that are sometimes connected to air sacs, and they have struts of bone to provide structural reinforcement. Pneumatic bones are not found in all birds, and they are more extensive in large birds than in small birds. Not all bones of the skeleton are pneumatic, although the skulls of almost all birds are.



Figure **34.8.2**: Many birds have hollow, pneumatic bones, which make flight easier.

Other modifications that reduce weight include the lack of a urinary bladder. Birds possess a cloaca, a structure that allows water to be reabsorbed from waste back into the bloodstream. Uric acid is not expelled as a liquid but is concentrated into urate salts, which are expelled along with fecal matter. In this way, water is not held in the urinary bladder, which would increase body weight. Most bird species only possess one ovary rather than two, further reducing body mass.

The air sacs that extend into bones to form pneumatic bones also join with the lungs and function in respiration. Unlike mammalian lungs in which air flows in two directions, as it is breathed in and out, airflow through bird lungs travels in one direction (Figure 34.8.3). Air sacs allow for this unidirectional airflow, which also creates a cross-current exchange system with the blood. In a cross-current or counter-current system, the air flows in one direction and the blood flows in the opposite direction, creating a very efficient means of gas exchange.

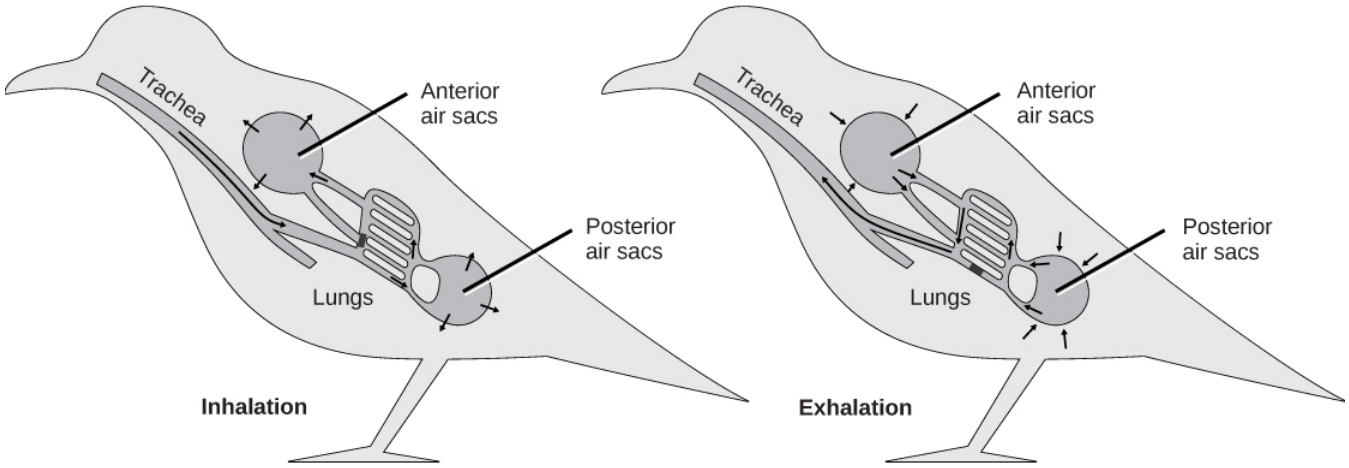


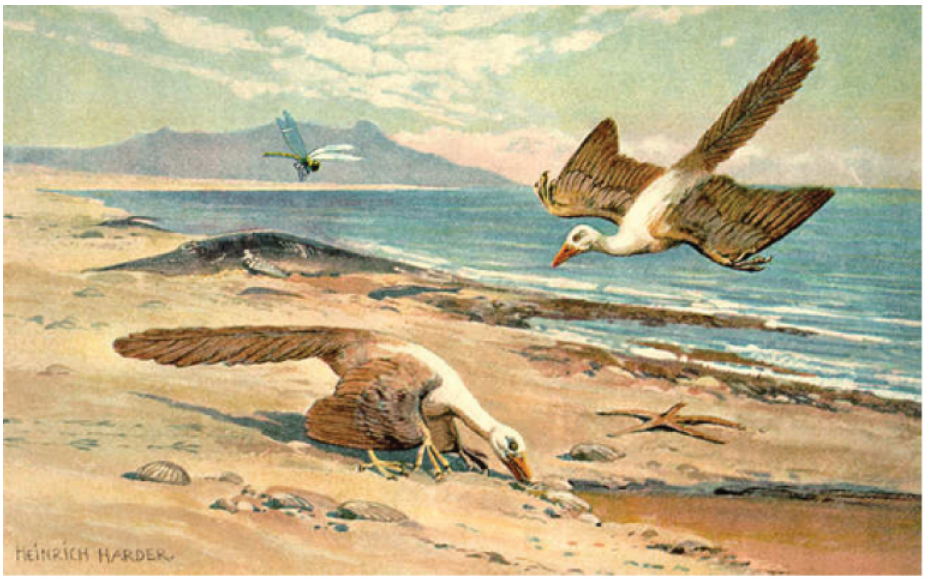
Figure 34.8.3: Avian respiration is an efficient system of gas exchange with air flowing unidirectionally. During inhalation, air passes from the trachea into posterior air sacs, then through the lungs to anterior air sacs. The air sacs are connected to the hollow interior of bones. During exhalation, air from air sacs passes into the lungs and out the trachea. (credit: modification of work by L. Shyamal)

Evolution of Birds

The evolutionary history of birds is still somewhat unclear. Due to the fragility of bird bones, they do not fossilize as well as other vertebrates. Birds are diapsids, meaning they have two fenestrations or openings in their skulls. Birds belong to a group of diapsids called the archosaurs, which also includes crocodiles and dinosaurs. It is commonly accepted that birds evolved from dinosaurs.

Dinosaurs (including birds) are further subdivided into two groups, the Saurischia ("lizard like") and the Ornithischia ("bird like"). Despite the names of these groups, it was not the bird-like dinosaurs that gave rise to modern birds. Rather, Saurischia diverged into two groups: One included the long-necked herbivorous dinosaurs, such as Apatosaurus. The second group, bipedal predators called theropods, includes birds. This course of evolution is suggested by similarities between theropod fossils and birds, specifically in the structure of the hip and wrist bones, as well as the presence of the wishbone, formed by the fusing of the clavicles.

One important fossil of an animal intermediate to dinosaurs and birds is *Archaeopteryx*, which is from the Jurassic period (Figure 34.8.4). *Archaeopteryx* is important in establishing the relationship between birds and dinosaurs, because it is an intermediate fossil, meaning it has characteristics of both dinosaurs and birds. Some scientists propose classifying it as a bird, but others prefer to classify it as a dinosaur. The fossilized skeleton of *Archaeopteryx* looks like that of a dinosaur, and it had teeth whereas birds do not, but it also had feathers modified for flight, a trait associated only with birds among modern animals. Fossils of older feathered dinosaurs exist, but the feathers do not have the characteristics of flight feathers.



(a)



(b)

Figure **34.8.4**: (a) *Archaeopteryx* lived in the late Jurassic Period around 150 million years ago. It had teeth like a dinosaur, but had (b) flight feathers like modern birds, which can be seen in this fossil.

It is still unclear exactly how flight evolved in birds. Two main theories exist, the arboreal ("tree") hypothesis and the terrestrial ("land") hypothesis. The arboreal hypothesis posits that tree-dwelling precursors to modern birds jumped from branch to branch using their feathers for gliding before becoming fully capable of flapping flight. In contrast to this, the terrestrial hypothesis holds that running was the stimulus for flight, as wings could be used to improve running and then became used for flapping flight. Like the question of how flight evolved, the question of how endothermy evolved in birds still is unanswered. Feathers provide insulation, but this is only beneficial if body heat is being produced internally. Similarly, internal heat production is only viable if insulation is present to retain that heat. It has been suggested that one or the other—feathers or endothermy—evolved in response to some other selective pressure.

During the Cretaceous period, a group known as the Enantiornithes was the dominant bird type (Figure **34.8.5**). Enantiornithes means "opposite birds," which refers to the fact that certain bones of the feet are joined differently than the way the bones are joined in modern birds. These birds formed an evolutionary line separate from modern birds, and they did not survive past the Cretaceous. Along with the Enantiornithes, Ornithurae birds (the evolutionary line that includes modern birds) were also present in the Cretaceous. After the extinction of Enantiornithes, modern birds became the dominant bird, with a large radiation occurring during the Cenozoic Era. Referred to as Neornithes ("new birds"), modern birds are now classified into two groups, the Paleognathae ("old jaw") or ratites, a group of flightless birds including ostriches, emus, rheas, and kiwis, and the Neognathae ("new jaw"), which includes all other birds.



Figure **34.8.5**: *Shanweiniao cooperorum* was a species of Enantiornithes that did not survive past the Cretaceous period. (credit: Nobu Tamura)

Career Connection: Veterinarian

Veterinarians treat diseases, disorders, and injuries in animals, primarily vertebrates. They treat pets, livestock, and animals in zoos and laboratories. Veterinarians usually treat dogs and cats, but also treat birds, reptiles, rabbits, and other animals that are kept as pets. Veterinarians that work with farms and ranches treat pigs, goats, cows, sheep, and horses.

Veterinarians are required to complete a degree in veterinary medicine, which includes taking courses in animal physiology, anatomy, microbiology, and pathology, among many other courses. The physiology and biochemistry of different vertebrate species differ greatly.

Veterinarians are also trained to perform surgery on many different vertebrate species, which requires an understanding of the vastly different anatomies of various species. For example, the stomach of ruminants like cows has four compartments versus one compartment for non-ruminants. Birds also have unique anatomical adaptations that allow for flight.

Some veterinarians conduct research in academic settings, broadening our knowledge of animals and medical science. One area of research involves understanding the transmission of animal diseases to humans, called zoonotic diseases. For example, one area of great concern is the transmission of the avian flu virus to humans. One type of avian flu virus, H5N1, is a highly pathogenic strain that has been spreading in birds in Asia, Europe, Africa, and the Middle East. Although the virus does not cross over easily to humans, there have been cases of bird-to-human transmission. More research is needed to understand how this virus can cross the species barrier and how its spread can be prevented.

Summary

Birds are endothermic, meaning they produce their own body heat and regulate their internal temperature independently of the external temperature. Feathers not only act as insulation but also allow for flight, providing lift with secondary feathers and thrust with primary feathers. Pneumatic bones are bones that are hollow rather than filled with tissue, containing air spaces that are sometimes connected to air sacs. Airflow through bird lungs travels in one direction, creating a cross-current exchange with the blood. Birds are diapsids and belong to a group called the archosaurs. Birds are thought to have evolved from theropod dinosaurs. The oldest known fossil of a bird is that of *Archaeopteryx*, which is from the Jurassic period. Modern birds are now classified into two groups, Paleognathae and Neognathae.

Glossary

Archaeopteryx
transition species from dinosaur to bird from the Jurassic period

contour feather
feather that creates an aerodynamic surface for efficient flight

down feather
feather specialized for insulation

Enantiornithes
dominant bird group during the Cretaceous period

flight feather
feather specialized for flight

furcula
wishbone formed by the fusing of the clavicles

Neognathae

birds other than the Paleognathae

Neornithes
modern birds

Paleognathae
ratites; flightless birds, including ostriches and emus

pneumatic bone
air-filled bone

primary feather
feather located at the tip of the wing that provides thrust

secondary feather
feather located at the base of the wing that provides lift

theropod
dinosaur group ancestral to birds

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34.9: Mammals

Skills to Develop

- Name and describe the distinguishing features of the three main groups of mammals
- Describe the proposed line of descent that produced mammals
- List some derived features that may have arisen in response to mammals' need for constant, high-level metabolism

Mammals are vertebrates that possess hair and mammary glands. Several other characteristics are distinctive to mammals, including certain features of the jaw, skeleton, integument, and internal anatomy. Modern mammals belong to three clades: monotremes, marsupials, and eutherians (or placental mammals).

Characteristics of Mammals

The presence of hair is one of the most obvious signs of a mammal. Although it is not very extensive on certain species, such as whales, hair has many important functions for mammals. Mammals are endothermic, and hair provides insulation to retain heat generated by metabolic work. Hair traps a layer of air close to the body, retaining heat. Along with insulation, hair can serve as a sensory mechanism via specialized hairs called vibrissae, better known as whiskers. These attach to nerves that transmit information about sensation, which is particularly useful to nocturnal or burrowing mammals. Hair can also provide protective coloration or be part of social signaling, such as when an animal's hair stands "on end."

Mammalian integument, or skin, includes secretory glands with various functions. Sebaceous glands produce a lipid mixture called sebum that is secreted onto the hair and skin for water resistance and lubrication. Sebaceous glands are located over most of the body. Eccrine glands produce sweat, or perspiration, which is mainly composed of water. In most mammals, eccrine glands are limited to certain areas of the body, and some mammals do not possess them at all. However, in primates, especially humans, sweat figures prominently in thermoregulation, regulating the body through evaporative cooling. Sweat glands are located over most of the body surface in primates. Apocrine glands, or scent glands, secrete substances that are used for chemical communication, such as in skunks. Mammary glands produce milk that is used to feed newborns. While male monotremes and eutherians possess mammary glands, male marsupials do not. Mammary glands likely are modified sebaceous or eccrine glands, but their evolutionary origin is not entirely clear.

The skeletal system of mammals possesses many unique features. The lower jaw of mammals consists of only one bone, the dentary. The jaws of other vertebrates are composed of more than one bone. In mammals, the dentary bone joins the skull at the squamosal bone, while in other vertebrates, the quadrate bone of the jaw joins with the articular bone of the skull. These bones are present in mammals, but they have been modified to function in hearing and form bones in the middle ear (Figure **34.9.1**). Other vertebrates possess only one middle ear bone, the stapes. Mammals have three: the malleus, incus, and stapes. The malleus originated from the articular bone, whereas the incus originated from the quadrate bone. This arrangement of jaw and ear bones aids in distinguishing fossil mammals from fossils of other synapsids.

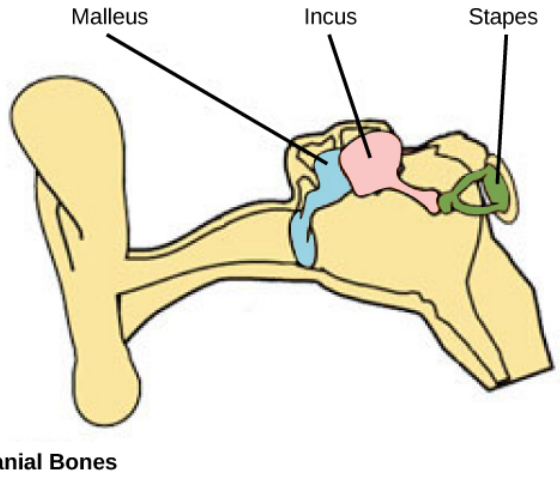


Figure **34.9.1**: Bones of the mammalian inner ear are modified from bones of the jaw and skull. (credit: NCI)

The adductor muscle that closes the jaw is composed of two muscles in mammals: the temporalis and the masseter. These allow side-to-side movement of the jaw, making chewing possible, which is unique to mammals. Most mammals have heterodont teeth, meaning that they have different types and shapes of teeth rather than just one type and shape of tooth. Most mammals are diphyodonts, meaning that they have two sets of teeth in their lifetime: deciduous or “baby” teeth, and permanent teeth. Other vertebrates are polyphyodonts, that is, their teeth are replaced throughout their entire life.

Mammals, like birds, possess a four-chambered heart. Mammals also have a specialized group of cardiac fibers located in the walls of their right atrium called the sinoatrial node, or pacemaker, which determines the rate at which the heart beats. Mammalian erythrocytes (red blood cells) do not have nuclei, whereas the erythrocytes of other vertebrates are nucleated.

The kidneys of mammals have a portion of the nephron called the loop of Henle or nephritic loop, which allows mammals to produce urine with a high concentration of solutes, higher than that of the blood. Mammals lack a renal portal system, which is a system of veins that moves blood from the hind or lower limbs and region of the tail to the kidneys. Renal portal systems are present in all other vertebrates except jawless fishes. A urinary bladder is present in all mammals.

Mammalian brains have certain characteristics that differ from other vertebrates. In some, but not all mammals, the cerebral cortex, the outermost part of the cerebrum, is highly folded, allowing for a greater surface area than is possible with a smooth cortex. The optic lobes, located in the midbrain, are divided into two parts in mammals, whereas other vertebrates possess a single, undivided lobe. Eutherian mammals also possess a specialized structure that links the two cerebral hemispheres, called the corpus callosum.

Evolution of Mammals

Mammals are synapsids, meaning they have a single opening in the skull. They are the only living synapsids, as earlier forms became extinct by the Jurassic period. The early non-mammalian synapsids can be divided into two groups, the pelycosaurs and the therapsids. Within the therapsids, a group called the cynodonts are thought to be the ancestors of mammals (Figure **34.9.2**).



Figure **34.9.2**: Cynodonts, which first appeared in the Late Permian period 260 million years ago, are thought to be the ancestors of modern mammals. (credit: Nobu Tamura)

A key characteristic of synapsids is endothermy, rather than the ectothermy seen in most other vertebrates. The increased metabolic rate required to internally modify body temperature went hand in hand with changes to certain skeletal structures. The later synapsids, which had more evolved characteristics unique to mammals, possess cheeks for holding food and heterodont teeth, which are specialized for chewing, mechanically breaking down food to speed digestion and releasing the energy needed to produce heat. Chewing also requires the ability to chew and breathe at the same time, which is facilitated by the presence of a secondary palate. A secondary palate separates the area of the mouth where chewing occurs from the area above where respiration occurs, allowing breathing to proceed uninterrupted during chewing. A secondary palate is not found in pelycosaurs but is present in cynodonts and mammals. The jawbone also shows changes from early synapsids to later ones. The zygomatic arch, or cheekbone, is present in mammals and advanced therapsids such as cynodonts, but is not present in pelycosaurs. The presence of the zygomatic arch suggests the presence of the masseter muscle, which closes the jaw and functions in chewing.

In the appendicular skeleton, the shoulder girdle of therian mammals is modified from that of other vertebrates in that it does not possess a procoracoid bone or an interclavicle, and the scapula is the dominant bone.

Mammals evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period, some 205 million years ago. Early mammals were small, about the size of a small rodent. Mammals first began to diversify in the Mesozoic Era, from the Jurassic to the Cretaceous periods, although most of these mammals were extinct by the end of the

Mesozoic. During the Cretaceous period, another radiation of mammals began and continued through the Cenozoic Era, about 65 million years ago.

Living Mammals

The eutherians, or placental mammals, and the marsupials together comprise the clade of therian mammals. Monotremes, or metatherians, form their sister clade.

There are three living species of monotremes: the platypus and two species of echidnas, or spiny anteaters. The leathery-beaked platypus belongs to the family Ornithorhynchidae ("bird beak"), whereas echidnas belong to the family Tachyglossidae ("sticky tongue") (Figure **34.9.3**). The platypus and one species of echidna are found in Australia, and the other species of echidna is found in New Guinea. Monotremes are unique among mammals as they lay eggs, rather than giving birth to live young. The shells of their eggs are not like the hard shells of birds, but are a leathery shell, similar to the shells of reptile eggs. Monotremes have no teeth.



Figure **34.9.3**: (a) The platypus, a monotreme, possesses a leathery beak and lays eggs rather than giving birth to live young. (b) The echidna is another monotreme. (credit b: modification of work by Barry Thomas)

Marsupials are found primarily in Australia, though the opossum is found in North America. Australian marsupials include the kangaroo, koala, bandicoot, Tasmanian devil (Figure **34.9.4**), and several other species. Most species of marsupials possess a pouch in which the very premature young reside after birth, receiving milk and continuing to develop. Marsupials differ from eutherians in that there is a less complex placental connection: The young are born at an extremely early age and latch onto the nipple within the pouch.



Figure **34.9.4**: The Tasmanian devil is one of several marsupials native to Australia. (credit: Wayne McLean)

Eutherians are the most widespread of the mammals, occurring throughout the world. There are 18 to 20 orders of placental mammals. Some examples are Insectivora, the insect eaters; Edentata, the toothless anteaters; Rodentia, the rodents; Cetacea, the aquatic mammals including whales; Carnivora, carnivorous mammals including dogs, cats, and bears; and Primates, which includes humans. Eutherian mammals are sometimes called placental mammals because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. While other mammals possess a less complex placenta or briefly have a placenta, all eutherians possess a complex placenta during gestation.

Summary

Mammals in general are vertebrates that possess hair and mammary glands. The mammalian integument includes various secretory glands, including sebaceous glands, eccrine glands, apocrine glands, and mammary glands. Mammals are synapsids, meaning that they have a single opening in the skull. A key characteristic of synapsids is endothermy rather than the ectothermy seen in other vertebrates. Mammals probably evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period. There are three groups of mammals living today: monotremes, marsupials, and eutherians. Monotremes are unique among mammals as they lay eggs, rather than giving birth to young. Eutherian mammals are sometimes called placental mammals, because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange.

Glossary

apocrine gland
: scent gland that secretes substances that are used for chemical communication

dentary
: single bone that comprises the lower jaw of mammals

diphyodont
: refers to the possession of two sets of teeth in a lifetime

eccrine gland
: sweat gland

eutherian mammal
: mammal that possesses a complex placenta, which connects a fetus to the mother; sometimes called placental mammals

heterodont tooth
: different types of teeth that are modified for different purposes

mammal

one of the groups of endothermic vertebrates that possesses hair and mammary glands

mammary gland
in female mammals, a gland that produces milk for newborns

marsupial
one of the groups of mammals that includes the kangaroo, koala, bandicoot, Tasmanian devil, and several other species; young develop within a pouch

monotreme
egg-laying mammal

Ornithorhynchidae
clade that includes the duck-billed platypus

sebaceous gland
in mammals, a skin gland that produce a lipid mixture called *sebum*

Tachyglossidae
clade that includes the echidna or spiny anteater

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34.10: Evolution of Primates

Skills to Develop

- Describe the derived features that distinguish primates from other animals
- Explain why scientists are having difficulty determining the true lines of descent in hominids

Order Primates of class Mammalia includes lemurs, tarsiers, monkeys, apes, and humans. Non-human primates live primarily in the tropical or subtropical regions of South America, Africa, and Asia. They range in size from the mouse lemur at 30 grams (1 ounce) to the mountain gorilla at 200 kilograms (441 pounds). The characteristics and evolution of primates is of particular interest to us as it allows us to understand the evolution of our own species.

Characteristics of Primates

All primate species possess adaptations for climbing trees, as they all descended from tree-dwellers. This arboreal heritage of primates has resulted in hands and feet that are adapted for brachiation, or climbing and swinging through trees. These adaptations include, but are not limited to: 1) a rotating shoulder joint, 2) a big toe that is widely separated from the other toes and thumbs, which are widely separated from fingers (except humans), which allow for gripping branches, 3) stereoscopic vision, two overlapping fields of vision from the eyes, which allows for the perception of depth and gauging distance. Other characteristics of primates are brains that are larger than those of most other mammals, claws that have been modified into flattened nails, typically only one offspring per pregnancy, and a trend toward holding the body upright.

Order Primates is divided into two groups: prosimians and anthropoids. Prosimians include the bush babies of Africa, the lemurs of Madagascar, and the lorises, pottos, and tarsiers of Southeast Asia. Anthropoids include monkeys, apes, and humans. In general, prosimians tend to be nocturnal (in contrast to diurnal anthropoids) and exhibit a smaller size and smaller brain than anthropoids.

Evolution of Primates

The first primate-like mammals are referred to as proto-primates. They were roughly similar to squirrels and tree shrews in size and appearance. The existing fossil evidence (mostly from North Africa) is very fragmented. These proto-primates remain largely mysterious creatures until more fossil evidence becomes available. The oldest known primate-like mammals with a relatively robust fossil record is *Plesiadapis* (although some researchers do not agree that *Plesiadapis* was a proto-primate). Fossils of this primate have been dated to approximately 55 million years ago. Plesiadapiforms were proto-primates that had some features of the teeth and skeleton in common with true primates. They were found in North America and Europe in the Cenozoic and went extinct by the end of the Eocene.

The first true primates were found in North America, Europe, Asia, and Africa in the Eocene Epoch. These early primates resembled present-day prosimians such as lemurs. Evolutionary changes continued in these early primates, with larger brains and eyes, and smaller muzzles being the trend. By the end of the Eocene Epoch, many of the early prosimian species went extinct due either to cooler temperatures or competition from the first monkeys.

Anthropoid monkeys evolved from prosimians during the Oligocene Epoch. By 40 million years ago, evidence indicates that monkeys were present in the New World (South America) and the Old World (Africa and Asia). New World monkeys are also called Platyrrhini—a reference to their broad noses (Figure **34.10.1**). Old World monkeys are called Catarrhini—a reference to their narrow noses. There is still quite a bit of uncertainty about the origins of the New World monkeys. At the time the platyrrhines arose, the continents of South American and Africa had drifted apart. Therefore, it is thought that monkeys arose in the Old World and reached the New World either by drifting on log rafts or by crossing land bridges. Due to this reproductive isolation, New World monkeys and Old World monkeys underwent separate adaptive radiations over millions of years. The New World monkeys are all arboreal, whereas Old World monkeys include arboreal and ground-dwelling species.



Figure 34.10.1: The howler monkey is native to Central and South America. It makes a call that sounds like a lion roaring. (credit: Xavi Talleda)

Apes evolved from the catarrhines in Africa midway through the Cenozoic, approximately 25 million years ago. Apes are generally larger than monkeys and they do not possess a tail. All apes are capable of moving through trees, although many species spend most their time on the ground. Apes are more intelligent than monkeys, and they have relatively larger brains proportionate to body size. The apes are divided into two groups. The lesser apes comprise the family Hylobatidae, including gibbons and siamangs. The great apes include the genera *Pan* (chimpanzees and bonobos) (Figure 34.10.2a), *Gorilla* (gorillas), *Pongo* (orangutans), and *Homo* (humans) (Figure 34.10.2b). The very arboreal gibbons are smaller than the great apes; they have low sexual dimorphism (that is, the genders are not markedly different in size); and they have relatively longer arms used for swinging through trees.

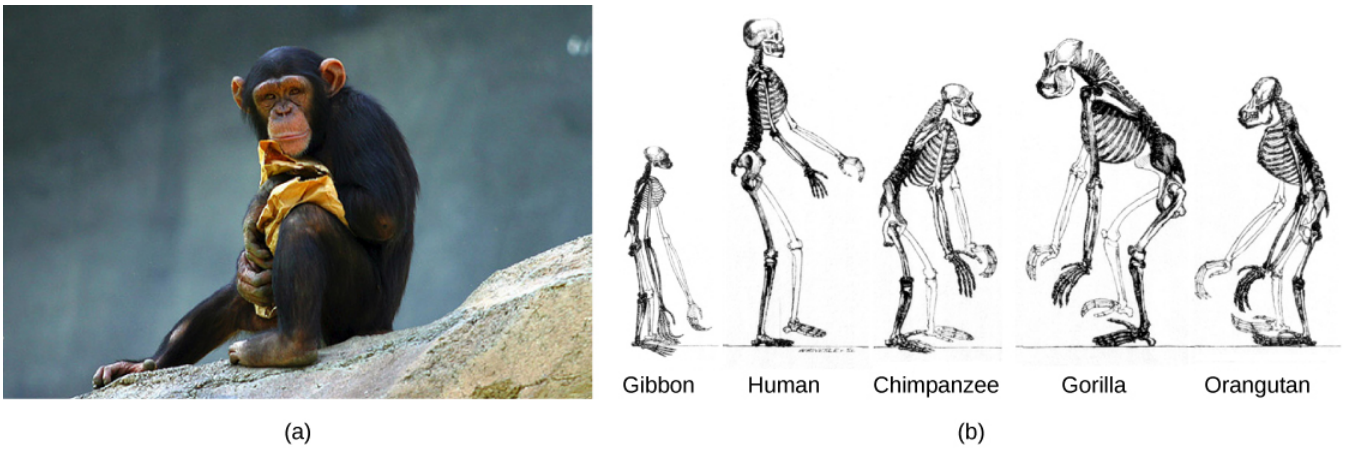


Figure 34.10.2: The (a) chimpanzee is one of the great apes. It possesses a relatively large brain and has no tail. (b) All great apes have a similar skeletal structure. (credit a: modification of work by Aaron Logan; credit b: modification of work by Tim Vickers)

Human Evolution

The family Hominidae of order Primates includes the hominoids: the great apes (Figure 34.10.3). Evidence from the fossil record and from a comparison of human and chimpanzee DNA suggests that humans and chimpanzees diverged from a common hominoid ancestor approximately 6 million years ago. Several species evolved from the evolutionary branch that includes humans, although our species is the only surviving member. The term hominin is used to refer to those species that evolved after this split of the primate line, thereby designating species that are more closely related to humans than to chimpanzees. Hominins were predominantly bipedal and include those groups that likely gave rise to our species—including *Australopithecus*, *Homo habilis*, and *Homo erectus*—and those non-ancestral groups that can be considered “cousins” of modern humans, such as Neanderthals. Determining the true lines of descent in hominins is difficult. In years past, when relatively few hominin fossils had been recovered, some scientists believed that considering them in order, from oldest to youngest, would demonstrate the course of evolution from early hominins to modern humans. In the past several years, however, many new fossils have been found, and it is clear that there was often more than one species alive at any one time and that many of the fossils found (and species named) represent hominin species that died out and are not ancestral to modern humans.

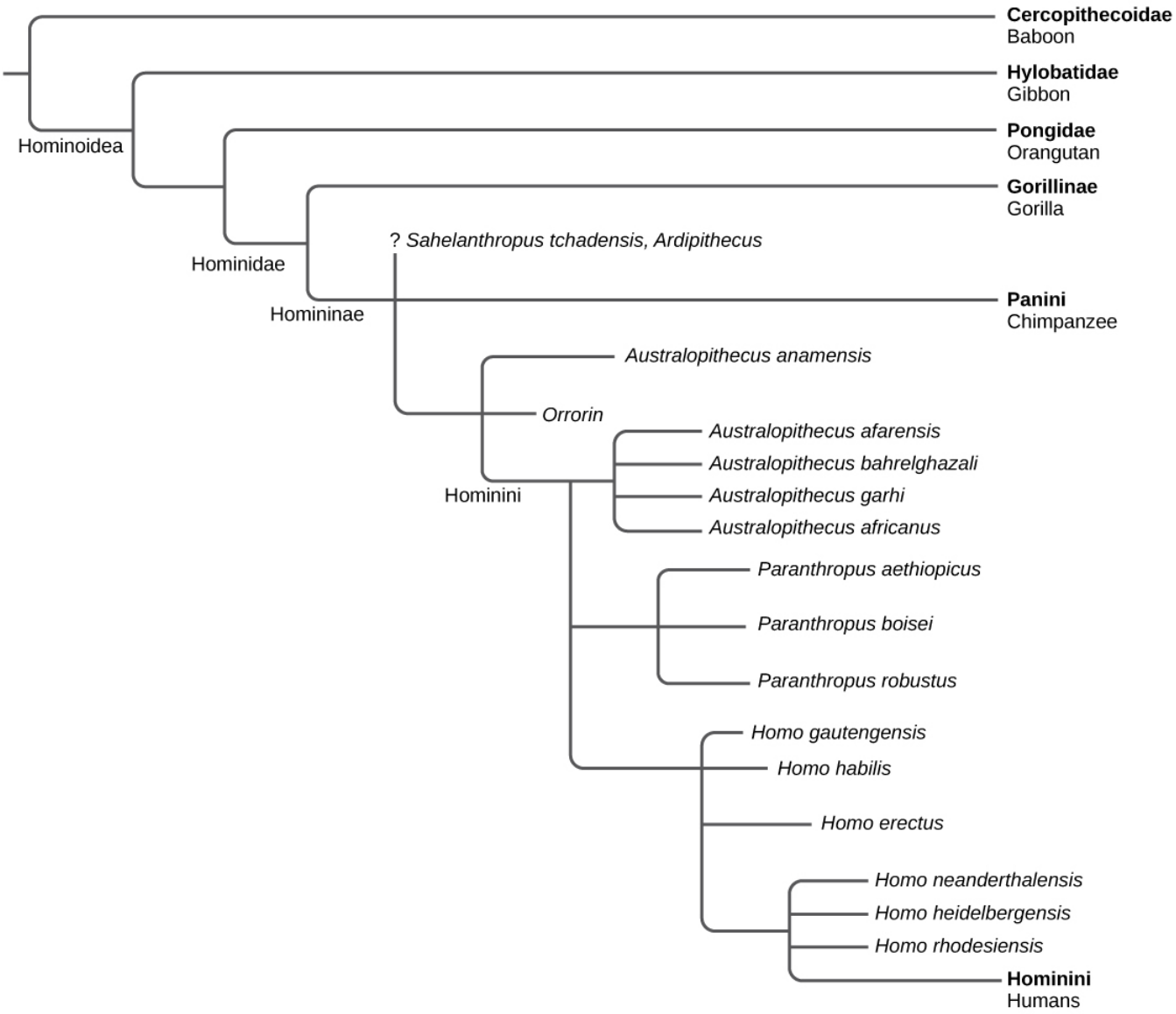


Figure **34.10.3**: This chart shows the evolution of modern humans.

Very Early Hominins

Three species of very early hominids have made news in the past few years. The oldest of these, *Sahelanthropus tchadensis*, has been dated to nearly 7 million years ago. There is a single specimen of this genus, a skull that was a surface find in Chad. The fossil, informally called “Toumai,” is a mosaic of primitive and evolved characteristics, and it is unclear how this fossil fits with the picture given by molecular data, namely that the line leading to modern humans and modern chimpanzees apparently bifurcated about 6 million years ago. It is not thought at this time that this species was an ancestor of modern humans.

A second, younger species, *Orrorin tugenensis*, is also a relatively recent discovery, found in 2000. There are several specimens of *Orrorin*. It is not known whether *Orrorin* was a human ancestor, but this possibility has not been ruled out. Some features of *Orrorin* are more similar to those of modern humans than are the australopiths, although *Orrorin* is much older.

A third genus, *Ardipithecus*, was discovered in the 1990s, and the scientists who discovered the first fossil found that some other scientists did not believe the organism to be a biped (thus, it would not be considered a hominid). In the intervening years, several more specimens of *Ardipithecus*, classified as two different species, demonstrated that the organism was bipedal. Again, the status of this genus as a human ancestor is uncertain.

Early Hominins: Genus *Australopithecus*

Australopithecus ("southern ape") is a genus of hominin that evolved in eastern Africa approximately 4 million years ago and went extinct about 2 million years ago. This genus is of particular interest to us as it is thought that our genus, genus *Homo*, evolved from *Australopithecus* about 2 million years ago (after likely passing through some transitional states). *Australopithecus* had a number of characteristics that were more similar to the great apes than to modern humans. For example, sexual dimorphism was more exaggerated than in modern humans. Males were up to 50 percent larger than females, a ratio that is similar to that seen in modern gorillas and orangutans. In contrast, modern human males are approximately 15 to 20 percent larger than females. The brain size of *Australopithecus* relative to its body mass was also smaller than modern humans and more similar to that seen in the great apes. A key feature that *Australopithecus* had in common with modern humans was bipedalism, although it is likely that *Australopithecus* also spent time in trees. Hominin footprints, similar to those of modern humans, were found in Laetoli, Tanzania and dated to 3.6 million years ago. They showed that hominins at the time of *Australopithecus* were walking upright.

There were a number of *Australopithecus* species, which are often referred to as *australopiths*. *Australopithecus anamensis* lived about 4.2 million years ago. More is known about another early species, *Australopithecus afarensis*, which lived between 3.9 and 2.9 million years ago. This species demonstrates a trend in human evolution: the reduction of the dentition and jaw in size. *A. afarensis* (Figure **34.10.4**) had smaller canines and molars compared to apes, but these were larger than those of modern humans. Its brain size was 380–450 cubic centimeters, approximately the size of a modern chimpanzee brain. It also had prognathic jaws, which is a relatively longer jaw than that of modern humans. In the mid-1970s, the fossil of an adult female *A. afarensis* was found in the Afar region of Ethiopia and dated to 3.24 million years ago (Figure **34.10.5**). The fossil, which is informally called "Lucy," is significant because it was the most complete australopith fossil found, with 40 percent of the skeleton recovered.



(a) (b)

Figure **34.10.4**: The skull of (a) *Australopithecus afarensis*, an early hominid that lived between two and three million years ago, resembled that of (b) modern humans but was smaller with a sloped forehead and prominent jaw.



Figure **34.10.5**: This adult female *Australopithecus afarensis* skeleton, nicknamed Lucy, was discovered in the mid 1970s. (credit: "120"/Wikimedia Commons)

Australopithecus africanus lived between 2 and 3 million years ago. It had a slender build and was bipedal, but had robust arm bones and, like other early hominids, may have spent significant time in trees. Its brain was larger than that of *A. afarensis* at 500 cubic centimeters, which is slightly less than one-third the size of modern human brains. Two other species, *Australopithecus bahrelghazali* and *Australopithecus garhi*, have been added to the roster of australopiths in recent years.

A Dead End: Genus *Paranthropus*

The australopiths had a relatively slender build and teeth that were suited for soft food. In the past several years, fossils of hominids of a different body type have been found and dated to approximately 2.5 million years ago. These hominids, of the genus *Paranthropus*, were relatively large and had large grinding teeth. Their molars showed heavy wear, suggesting that they had a

coarse and fibrous vegetarian diet as opposed to the partially carnivorous diet of the australopiths. *Paranthropus* includes *Paranthropus robustus* of South Africa, and *Paranthropus aethiopicus* and *Paranthropus boisei* of East Africa. The hominids in this genus went extinct more than 1 million years ago and are not thought to be ancestral to modern humans, but rather members of an evolutionary branch on the hominin tree that left no descendants.

Early Hominins: Genus *Homo*

The human genus, *Homo*, first appeared between 2.5 and 3 million years ago. For many years, fossils of a species called *H. habilis* were the oldest examples in the genus *Homo*, but in 2010, a new species called *Homo gautengensis* was discovered and may be older. Compared to *A. africanus*, *H. habilis* had a number of features more similar to modern humans. *H. habilis* had a jaw that was less prognathic than the australopiths and a larger brain, at 600–750 cubic centimeters. However, *H. habilis* retained some features of older hominin species, such as long arms. The name *H. habilis* means "handy man," which is a reference to the stone tools that have been found with its remains.

Link to Learning



Visit this site for a video about Smithsonian paleontologist Briana Pobiner explaining the link between hominin eating of meat and evolutionary trends.

H. erectus appeared approximately 1.8 million years ago (Figure **34.10.6**). It is believed to have originated in East Africa and was the first hominin species to migrate out of Africa. Fossils of *H. erectus* have been found in India, China, Java, and Europe, and were known in the past as "Java Man" or "Peking Man." *H. erectus* had a number of features that were more similar to modern humans than those of *H. habilis*. *H. erectus* was larger in size than earlier hominins, reaching heights up to 1.85 meters and weighing up to 65 kilograms, which are sizes similar to those of modern humans. Its degree of sexual dimorphism was less than earlier species, with males being 20 to 30 percent larger than females, which is close to the size difference seen in our species. *H. erectus* had a larger brain than earlier species at 775–1,100 cubic centimeters, which compares to the 1,130–1,260 cubic centimeters seen in modern human brains. *H. erectus* also had a nose with downward-facing nostrils similar to modern humans, rather than the forward facing nostrils found in other primates. Longer, downward-facing nostrils allow for the warming of cold air before it enters the lungs and may have been an adaptation to colder climates. Artifacts found with fossils of *H. erectus* suggest that it was the first hominin to use fire, hunt, and have a home base. *H. erectus* is generally thought to have lived until about 50,000 years ago.



Figure **34.10.6**: *Homo erectus* had a prominent brow and a nose that pointed downward rather than forward.

Humans: *Homo sapiens*

A number of species, sometimes called archaic *Homo sapiens*, apparently evolved from *H. erectus* starting about 500,000 years ago. These species include *Homo heidelbergensis*, *Homo rhodesiensis*, and *Homo neanderthalensis*. These archaic *H. sapiens* had a brain size similar to that of modern humans, averaging 1,200–1,400 cubic centimeters. They differed from modern humans by having a thick skull, a prominent brow ridge, and a receding chin. Some of these species survived until 30,000–10,000 years ago, overlapping with modern humans (Figure **34.10.7**).



Figure **34.10.7**: The *Homo neanderthalensis* used tools and may have worn clothing.

There is considerable debate about the origins of anatomically modern humans or *Homo sapiens sapiens*. As discussed earlier, *H. erectus* migrated out of Africa and into Asia and Europe in the first major wave of migration about 1.5 million years ago. It is thought that modern humans arose in Africa from *H. erectus* and migrated out of Africa about 100,000 years ago in a second major migration wave. Then, modern humans replaced *H. erectus* species that had migrated into Asia and Europe in the first wave.

This evolutionary timeline is supported by molecular evidence. One approach to studying the origins of modern humans is to examine mitochondrial DNA (mtDNA) from populations around the world. Because a fetus develops from an egg containing its mother's mitochondria (which have their own, non-nuclear DNA), mtDNA is passed entirely through the maternal line. Mutations

in mtDNA can now be used to estimate the timeline of genetic divergence. The resulting evidence suggests that all modern humans have mtDNA inherited from a common ancestor that lived in Africa about 160,000 years ago. Another approach to the molecular understanding of human evolution is to examine the Y chromosome, which is passed from father to son. This evidence suggests that all men today inherited a Y chromosome from a male that lived in Africa about 140,000 years ago.

Summary

All primate species possess adaptations for climbing trees, as they all probably descended from tree-dwellers, although not all species are arboreal. Other characteristics of primates are brains that are larger than those of other mammals, claws that have been modified into flattened nails, typically only one young per pregnancy, stereoscopic vision, and a trend toward holding the body upright. Primates are divided into two groups: prosimians and anthropoids. Monkeys evolved from prosimians during the Oligocene Epoch. Apes evolved from catarrhines in Africa during the Miocene Epoch. Apes are divided into the lesser apes and the greater apes. Hominins include those groups that gave rise to our species, such as *Australopithecus* and *H. erectus*, and those groups that can be considered "cousins" of humans, such as Neanderthals. Fossil evidence shows that hominins at the time of *Australopithecus* were walking upright, the first evidence of bipedal hominins. A number of species, sometimes called archaic *H. sapiens*, evolved from *H. erectus* approximately 500,000 years ago. There is considerable debate about the origins of anatomically modern humans or *H. sapiens sapiens*.

Glossary

anthropoid
: monkeys, apes, and humans

Australopithecus
: genus of hominins that evolved in eastern Africa approximately 4 million years ago

brachiation
: movement through trees branches via suspension from the arms

Catarrhini
: clade of Old World monkeys

Gorilla
: genus of gorillas

hominin
: species that are more closely related to humans than chimpanzees

hominoid
: pertaining to great apes and humans

Homo
: genus of humans

Homo sapiens sapiens
: anatomically modern humans

Hylobatidae
: family of gibbons

Pan
: genus of chimpanzees and bonobos

Platyrrhini

clade of New World monkeys

Plesiadapis
oldest known primate-like mammal

Pongo
genus of orangutans

Primates
order of lemurs, tarsiers, monkeys, apes, and humans

prognathic jaw
long jaw

prosimian
division of primates that includes bush babies of Africa, lemurs of Madagascar, and lorises, pottos, and tarsiers of Southeast Asia

stereoscopic vision
two overlapping fields of vision from the eyes that produces depth perception

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CHAPTER OVERVIEW

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35.5.1: Leaf Structure and Arrangment

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35.5.3: Leaf Structure, Function, and Adaptation

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35.1: Organization of the Plant Body- An Overview

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35.1.1: Plant Tissues and Organ Systems

Learning Objectives

- Differentiate among the types of plant tissues and organs

Plant Tissues

Plants are multicellular eukaryotes with tissue systems made of various cell types that carry out specific functions. Plant tissue systems fall into one of two general types: meristematic tissue and permanent (or non-meristematic) tissue. Cells of the meristematic tissue are found in meristems, which are plant regions of continuous cell division and growth. Meristematic tissue cells are either undifferentiated or incompletely differentiated; they continue to divide and contribute to the growth of the plant. In contrast, permanent tissue consists of plant cells that are no longer actively dividing.

Meristematic tissues consist of three types, based on their location in the plant. Apical meristems contain meristematic tissue located at the tips of stems and roots, which enable a plant to extend in length. Lateral meristems facilitate growth in thickness or girth in a maturing plant. Intercalary meristems occur only in monocots at the bases of leaf blades and at nodes (the areas where leaves attach to a stem). This tissue enables the monocot leaf blade to increase in length from the leaf base; for example, it allows lawn grass leaves to elongate even after repeated mowing.

Meristems produce cells that quickly differentiate, or specialize, and become permanent tissue. Such cells take on specific roles and lose their ability to divide further. They differentiate into three main types: dermal, vascular, and ground tissue. Dermal tissue covers and protects the plant. Vascular tissue transports water, minerals, and sugars to different parts of the plant. Ground tissue serves as a site for photosynthesis, provides a supporting matrix for the vascular tissue, and helps to store water and sugars.

Plant tissues are either simple (composed of similar cell types) or complex (composed of different cell types). Dermal tissue, for example, is a simple tissue that covers the outer surface of the plant and controls gas exchange. Vascular tissue is an example of a complex tissue. It is made of two specialized conducting tissues: xylem and phloem. Xylem tissue transports water and nutrients from the roots to different parts of the plant. It includes three different cell types: vessel elements and tracheids (both of which conduct water) and xylem parenchyma. Phloem tissue, which transports organic compounds from the site of photosynthesis to other parts of the plant, consists of four different cell types: sieve cells (which conduct photosynthates), companion cells, phloem parenchyma, and phloem fibers. Unlike xylem-conducting cells, phloem-conducting cells are alive at maturity. The xylem and phloem always lie adjacent to each other. In stems, the xylem and the phloem form a structure called a vascular bundle; in roots, this is termed the vascular stele or vascular cylinder.

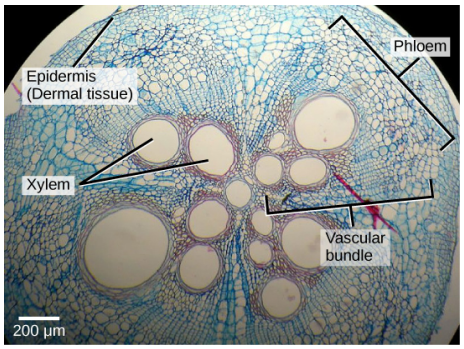


Figure **35.1.1.1**: Cross section of a squash stem showing a vascular bundle: This light micrograph shows a cross section of a squash (Curcurbita maxima) stem. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest of the plant, are dead at functional maturity. Phloem cells, which transport sugars and other organic compounds from photosynthetic tissue to the rest of the plant, are living. The vascular bundles are encased in ground tissue and surrounded by dermal tissue.

Plant Organ Systems

In plants, just as in animals, similar cells working together form a tissue. When different types of tissues work together to perform a unique function, they form an organ; organs working together form organ systems. Vascular plants have two distinct organ systems:

a shoot system and a root system. The shoot system consists of two portions: the vegetative (non-reproductive) parts of the plant, such as the leaves and the stems; and the reproductive parts of the plant, which include flowers and fruits. The shoot system generally grows above ground, where it absorbs the light needed for photosynthesis. The root system, which supports the plants and absorbs water and minerals, is usually underground.

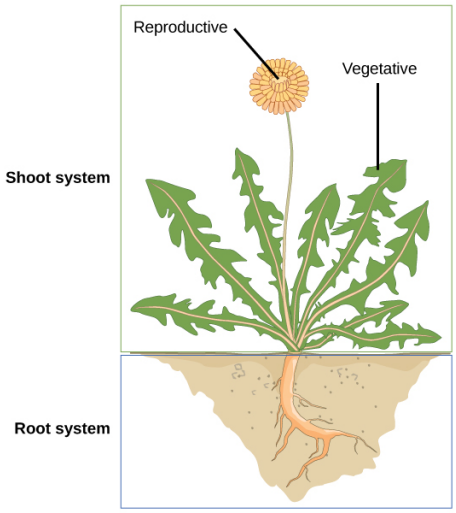


Figure **35.1.1.1**: Example plant organ systems: The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil.

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Key Points

- There are two types of plant tissues: meristematic tissue found in plant regions of continuous cell division and growth, and permanent (or non-meristematic) tissue consisting of cells that are no longer actively dividing.
- Meristems produce cells that differentiate into three secondary tissue types: dermal tissue which covers and protects the plant, vascular tissue which transports water, minerals, and sugars and ground tissue which serves as a site for photosynthesis, supports vascular tissue, and stores nutrients.
- Vascular tissue is made of xylem tissue which transports water and nutrients from the roots to different parts of the plant and phloem tissue which transports organic compounds from the site of photosynthesis to other parts of the plant.
- The xylem and phloem always lie next to each other forming a structure called a vascular bundle in stems and a vascular stele or vascular cylinder in roots.
- Parts of the shoot system include the vegetative parts, such as the leaves and the stems, and the reproductive parts, such as the flowers and fruits.

Key Terms

- **meristem**: the plant tissue composed of totipotent cells that allows plant growth
- **parenchyma**: the ground tissue making up most of the non-woody parts of a plant
- **xylem**: a vascular tissue in land plants primarily responsible for the distribution of water and minerals taken up by the roots; also the primary component of wood

- **phloem**: a vascular tissue in land plants primarily responsible for the distribution of sugars and nutrients manufactured in the shoot
- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts

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35.2: Plant Tissues

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35.2.1: Plant Tissues

This page explains the different types of plant tissues and their roles: meristematic tissue enables growth; protective tissue covers surfaces; parenchyma aids in storage and photosynthesis; sclerenchyma offers support; collenchyma strengthens growth areas; xylem transports water and minerals; and phloem carries sugars. Each tissue type is essential to the overall structure and function of plants.

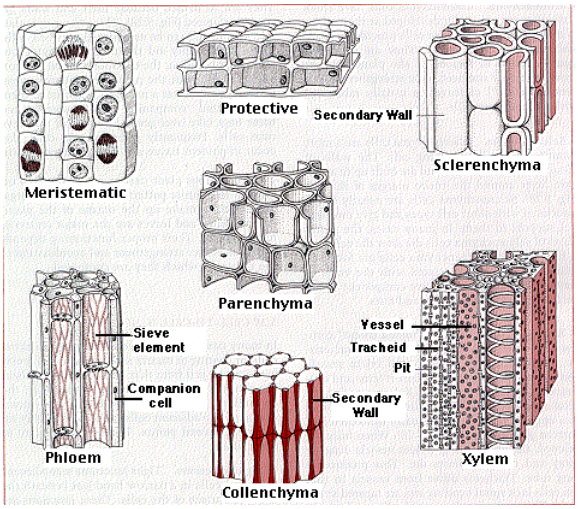


Figure 16.1.1.1 Types of plant tissues

Meristematic

The main function of meristematic tissue is mitosis. The cells are small, thin-walled, with no central vacuole and no specialized features.

Meristematic tissue is located in

- the **apical meristems** at the growing points of roots and stems.
- the **secondary meristems** (lateral buds) at the **nodes** of stems (where branching occurs), and in some plants,
- meristematic tissue, called the **cambium**, that is found within mature stems and roots.

The cells produced in the meristems soon become differentiated into one or another of several types.

Protective

Protective tissue covers the surface of leaves and the living cells of roots and stems. Its cells are flattened with their top and bottom surfaces parallel. The upper and lower **epidermis of the leaf** are examples of protective tissue.

Parenchyma

The cells of parenchyma are large, thin-walled, and usually have a large central vacuole. They are often partially separated from each other and are usually stuffed with plastids. In areas not exposed to light, colorless plastids predominate and food storage is the main function. The cells of the white potato are parenchyma cells. Where light is present, e.g., in leaves, chloroplasts predominate and photosynthesis is the main function.

Sclerenchyma

The walls of these cells are very thick and built up in a uniform layer around the entire margin of the cell. Often, the cell dies after its cell wall is fully formed. Sclerenchyma cells are usually found associated with other cells types and give them mechanical support.

Sclerenchyma is found in stems and also in leaf veins. Sclerenchyma also makes up the hard outer covering of seeds and nuts.

Collenchyma

Collenchyma cells have thick walls that are especially thick at their corners. These cells provide mechanical support for the plant. They are most often found in areas that are growing rapidly and need to be strengthened. The **petiole** ("stalk") of leaves is usually reinforced with collenchyma.

Xylem

Xylem conducts water and dissolved minerals from the roots to all the other parts of the plant.

In angiosperms, most of the water travels in the **xylem vessels**. These are thick-walled tubes that can extend vertically through several feet of xylem tissue. Their diameter may be as large as 0.7 mm. Their walls are thickened with secondary deposits of cellulose and are usually further strengthened by impregnation with **lignin**. The secondary walls of the xylem vessels are deposited in spirals and rings and are usually perforated by pits. Xylem vessels arise from individual cylindrical cells oriented end to end. At maturity the end walls of these cells dissolve away, and the cytoplasmic contents die. The result is the xylem vessel, a continuous nonliving duct.

Xylem also contains **tracheids**. These are individual cells tapered at each end so the tapered end of one cell overlaps that of the adjacent cell. Like xylem vessels, they have thick, lignified walls and, at maturity, no cytoplasm. Their walls are perforated so that water can flow from one tracheid to the next. The xylem of ferns and conifers contains only tracheids.

In woody plants, the older xylem ceases to participate in water transport and simply serves to give strength to the trunk. Wood is xylem. When counting the annual rings of a tree, one is counting rings of xylem.

Phloem

The main components of phloem are **sieve elements** and **companion cells**.

Sieve elements are so named because their end walls are perforated. This allows cytoplasmic connections between vertically-stacked cells. The result is a **sieve tube** that conducts the products of photosynthesis - sugars and amino acids - from the place where they are manufactured (a "source"), e.g., leaves, to the places ("sinks") where they are consumed or stored; such as

- roots
- growing tips of stems and leaves
- flowers
- fruits, tubers, corms, etc.

Sieve elements have no nucleus and only a sparse collection of other organelles. They depend on the adjacent companion cells for many functions. **Companion cells** move sugars, amino acids and a variety of macromolecules into and out of the sieve elements. In "source" tissue, such as a leaf, the companion cells use transmembrane proteins to take up - by active transport - sugars and other organic molecules from the cells manufacturing them. Water follows by osmosis. These materials then move into adjacent sieve elements through plasmodesmata. The pressure created by osmosis drives the flow of materials through the sieve tubes.

In "sink" tissue, the sugars and other organic molecules leave the sieve elements through plasmodesmata connecting the sieve elements to their companion cells and then pass on to the cells of their destination. Again, water follows by osmosis where it may leave the plant by transpiration or increase the volume of the cells or move into the xylem for recycling through the plant.

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35.3: Roots- Anchoring and Absorption Structures

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35.3.1: Types of Root Systems and Zones of Growth

Learning Objectives

- Describe the three zones of the root tip and summarize the role of each zone in root growth

Types of Root Systems

There are two main types of root systems. Dicots have a tap root system, while monocots have a fibrous root system, which is also known as an adventitious root system. A tap root system has a main root that grows down vertically, from which many smaller lateral roots arise. Dandelions are a common example; their tap roots usually break off when these weeds are pulled from the ground; they can regrow another shoot from the remaining root. A tap root system penetrates deep into the soil. In contrast, a fibrous root system is located closer to the soil surface where it forms a dense network of roots that also helps prevent soil erosion (lawn grasses are a good example, as are wheat, rice, and corn). Some plants have a combination of tap roots and fibrous roots. Plants that grow in dry areas often have deep root systems, whereas plants that grow in areas with abundant water are likely to have shallower root systems.

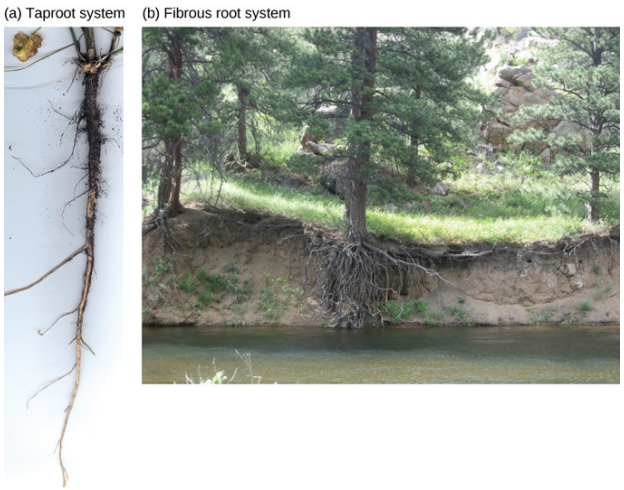


Figure **35.3.1.1**: Main types of root systems: (a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots.

Zones of the Root Tip

Root growth begins with seed germination. When the plant embryo emerges from the seed, the radicle of the embryo forms the root system. The tip of the root is protected by the root cap, a structure exclusive to roots and unlike any other plant structure. The root cap is continuously replaced because it is easily damaged as the root pushes through soil. The root tip can be divided into three zones: a zone of cell division, a zone of elongation, and a zone of maturation. The zone of cell division is closest to the root tip and is made up of the actively-dividing cells of the root meristem, which contains the undifferentiated cells of the germinating plant. The zone of elongation is where the newly-formed cells increase in length, thereby lengthening the root. Beginning at the first root hair is the zone of cell maturation where the root cells differentiate into specialized cell types. All three zones are in approximately the first centimeter of the root tip.

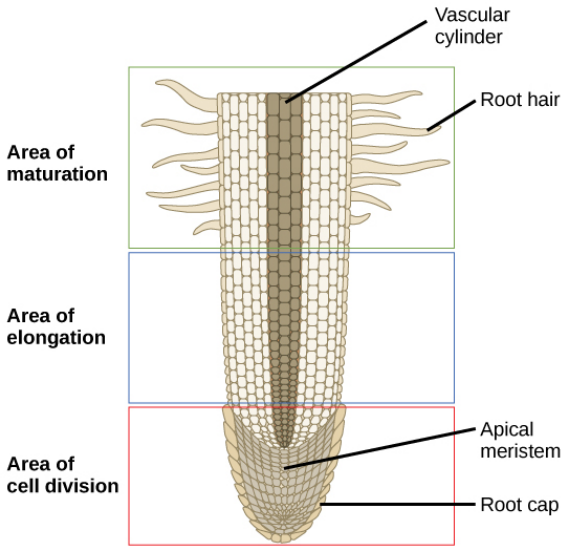


Figure **35.3.1.1**: Zones of the root tip: A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem.

Key Points

- Root tips ultimately develop into two main types of root systems: tap roots and fibrous roots.
- The growing root tip is protected by a root cap.
- Within the root tip, cells differentiate, actively divide, and increase in length, depending on in which zone the cells are located.
- Dividing cells make up the zone of cell division in a germinating plant.
- The newly-forming root increases in size in the zone of elongation.
- Differentiating cells make up the zone of cell maturation.

Key Terms

- **radicle**: the rudimentary shoot of a plant that supports the cotyledons in the seed and from which the root is developed downward; the root of the embryo
- **meristem**: the plant tissue composed of totipotent cells that allows plant growth
- **germination**: the beginning of vegetation or growth from a seed or spore

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35.3.2: Root Modifications

Learning Objectives

- Explain the reasons for root modifications

Plants have different root structures for specific purposes. There are many different types of specialized roots, but two of the more familiar types of roots include aerial roots and storage roots. Aerial roots grow above the ground, typically providing structural support. Storage roots (for example, taproots and tuberous roots) are modified for food storage.

Aerial roots are found in many different kinds of plants, offering varying functions depending on the location of the plant. Epiphytic roots are a type of aerial root that enable a plant to grow on another plant in a non-parasitic manner. The banyan tree begins as an epiphyte, germinating in the branches of a host tree. Aerial prop roots develop from the branches and eventually reach the ground, providing additional support. Over time, many roots will come together to form what appears to be a trunk. The epiphytic roots of orchids develop a spongy tissue to absorb moisture and nutrients from any organic material on their roots. In screwpine, a palm-like tree that grows in sandy tropical soils, aerial roots develop to provide additional support that help the tree remain upright in shifting sand and water conditions.



Figure **35.3.2.1**: Aerial roots: The (a) banyan tree, also known as the strangler fig, begins life as an epiphyte in a host tree. Aerial roots extend to the ground, supporting the growing plant, which eventually strangles the host tree. The (b) screwpine develops aerial roots that help support the plant in sandy soils.

Storage roots, such as carrots, beets, and sweet potatoes, are examples of roots that are specially modified for storage of starch and water. They usually grow underground as protection from plant-eating animals. Some plants, however, such as leaf succulents and cacti, store energy in their leaves and stems, respectively, instead of in their roots.



Figure **35.3.2.1**: Storage roots: Many vegetables, such as carrots and beets, are modified roots that store food and water.

Other examples of modified roots are aerating roots and haustorial roots. Aerating roots, which rise above the ground, especially above water, are commonly seen in mangrove forests that grow along salt water coastlines. Haustorial roots are often seen in parasitic plants such as mistletoe. Their roots allow the plants to absorb water and nutrients from other plants.

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Key Points

- Storage roots, which include a large number of edible vegetables such as potatoes and carrots, are some of the most commonly-known types of modified roots.
- Aerial roots encompass a variety of shapes, yet function similarly as structural support for the plant.
- Parasitic plants have special haustorial roots that allow the plant to absorb nutrients from a host plant.

Key Terms

- **succulent**: having fleshy leaves or other tissues that store water
- **epiphyte**: a plant that grows on another, using it as a physical support but neither obtaining nutrients from it nor causing it any damage if also offering no benefit

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35.4: Stems- Support for Above Ground Organs

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35.4.1: Functions of Stems

Learning Objectives

- Summarize the main function and basic structure of stems

Stems

Stems are a part of the shoot system of a plant. They may range in length from a few millimeters to hundreds of meters. They also vary in diameter, depending on the plant type. Stems are usually above ground, although the stems of some plants, such as the potato, also grow underground. Stems may be herbaceous (soft) or woody in nature. Their main function is to provide support to the plant, holding leaves, flowers, and buds; in some cases, stems also store food for the plant. A stem may be unbranched, like that of a palm tree, or it may be highly branched, like that of a magnolia tree. The stem of the plant connects the roots to the leaves, helping to transport absorbed water and minerals to different parts of the plant. The stem also helps to transport the products of photosynthesis (i.e., sugars) from the leaves to the rest of the plant.

Plant stems, whether above or below ground, are characterized by the presence of nodes and internodes. Nodes are points of attachment for leaves, aerial roots, and flowers. The stem region between two nodes is called an internode. The stalk that extends from the stem to the base of the leaf is the petiole. An axillary bud is usually found in the axil (the area between the base of a leaf and the stem) where it can give rise to a branch or a flower. The apex (tip) of the shoot contains the apical meristem within the apical bud.

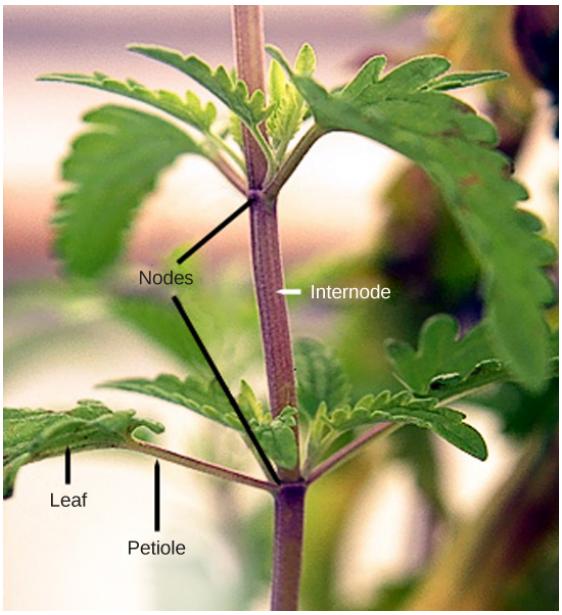


Figure **35.4.1.1**: Parts of a stem: Leaves are attached to the plant stem at areas called nodes. An internode is the stem region between two nodes. The petiole is the stalk connecting the leaf to the stem. The leaves just above the nodes arise from axillary buds.

Key Points

- Most stems are found above ground, but some of them grow underground.
- Stems can be either unbranched or highly branched; they may be herbaceous or woody.
- Stems connect the roots to the leaves, helping to transport water, minerals, and sugars to different parts of the plant.
- Plant stems always have nodes (points of attachments for leaves, roots, and flowers) and internodes (regions between nodes).
- The petiole is the stalk that extends from the stem to the base of the leaf.
- An axillary bud gives rise to a branch or a flower; it is usually found in the axil: the junction of the stem and petiole.

Key Terms

- **node**: points of attachment for leaves, aerial roots, and flowers
- **internode**: a section of stem between two stem nodes
- **petiole**: stalk that extends from the stem to the base of the leaf
- **axillary bud**: embryonic shoot that lies at the junction of the stem and petiole that gives rise to a branch or flower

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35.4.2: Stem Anatomy

Learning Objectives

- Summarize the roles of dermal tissue, vascular tissue, and ground tissue

Stem Anatomy

The stem and other plant organs are primarily made from three simple cell types: parenchyma, collenchyma, and sclerenchyma cells. Parenchyma cells are the most common plant cells. They are found in the stem, the root, the inside of the leaf, and the pulp of the fruit. Parenchyma cells are responsible for metabolic functions, such as photosynthesis. They also help repair and heal wounds. In addition, some parenchyma cells store starch.



Figure **35.4.2.1**: Parenchyma cells in plants: The stem of common St John's Wort (*Hypericum perforatum*) is shown in cross section in this light micrograph. The central pith (greenish-blue, in the center) and peripheral cortex (narrow zone 3–5 cells thick, just inside the epidermis) are composed of parenchyma cells. Vascular tissue composed of xylem (red) and phloem tissue (green, between the xylem and cortex) surrounds the pith.

Collenchyma cells are elongated cells with unevenly-thickened walls. They provide structural support, mainly to the stem and leaves. These cells are alive at maturity and are usually found below the epidermis. The "strings" of a celery stalk are an example of collenchyma cells.

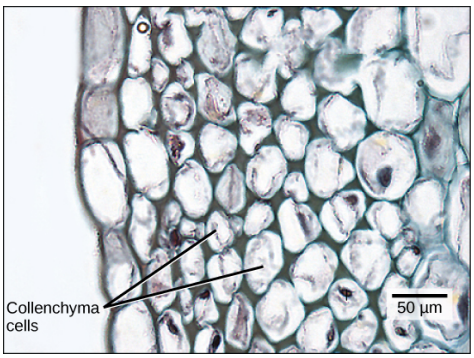


Figure **35.4.2.1**: Collenchyma cells in plants: Collenchyma cell walls are uneven in thickness, as seen in this light micrograph. They provide support to plant structures.

Sclerenchyma cells also provide support to the plant, but unlike collenchyma cells, many of them are dead at maturity. There are two types of sclerenchyma cells: fibers and sclereids. Both types have secondary cell walls that are thickened with deposits of lignin, an organic compound that is a key component of wood. Fibers are long, slender cells; sclereids are smaller-sized. Sclereids give pears their gritty texture. Humans use sclerenchyma fibers to make linen and rope.

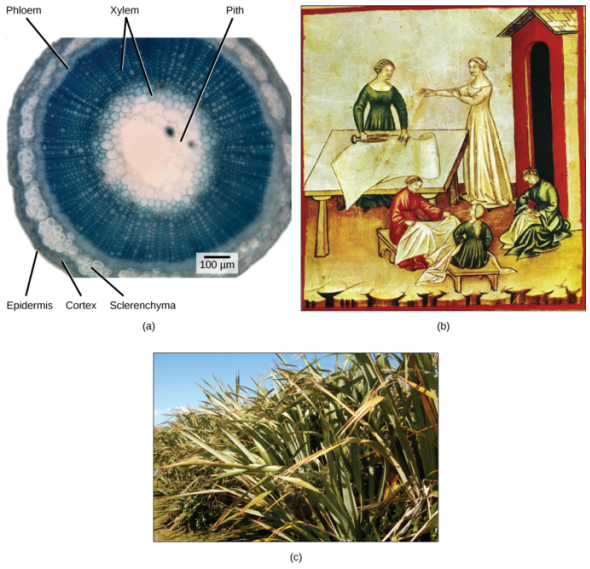


Figure 35.4.2.1: Sclerenchyma cells in plants: The central pith and outer cortex of the (a) flax stem are made up of parenchyma cells. Inside the cortex is a layer of sclerenchyma cells, which make up the fibers in flax rope and clothing. Humans have grown and harvested flax for thousands of years. In (b) this drawing, fourteenth-century women prepare linen. The (c) flax plant is grown and harvested for its fibers, which are used to weave linen, and for its seeds, which are the source of linseed oil.

As with the rest of the plant, the stem has three tissue systems: dermal, vascular, and ground tissue. Each is distinguished by characteristic cell types that perform specific tasks necessary for the plant's growth and survival.

Dermal Tissue

The dermal tissue of the stem consists primarily of epidermis: a single layer of cells covering and protecting the underlying tissue. Woody plants have a tough, waterproof outer layer of cork cells commonly known as bark, which further protects the plant from damage. Epidermal cells are the most-numerous and least-differentiated of the cells in the epidermis. The epidermis of a leaf also contains openings, known as stomata, through which the exchange of gases takes place. Two cells, known as guard cells, surround each leaf stoma, controlling its opening and closing and, thus, regulating the uptake of carbon dioxide and the release of oxygen and water vapor. Trichomes are hair-like structures on the epidermal surface. They help to reduce transpiration (the loss of water by aboveground plant parts), increase solar reflectance, and store compounds that defend the leaves against predation by herbivores.

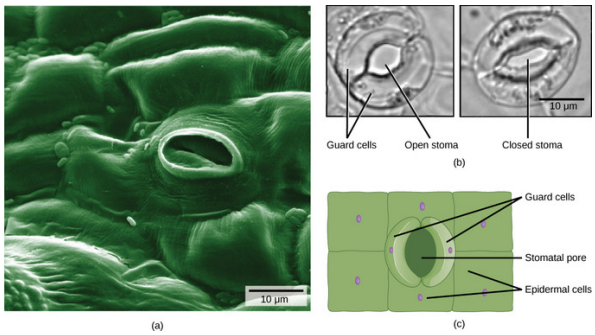


Figure 35.4.2.1: Stomata: Openings called stomata (singular: stoma) allow a plant to take up carbon dioxide and release oxygen and water vapor. The (a) colorized scanning-electron micrograph shows a closed stoma of a dicot. Each stoma is flanked by two guard cells that regulate its (b) opening and closing. The (c) guard cells sit within the layer of epidermal cells.

Vascular Tissue

The xylem and phloem that make up the vascular tissue of the stem are arranged in distinct strands called vascular bundles, which run up and down the length of the stem. Both are considered complex plant tissue because they are composed of more than one simple cell type that work in concert with each other. When the stem is viewed in cross section, the vascular bundles of dicot stems are arranged in a ring. In plants with stems that live for more than one year, the individual bundles grow together and produce the characteristic growth rings. In monocot stems, the vascular bundles are randomly scattered throughout the ground tissue.

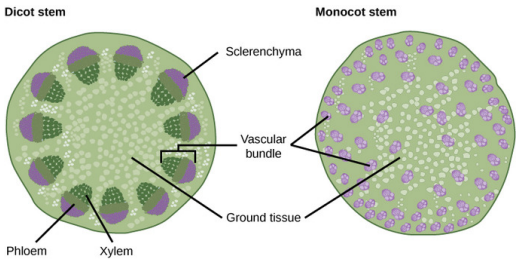


Figure **35.4.2.1**: Vascular bundles: In (a) dicot stems, vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle; phloem is located toward the exterior. Sclerenchyma fibers cap the vascular bundles. In (b) monocot stems, vascular bundles composed of xylem and phloem tissues are scattered throughout the ground tissue.

Xylem tissue has three types of cells: xylem parenchyma, tracheids, and vessel elements. The latter two types conduct water and are dead at maturity. Tracheids are xylem cells with thick secondary cell walls that are lignified. Water moves from one tracheid to another through regions on the side walls known as pits where secondary walls are absent. Vessel elements are xylem cells with thinner walls; they are shorter than tracheids. Each vessel element is connected to the next by means of a perforation plate at the end walls of the element. Water moves through the perforation plates to travel up the plant.

Phloem tissue is composed of sieve-tube cells, companion cells, phloem parenchyma, and phloem fibers. A series of sieve-tube cells (also called sieve-tube elements) are arranged end-to-end to create a long sieve tube, which transports organic substances such as sugars and amino acids. The sugars flow from one sieve-tube cell to the next through perforated sieve plates, which are found at the end junctions between two cells. Although still alive at maturity, the nucleus and other cell components of the sieve-tube cells have disintegrated. Companion cells are found alongside the sieve-tube cells, providing them with metabolic support. The companion cells contain more ribosomes and mitochondria than do the sieve-tube cells, which lack some cellular organelles.

Ground Tissue

Ground tissue is mostly made up of parenchyma cells, but may also contain collenchyma and sclerenchyma cells that help support the stem. The ground tissue towards the interior of the vascular tissue in a stem or root is known as pith, while the layer of tissue between the vascular tissue and the epidermis is known as the cortex.

Key Points

- The stem has three simple cell types: the parenchyma, collenchyma, and sclerenchyma cells that are responsible for metabolic functions, repairing and healing wounds, and storing starch.
- The stem is composed of three tissue systems that include the epidermis, vascular, and ground tissues, all of which are made from the simple cell types..
- The xylem and phloem carry water and nutrients up and down the length of the stem and are arranged in distinct strands called vascular bundles.
- The epidermis is a single layer of cells that makes up the dermal tissue covering the stem and protecting the underlying tissue. Woody plants have an extra layer of protection on top of the epidermis made of cork cells known as bark.
- The vascular tissue of the stem consists of the complex tissues xylem and phloem which carry water and nutrients up and down the length of the stem and are arranged in distinct strands called vascular bundles.
- Ground tissue helps support the stem and is called pith when it is located towards the middle of the stem and called the cortex when it is between the vascular tissue and the epidermis.

Key Terms

- **collenchyma**: a supporting ground tissue just under the surface of various leaf structures formed before vascular differentiation
- **sclerenchyma**: a mechanical, supportive ground tissue in plants consisting of aggregates of cells having thick, often mineralized walls
- **sclereid**: a reduced form of sclerenchyma cells with highly-thickened, lignified walls
- **lignin**: a complex, non-carbohydrate, aromatic polymer present in all wood
- **stoma**: a pore found in the leaf and stem epidermis used for gaseous exchange
- **trichome**: a hair- or scale-like extension of the epidermis of a plant

- **xylem**: a vascular tissue in land plants primarily responsible for the distribution of water and minerals taken up by the roots; also the primary component of wood
- **phloem**: a vascular tissue in land plants primarily responsible for the distribution of sugars and nutrients manufactured in the shoot
- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts
- **pith**: the soft spongy substance in the center of the stems of many plants and trees
- **cortex**: the tissue of a stem or root that lies inward from the epidermis, but exterior to the vascular tissue
- **parenchyma**: the ground tissue making up most of the non-woody parts of a plant

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35.4.3: Primary and Secondary Growth in Stems

Learning Objectives

- Distinguish between primary and secondary growth in stems

Growth in plants occurs as the stems and roots lengthen. Some plants, especially those that are woody, also increase in thickness during their life span. The increase in length of the shoot and the root is referred to as primary growth. It is the result of cell division in the shoot apical meristem. Secondary growth is characterized by an increase in thickness or girth of the plant. It is caused by cell division in the lateral meristem. Herbaceous plants mostly undergo primary growth, with little secondary growth or increase in thickness. Secondary growth, or “wood”, is noticeable in woody plants; it occurs in some dicots, but occurs very rarely in monocots.

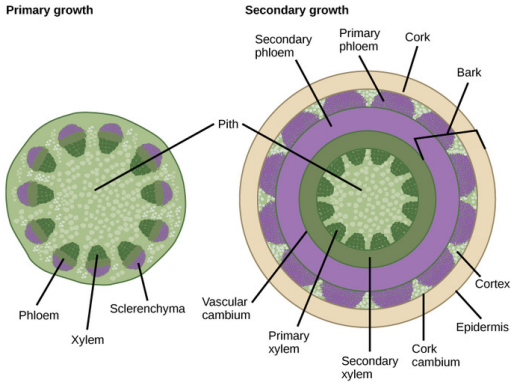


Figure **35.4.3.1**: Primary and secondary growth: In woody plants, primary growth is followed by secondary growth, which allows the plant stem to increase in thickness or girth. Secondary vascular tissue is added as the plant grows, as well as a cork layer. The bark of a tree extends from the vascular cambium to the epidermis.

Some plant parts, such as stems and roots, continue to grow throughout a plant’s life: a phenomenon called indeterminate growth. Other plant parts, such as leaves and flowers, exhibit determinate growth, which ceases when a plant part reaches a particular size.

Primary Growth

Most primary growth occurs at the apices, or tips, of stems and roots. Primary growth is a result of rapidly-dividing cells in the apical meristems at the shoot tip and root tip. Subsequent cell elongation also contributes to primary growth. The growth of shoots and roots during primary growth enables plants to continuously seek water (roots) or sunlight (shoots).

The influence of the apical bud on overall plant growth is known as apical dominance, which diminishes the growth of axillary buds that form along the sides of branches and stems. Most coniferous trees exhibit strong apical dominance, thus producing the typical conical Christmas tree shape. If the apical bud is removed, then the axillary buds will start forming lateral branches. Gardeners make use of this fact when they prune plants by cutting off the tops of branches, thus encouraging the axillary buds to grow out, giving the plant a bushy shape.

Secondary Growth

The increase in stem thickness that results from secondary growth is due to the activity of the lateral meristems, which are lacking in herbaceous plants. Lateral meristems include the vascular cambium and, in woody plants, the cork cambium. The vascular cambium is located just outside the primary xylem and to the interior of the primary phloem. The cells of the vascular cambium divide and form secondary xylem (tracheids and vessel elements) to the inside and secondary phloem (sieve elements and companion cells) to the outside. The thickening of the stem that occurs in secondary growth is due to the formation of secondary phloem and secondary xylem by the vascular cambium, plus the action of cork cambium, which forms the tough outermost layer of the stem. The cells of the secondary xylem contain lignin, which provides hardiness and strength.

In woody plants, cork cambium is the outermost lateral meristem. It produces cork cells (bark) containing a waxy substance known as suberin that can repel water. The bark protects the plant against physical damage and helps reduce water loss. The cork cambium

also produces a layer of cells known as phelloderm, which grows inward from the cambium. The cork cambium, cork cells, and phelloderm are collectively termed the periderm. The periderm substitutes for the epidermis in mature plants. In some plants, the periderm has many openings, known as lenticels, which allow the interior cells to exchange gases with the outside atmosphere. This supplies oxygen to the living- and metabolically-active cells of the cortex, xylem, and phloem.



Figure **35.4.3.1**: Example of lenticels: Lenticels on the bark of this cherry tree enable the woody stem to exchange gases with the surrounding atmosphere.

Annual Rings

The activity of the vascular cambium gives rise to annual growth rings. During the spring growing season, cells of the secondary xylem have a large internal diameter; their primary cell walls are not extensively thickened. This is known as early wood, or spring wood. During the fall season, the secondary xylem develops thickened cell walls, forming late wood, or autumn wood, which is denser than early wood. This alternation of early and late wood is due largely to a seasonal decrease in the number of vessel elements and a seasonal increase in the number of tracheids. It results in the formation of an annual ring, which can be seen as a circular ring in the cross section of the stem. An examination of the number of annual rings and their nature (such as their size and cell wall thickness) can reveal the age of the tree and the prevailing climatic conditions during each season.

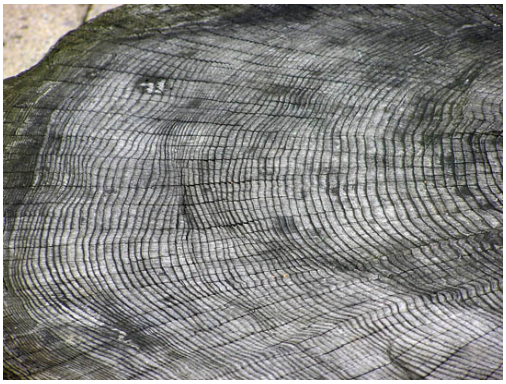


Figure **35.4.3.1**: Annual growth rings: The rate of wood growth increases in summer and decreases in winter, producing a characteristic ring for each year of growth. Seasonal changes in weather patterns can also affect the growth rate. Note how the rings vary in thickness.

Key Points

- Indeterminate growth continues throughout a plant's life, while determinate growth stops when a plant element (such as a leaf) reaches a particular size.
- Primary growth of stems is a result of rapidly-dividing cells in the apical meristems at the shoot tips.
- Apical dominance reduces the growth along the sides of branches and stems, giving the tree a conical shape.

- The growth of the lateral meristems, which includes the vascular cambium and the cork cambium (in woody plants), increases the thickness of the stem during secondary growth.
- Cork cells (bark) protect the plant against physical damage and water loss; they contain a waxy substance known as suberin that prevents water from penetrating the tissue.
- The secondary xylem develops dense wood during the fall and thin wood during the spring, which produces a characteristic ring for each year of growth.

Key Terms

- **lenticel**: small, oval, rounded spots upon the stem or branch of a plant that allow the exchange of gases with the surrounding atmosphere
- **periderm**: the outer layer of plant tissue; the outer bark
- **suberin**: a waxy material found in bark that can repel water

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35.4.4: Stem Modifications

Learning Objectives

- Explain the reasons for stem modifications

Some plant species have modified stems that are especially suited to a particular habitat and environment. A rhizome is a modified stem that grows horizontally underground; it has nodes and internodes. Vertical shoots may arise from the buds on the rhizome of some plants, such as ginger and ferns. Corms are similar to rhizomes, except they are more rounded and fleshy (such as in gladiolus). Corms contain stored food that enables some plants to survive the winter. Stolons are stems that run almost parallel to the ground, or just below the surface, and can give rise to new plants at the nodes. Runners are a type of stolon that runs above the ground and produces new clone plants at nodes at varying intervals: strawberries are an example. Tubers are modified stems that may store starch, as seen in the potato. Tubers arise as swollen ends of stolons, and contain many adventitious or unusual buds (familiar to us as the "eyes" on potatoes). A bulb, which functions as an underground storage unit, is a modification of a stem that has the appearance of enlarged fleshy leaves emerging from the stem or surrounding the base of the stem, as seen in the iris.

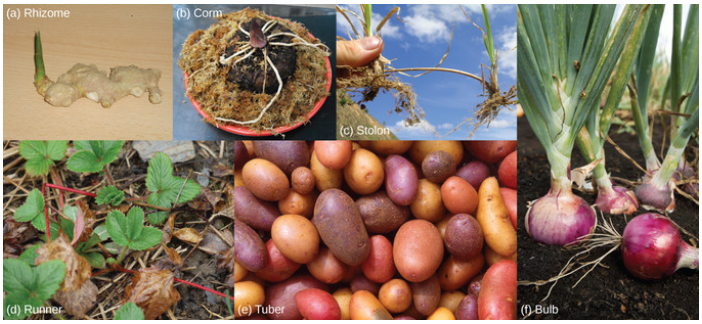


Figure **35.4.4.1**: Stem modifications: Stem modifications enable plants to thrive in a variety of environments. Shown are (a) ginger (Zingiber officinale) rhizomes, (b) a carrion flower (Amorphophallus titanum) corm (c) Rhodes grass (Chloris gayana) stolons, (d) strawberry (Fragaria ananassa) runners, (e) potato (Solanum tuberosum) tubers, and (f) red onion (Allium) bulbs.

Modifications to the aerial stems, vegetative buds, and floral buds of plants perform functions such as climbing, protection, and synthesis of food vegetative propagation. Aerial modifications of stems include the following:



Figure **35.4.4.1**: Aerial modifications of stems: Found in southeastern United States, (a) buckwheat vine (Brunnichia ovata) is a weedy plant that climbs with the aid of tendrils. This one is shown climbing up a wooden stake. (b) Thorns are modified branches.

- Tendrils are slender, twining strands that enable a plant (like the buckwheat vine) to seek support by climbing on other surfaces. These may develop from either the axillary bud or the terminal bud of the stem.
- Thorns are modified branches appearing as hard, woody, sharp outgrowths that protect the plant; common examples include roses, osage orange, and devil's walking stick.
- Bulbils are axillary buds that have become fleshy and rounded due to storage of food. They become detached from the plant, fall on ground and develop into a new plant.
- Cladodes are green branches of limited growth (usually one internode long) which have taken up the functions of photosynthesis.

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Key Points

- Modified stems that grow horizontally underground are either rhizomes, from which vertical shoots grow, or fleshier, food-storing corms.
- New plants can arise from the nodes of stolons and runners (an aboveground stolon): stems that run parallel to the ground, or just below the surface.
- Potatoes are examples of tubers: the swollen ends of stolons that may store starch.
- The stem modification that has enlarged fleshy leaves emerging from the stem or surrounding the base of the stem is called a bulb; it is also used to store food.
- Aerial modifications of stems include tendrils, thorns, bulbils, and cladodes..

Key Terms

- **stolon**: a shoot that grows along the ground and produces roots at its nodes; a runner
- **tuber**: a fleshy, thickened, underground stem of a plant, usually containing stored starch, as for example a potato or arrowroot
- **cladode**: green branches of limited growth which have taken up the functions of photosynthesis
- **rhizome**: a horizontal underground stem of some plants that sends out roots and shoots from its nodes
- **corm**: a short, vertical, swollen underground stem of a plant that serves as a storage organ to enable the plant to survive winter or other adverse conditions such as drought
- **bulb**: the bulb-shaped root portion of a plant such as a tulip, from which the rest of the plant may be regrown
- **tendril**: a thin, spirally-coiling stem that attaches a plant to its support
- **thorn**: a sharp, protective spine of a plant
- **bulbil**: a bulb-shaped bud in the place of a flower or in a leaf axil

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35.5: Leaves- Photosynthetic Organs

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35.5.1: Leaf Structure and Arrangment

Learning Objectives

- Sketch the basic structure of a typical leaf

Structure of a Typical Leaf

Each leaf typically has a leaf blade called the lamina, which is also the widest part of the leaf. Some leaves are attached to the plant stem by a petiole. Leaves that do not have a petiole and are directly attached to the plant stem are called sessile leaves. Leaves also have stipules, small green appendages usually found at the base of the petiole. Most leaves have a midrib, which travels the length of the leaf and branches to each side to produce veins of vascular tissue. The edge of the leaf is called the **margin**.

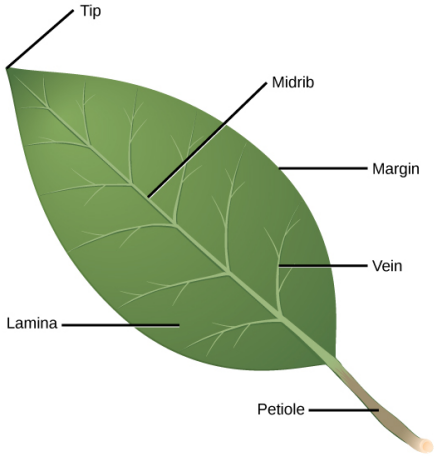


Figure 35.5.1.1: Parts of a leaf: A leaf may seem simple in appearance, but it is a highly-efficient structure. Petioles, stipules, veins, and a midrib are all essential structures of a leaf.

Within each leaf, the vascular tissue forms veins. The arrangement of veins in a leaf is called the **venation pattern**. Monocots and dicots differ in their patterns of venation. Monocots have parallel venation in which the veins run in straight lines across the length of the leaf without converging. In dicots, however, the veins of the leaf have a net-like appearance, forming a pattern known as reticulate venation. *Ginkgo biloba* is an example of a plant with dichotomous venation.

Leaf Arrangement

The arrangement of leaves on a stem is known as **phyllotaxy**. The number and placement of a plant's leaves will vary depending on the species, with each species exhibiting a characteristic leaf arrangement. Leaves are classified as either alternate, spiral, opposite, or whorled. Plants that have only one leaf per node have leaves that are said to be either alternate or spiral. Alternate leaves alternate on each side of the stem in a flat plane, and spiral leaves are arranged in a spiral along the stem. In an opposite leaf arrangement, two leaves arise at the same point, with the leaves connecting opposite each other along the branch. If there are three or more leaves connected at a node, the leaf arrangement is classified as whorled.

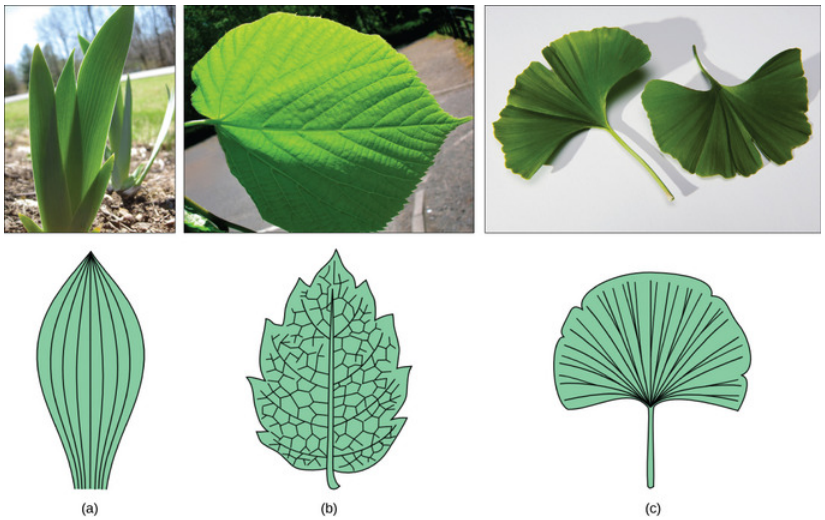


Figure **35.5.1.1**: Venation patterns: (a) Tulip (*Tulipa*), a monocot, has leaves with parallel venation. (b) The netlike venation in this linden (*Tilia cordata*) leaf distinguishes it as a dicot. (c) The Ginkgo biloba tree has dichotomous venation.

Key Points

- Each leaf typically has a leaf blade (lamina), stipules, a midrib, and a margin.
- Some leaves have a petiole, which attaches the leaf to the stem; leaves that do not have petioles are directly attached to the plant stem and are called sessile leaves.
- The arrangement of veins in a leaf is called the venation pattern; monocots have parallel venation, while dicots have reticulate venation.
- The arrangement of leaves on a stem is known as phyllotaxy; leaves can be classified as either alternate, spiral, opposite, or whorled.
- Plants with alternate and spiral leaf arrangements have only one leaf per node.
- In an opposite leaf arrangement, two leaves connect at a node. In a whorled arrangement, three or more leaves connect at a node.

Key Terms

- **petiole**: stalk that extends from the stem to the base of the leaf
- **lamina**: the flat part of a leaf; the blade, which is the widest part of the leaf
- **stipule**: small green appendage usually found at the base of the petiole

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35.5.2: Types of Leaf Forms

Learning Objectives

- Differentiate among the types of leaf forms

Leaf Form

There are two basic forms of leaves that can be described considering the way the blade (or lamina) is divided. Leaves may be simple or compound.

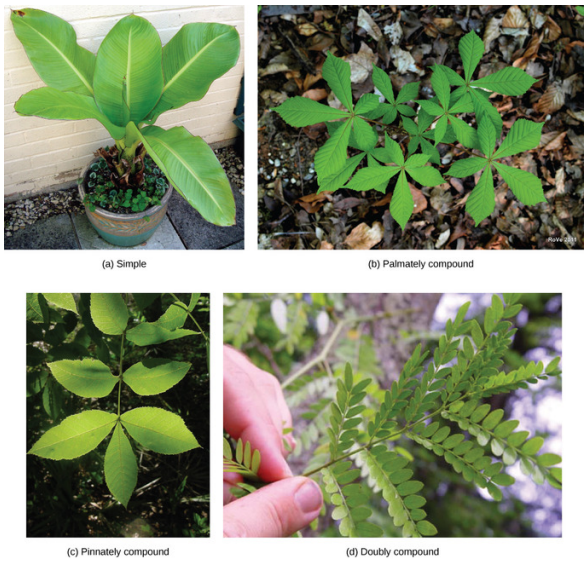


Figure **35.5.2.1**: Simple and compound leaves: Leaves may be simple or compound. In simple leaves, the lamina is continuous. (a) The banana plant (*Musa sp.*) has simple leaves. In compound leaves, the lamina is separated into leaflets. Compound leaves may be palmate or pinnate. (b) In palmately compound leaves, such as those of the horse chestnut (*Aesculus hippocastanum*), the leaflets branch from the petiole. (c) In pinnately compound leaves, the leaflets branch from the midrib, as on a scrub hickory (*Carya floridana*). (d) The honey locust has double compound leaves, in which leaflets branch from the veins.

In a simple leaf, such as the banana leaf, the blade is completely undivided. The leaf shape may also be formed of lobes where the gaps between lobes do not reach to the main vein. An example of this type is the maple leaf.

In a compound leaf, the leaf blade is completely divided, forming leaflets, as in the locust tree. Compound leaves are a characteristic of some families of higher plants. Each leaflet is attached to the rachis (middle vein), but may have its own stalk. A palmately compound leaf has its leaflets radiating outwards from the end of the petiole, like fingers off the palm of a hand. Examples of plants with palmately compound leaves include poison ivy, the buckeye tree, or the familiar house plant *Schefflera sp.* (commonly called “umbrella plant”). Pinnately compound leaves take their name from their feather-like appearance; the leaflets are arranged along the middle vein, as in rose leaves or the leaves of hickory, pecan, ash, or walnut trees. In a pinnately compound leaf, the middle vein is called the midrib. Bipinnately compound (or double compound) leaves are twice divided; the leaflets are arranged along a secondary vein, which is one of several veins branching off the middle vein. Each leaflet is called a “pinnule”. The pinnules on one secondary vein are called “pinna”. The silk tree (*Albizia*) is an example of a plant with bipinnate leaves.

Key Points

- In a simple leaf, the blade is completely undivided; leaves may also be formed of lobes where the gaps between lobes do not reach to the main vein.
- In a compound leaf, the leaf blade is divided, forming leaflets that are attached to the middle vein, but have their own stalks.
- The leaflets of palmately-compound leaves radiate outwards from the end of the petiole.
- Pinnately-compound leaves have their leaflets arranged along the middle vein.
- Bipinnately-compound (double-compound) leaves have their leaflets arranged along a secondary vein, which is one of several veins branching off the middle vein.

Key Terms

- **simple leaf**: a leaf with an undivided blade
- **compound leaf**: a leaf where the blade is divided, forming leaflets
- **palmately compound leaf**: leaf that has its leaflets radiating outwards from the end of the petiole
- **pinnately compound leaf**: a leaf where the leaflets are arranged along the middle vein

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35.5.3: Leaf Structure, Function, and Adaptation

Learning Objectives

- Describe the internal structure and function of a leaf

Leaf Structure and Function

The outermost layer of the leaf is the epidermis. It consists of the upper and lower epidermis, which are present on either side of the leaf. Botanists call the upper side the adaxial surface (or adaxis) and the lower side the abaxial surface (or abaxis). The epidermis aids in the regulation of gas exchange. It contains stomata, which are openings through which the exchange of gases takes place. Two guard cells surround each stoma, regulating its opening and closing. Guard cells are the only epidermal cells to contain chloroplasts.

The epidermis is usually one cell layer thick. However, in plants that grow in very hot or very cold conditions, the epidermis may be several layers thick to protect against excessive water loss from transpiration. A waxy layer known as the cuticle covers the leaves of all plant species. The cuticle reduces the rate of water loss from the leaf surface. Other leaves may have small hairs (trichomes) on the leaf surface. Trichomes help to avert herbivory by restricting insect movements or by storing toxic or bad-tasting compounds. They can also reduce the rate of transpiration by blocking air flow across the leaf surface.

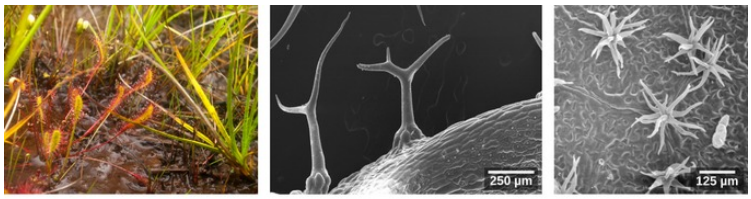
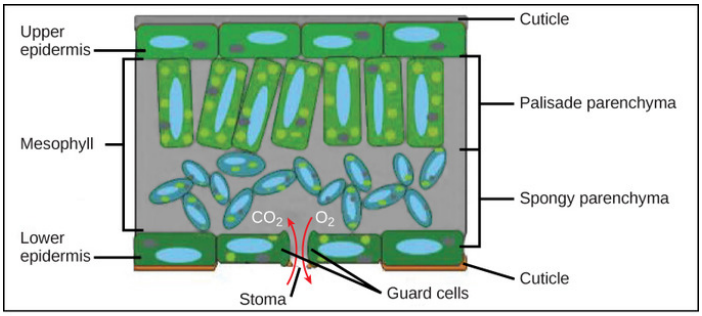
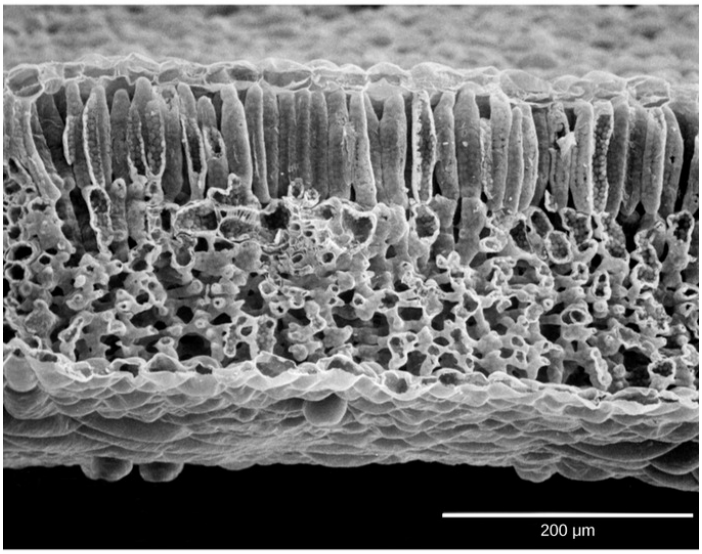


Figure 35.5.3.1: Trichomes: Trichomes give leaves a fuzzy appearance as in this (a) sundew *(Drosera sp*.). Leaf trichomes include (b) branched trichomes on the leaf of *Arabidopsis lyrata* and (c) multibranched trichomes on a mature *Quercus marilandica* leaf.

Below the epidermis of dicot leaves are layers of cells known as the mesophyll, or “middle leaf.” The mesophyll of most leaves typically contains two arrangements of parenchyma cells: the palisade parenchyma and spongy parenchyma. The palisade parenchyma (also called the palisade mesophyll) aids in photosynthesis and has column-shaped, tightly-packed cells. It may be present in one, two, or three layers. Below the palisade parenchyma are loosely-arranged cells of an irregular shape. These are the cells of the spongy parenchyma (or spongy mesophyll). The air space found between the spongy parenchyma cells allows gaseous exchange between the leaf and the outside atmosphere through the stomata. In aquatic plants, the intercellular spaces in the spongy parenchyma help the leaf float. Both layers of the mesophyll contain many chloroplasts.



(a)



(b)

Figure **35.5.3.1**: Mesophyll: (a) (top) The central mesophyll is sandwiched between an upper and lower epidermis. The mesophyll has two layers: an upper palisade layer and a lower spongy layer. Stomata on the leaf underside allow gas exchange. A waxy cuticle covers all aerial surfaces of land plants to minimize water loss. (b) (bottom) These leaf layers are clearly visible in the scanning electron micrograph. The numerous small bumps in the palisade parenchyma cells are chloroplasts. The bumps protruding from the lower surface of the leaf are glandular trichomes.

Similar to the stem, the leaf contains vascular bundles composed of xylem and phloem. The xylem consists of tracheids and vessels, which transport water and minerals to the leaves. The phloem transports the photosynthetic products from the leaf to the other parts of the plant. A single vascular bundle, no matter how large or small, always contains both xylem and phloem tissues.

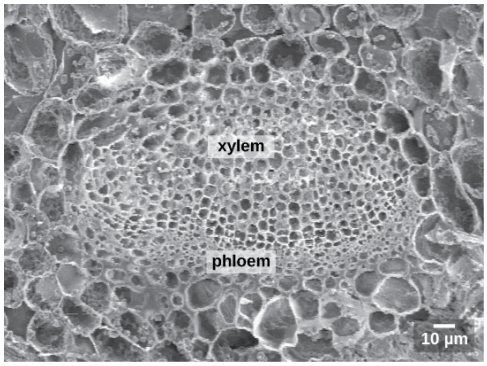


Figure **35.5.3.1**: Xylem and phloem: This scanning electron micrograph shows xylem and phloem in the leaf vascular bundle.

Leaf Adaptations

Coniferous plant species that thrive in cold environments, such as spruce, fir, and pine, have leaves that are reduced in size and needle-like in appearance. These needle-like leaves have sunken stomata and a smaller surface area, two attributes that aid in

reducing water loss. In hot climates, plants such as cacti have succulent leaves that help to conserve water. Many aquatic plants have leaves with wide lamina that can float on the surface of the water; a thick waxy cuticle on the leaf surface that repels water.

Key Points

- The epidermis consists of the upper and lower epidermis; it aids in the regulation of gas exchange via stomata.
- The epidermis is one layer thick, but may have more layers to prevent transpiration.
- The cuticle is located outside the epidermis and protects against water loss; trichomes discourage predation.
- The mesophyll is found between the upper and lower epidermis; it aids in gas exchange and photosynthesis via chloroplasts.
- The xylem transports water and minerals to the leaves; the phloem transports the photosynthetic products to the other parts of the plant.
- Plants in cold climates have needle-like leaves that are reduced in size; plants in hot climates have succulent leaves that help to conserve water.

Key Terms

- **trichome**: a hair- or scale-like extension of the epidermis of a plant
- **cuticle**: a noncellular protective covering outside the epidermis of many invertebrates and plants
- **mesophyll**: the inner tissue (parenchyma) of a leaf, containing many chloroplasts.

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CHAPTER OVERVIEW

36: Transport in Plants

36.1: Transport Mechanisms

36.2: Water and Mineral Absorption

36.2.1: Movement of Water and Minerals in the Xylem

36.3: Xylem Transport

36.4: Rate of Transpiration

36.4.1: Stomatal Opening and Closing

36.5: Water-Stress Responses

36.5.1: Response to Water Stress

36.6: Phloem Transport

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36.1: Transport Mechanisms

Skills to Develop

- Define water potential and explain how it is influenced by solutes, pressure, gravity, and the matric potential
- Describe how water potential, evapotranspiration, and stomatal regulation influence how water is transported in plants
- Explain how photosynthates are transported in plants

The structure of plant roots, stems, and leaves facilitates the transport of water, nutrients, and photosynthates throughout the plant. The phloem and xylem are the main tissues responsible for this movement. Water potential, evapotranspiration, and stomatal regulation influence how water and nutrients are transported in plants. To understand how these processes work, we must first understand the energetics of water potential.

Water Potential

Plants are phenomenal hydraulic engineers. Using only the basic laws of physics and the simple manipulation of potential energy, plants can move water to the top of a 116-meter-tall tree (Figure **36.1.1**a). Plants can also use hydraulics to generate enough force to split rocks and buckle sidewalks (Figure **36.1.1**b). Plants achieve this because of water potential.



(a) (b)

Figure **36.1.1**: With heights nearing 116 meters, (a) coastal redwoods (*Sequoia sempervirens*) are the tallest trees in the world. Plant roots can easily generate enough force to (b) buckle and break concrete sidewalks, much to the dismay of homeowners and city maintenance departments. (credit a: modification of work by Bernt Rostad; credit b: modification of work by Pedestrians Educating Drivers on Safety, Inc.)

Water potential is a measure of the potential energy in water. Plant physiologists are not interested in the energy in any one particular aqueous system, but are very interested in water movement between two systems. In practical terms, therefore, water potential is the difference in potential energy between a given water sample and pure water (at atmospheric pressure and ambient temperature). Water potential is denoted by the Greek letter ψ (*psi*) and is expressed in units of pressure (pressure is a form of energy) called megapascals (MPa). The potential of pure water ($\Psi_w^{\text{pure H2O}}$) is, by convenience of definition, designated a value of zero (even though pure water contains plenty of potential energy, that energy is ignored). Water potential values for the water in a plant root, stem, or leaf are therefore expressed relative to $\Psi_w^{\text{pure H2O}}$.

The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects. Water potential can be broken down into its individual components using the following equation:

$$\psi_{system} = \psi_{total} = \psi_s + \psi_p + \psi_g + \psi_m$$

where Ψ_s, Ψ_p, Ψ_g, and Ψ_m refer to the solute, pressure, gravity, and matric potentials, respectively. "System" can refer to the water potential of the soil water (Ψ^{soil}), root water (Ψ^{root}), stem water (Ψ^{stem}), leaf water (Ψ^{leaf}) or the water in the atmosphere ($\Psi^{atmosphere}$): whichever aqueous system is under consideration. As the individual components change, they raise or lower the total water potential of a system. When this happens, water moves to equilibrate, moving from the system or compartment with a higher water potential to the system or compartment with a lower water potential. This brings the difference in water potential between the two systems ($\Delta\Psi$) back to zero ($\Delta\Psi = 0$). Therefore, for water to move through the plant from the soil to the air (a process called transpiration), Ψ^{soil} must be $> \Psi^{root} > \Psi^{stem} > \Psi^{leaf} > \Psi^{atmosphere}$.

Water only moves in response to $\Delta\Psi$, not in response to the individual components. However, because the individual components influence the total Ψ_{system}, by manipulating the individual components (especially Ψ_s), a plant can control water movement.

Solute Potential

Solute potential (Ψ_s), also called osmotic potential, is negative in a plant cell and zero in distilled water. Typical values for cell cytoplasm are –0.5 to –1.0 MPa. Solutes reduce water potential (resulting in a negative Ψ_w) by consuming some of the potential energy available in the water. Solute molecules can dissolve in water because water molecules can bind to them via hydrogen bonds; a hydrophobic molecule like oil, which cannot bind to water, cannot go into solution. The energy in the hydrogen bonds between solute molecules and water is no longer available to do work in the system because it is tied up in the bond. In other words, the amount of available potential energy is reduced when solutes are added to an aqueous system. Thus, Ψ_s decreases with increasing solute concentration. Because Ψ_s is one of the four components of Ψ_{system} or Ψ_{total}, a decrease in Ψ_s will cause a decrease in Ψ_{total}. The internal water potential of a plant cell is more negative than pure water because of the cytoplasm's high solute content (Figure **36.1.2**). Because of this difference in water potential water will move from the soil into a plant's root cells via the process of osmosis. This is why solute potential is sometimes called osmotic potential.

Plant cells can metabolically manipulate Ψ_s (and by extension, Ψ_{total}) by adding or removing solute molecules. Therefore, plants have control over Ψ_{total} via their ability to exert metabolic control over Ψ_s.

Art Connection

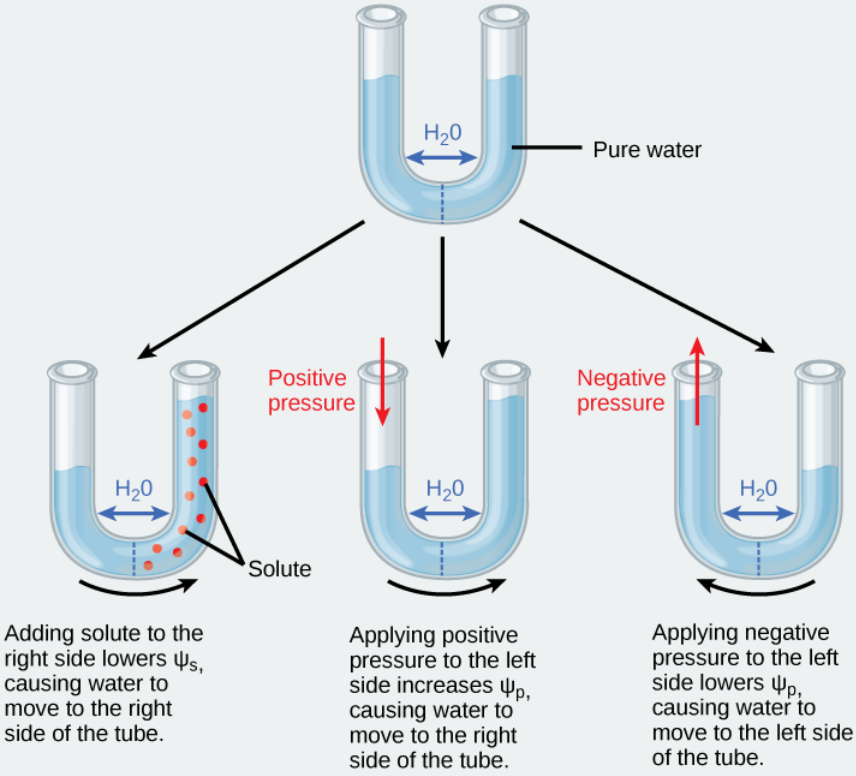


Figure **36.1.2**: In this example with a semipermeable membrane between two aqueous systems, water will move from a region of higher to lower water potential until equilibrium is reached. Solutes (Ψ_s), pressure (Ψ_p), and gravity (Ψ_g) influence total water potential for each side of the tube (Ψ_{total} $^{right\ or\ left}$), and therefore, the difference between Ψ_{total} on each side ($\Delta\Psi$). (Ψ_m , the potential due to interaction of water with solid substrates, is ignored in this example because glass is not especially hydrophilic). Water moves in response to the difference in water potential between two systems (the left and right sides of the tube).

Positive water potential is placed on the left side of the tube by increasing Ψ_p such that the water level rises on the right side. Could you equalize the water level on each side of the tube by adding solute, and if so, how?

Pressure Potential

Pressure potential (Ψ_p), also called turgor potential, may be positive or negative (Figure **36.1.3**). Because pressure is an expression of energy, the higher the pressure, the more potential energy in a system, and vice versa. Therefore, a positive Ψp (compression) increases Ψ_{total}, and a negative Ψ_p (tension) decreases Ψ_{total}. Positive pressure inside cells is contained by the cell wall, producing turgor pressure. Pressure potentials are typically around 0.6–0.8 MPa, but can reach as high as 1.5 MPa in a well-watered plant. A Ψ_p of 1.5 MPa equates to 210 pounds per square inch (1.5 MPa x 140 lb in^{-2} MPa^{-1} = 210 lb/in^{-2}). As a comparison, most automobile tires are kept at a pressure of 30–34 psi. An example of the effect of turgor pressure is the wilting of leaves and their restoration after the plant has been watered (Figure **36.1.3**). Water is lost from the leaves via transpiration (approaching Ψ_p = 0 MPa at the wilting point) and restored by uptake via the roots.

A plant can manipulate Ψ_p via its ability to manipulate Ψ_s and by the process of osmosis. If a plant cell increases the cytoplasmic solute concentration, Ψ_s will decline, Ψ_{total} will decline, the $\Delta\Psi$ between the cell and the surrounding tissue will decline, water will move into the cell by osmosis, and Ψ_p will increase. Ψ_p is also under indirect plant control via the opening and closing of stomata. Stomatal openings allow water to evaporate from the leaf, reducing Ψ_p and Ψ_{total} of the leaf and increasing ii between the water in the leaf and the petiole, thereby allowing water to flow from the petiole into the leaf.



(a) (b)

Figure **36.1.3**: When (a) total water potential (Ψ_{total}) is lower outside the cells than inside, water moves out of the cells and the plant wilts. When (b) the total water potential is higher outside the plant cells than inside, water moves into the cells, resulting in turgor pressure (Ψ_p) and keeping the plant erect. (credit: modification of work by Victor M. Vicente Selvas)

Gravity Potential

Gravity potential (Ψ_g) is always negative to zero in a plant with no height. It always removes or consumes potential energy from the system. The force of gravity pulls water downwards to the soil, reducing the total amount of potential energy in the water in the plant (Ψ_{total}). The taller the plant, the taller the water column, and the more influential Ψ_g becomes. On a cellular scale and in short plants, this effect is negligible and easily ignored. However, over the height of a tall tree like a giant coastal redwood, the gravitational pull of –0.1 MPa m^{-1} is equivalent to an extra 1 MPa of resistance that must be overcome for water to reach the leaves of the tallest trees. Plants are unable to manipulate Ψ_g.

Matric Potential

Matric potential (Ψ_m) is always negative to zero. In a dry system, it can be as low as –2 MPa in a dry seed, and it is zero in a water-saturated system. The binding of water to a matrix always removes or consumes potential energy from the system. Ψ_m is similar to solute potential because it involves tying up the energy in an aqueous system by forming hydrogen bonds between the water and some other component. However, in solute potential, the other components are soluble, hydrophilic solute molecules, whereas in Ψ_m, the other components are insoluble, hydrophilic molecules of the plant cell wall. Every plant cell has a cellulosic cell wall and the cellulose in the cell walls is hydrophilic, producing a matrix for adhesion of water: hence the name matric potential. Ψ_m is very large (negative) in dry tissues such as seeds or drought-affected soils. However, it quickly goes to zero as the seed takes up water or the soil hydrates. Ψ_m cannot be manipulated by the plant and is typically ignored in well-watered roots, stems, and leaves.

Movement of Water and Minerals in the Xylem

Solutes, pressure, gravity, and matric potential are all important for the transport of water in plants. Water moves from an area of higher total water potential (higher Gibbs free energy) to an area of lower total water potential. Gibbs free energy is the energy associated with a chemical reaction that can be used to do work. This is expressed as $\Delta\Psi$.

Transpiration is the loss of water from the plant through evaporation at the leaf surface. It is the main driver of water movement in the xylem. Transpiration is caused by the evaporation of water at the leaf–atmosphere interface; it creates negative pressure (tension) equivalent to –2 MPa at the leaf surface. This value varies greatly depending on the vapor pressure deficit, which can be negligible at high relative humidity (RH) and substantial at low RH. Water from the roots is pulled up by this tension. At night, when stomata shut and transpiration stops, the water is held in the stem and leaf by the adhesion of water to the cell walls of the xylem vessels and tracheids, and the cohesion of water molecules to each other. This is called the cohesion–tension theory of sap ascent.

Inside the leaf at the cellular level, water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to this leaf internal air space, and the water on the surface of the cells evaporates into

the air spaces, decreasing the thin film on the surface of the mesophyll cells. This decrease creates a greater tension on the water in the mesophyll cells (Figure **36.1.4**), thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Rings in the vessels maintain their tubular shape, much like the rings on a vacuum cleaner hose keep the hose open while it is under pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that can form via a process called cavitation. The formation of gas bubbles in xylem interrupts the continuous stream of water from the base to the top of the plant, causing a break termed an embolism in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water, and the more cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them non-functional.

Art Connection

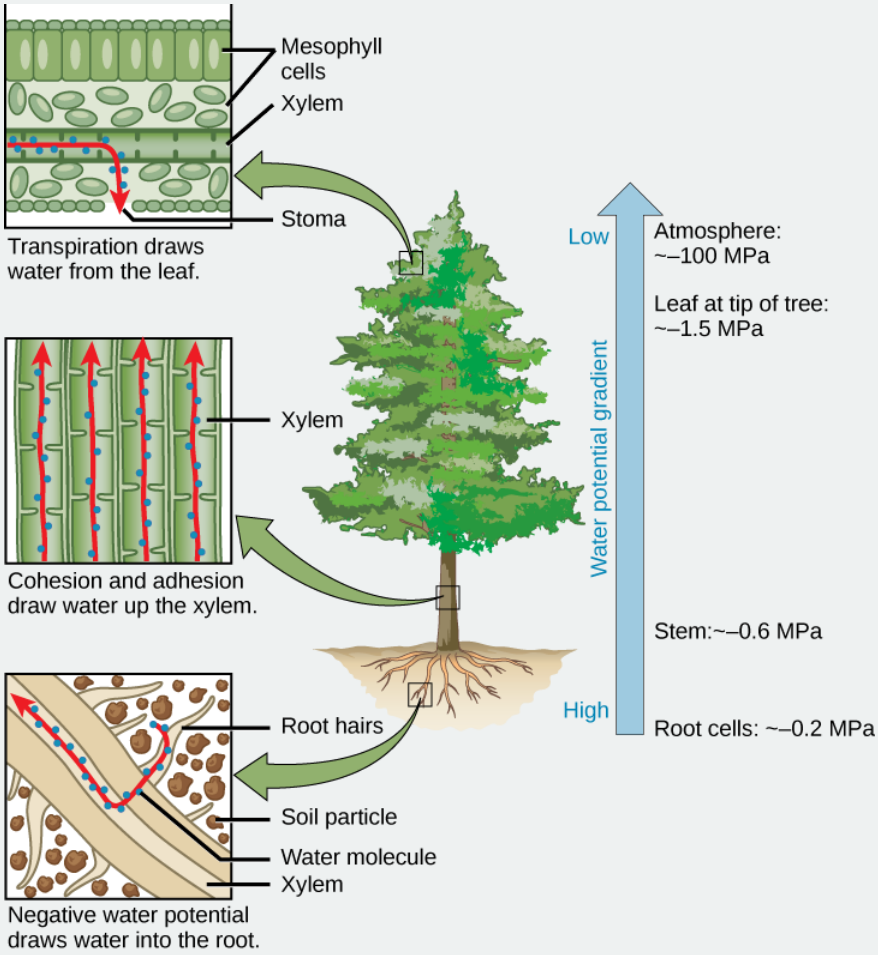


Figure **36.1.4**: The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.

Which of the following statements is false?

A. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf.
B. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the phloem. Transpiration draws water from the leaf.
C. Water potential decreases from the roots to the top of the plant.
D. Water enters the plants through root hairs and exits through stoma.

Transpiration—the loss of water vapor to the atmosphere through stomata—is a passive process, meaning that metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in energy between the water in the soil and the water in the atmosphere. However, transpiration is tightly controlled.

Control of Transpiration

The atmosphere to which the leaf is exposed drives transpiration, but also causes massive water loss from the plant. Up to 90 percent of the water taken up by roots may be lost through transpiration.

Leaves are covered by a waxy cuticle on the outer surface that prevents the loss of water. Regulation of transpiration, therefore, is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells, which open and close in response to environmental cues such as light intensity and quality, leaf water status, and carbon dioxide concentrations. Stomata must open to allow air containing carbon dioxide and oxygen to diffuse into the leaf for photosynthesis and respiration. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between efficient photosynthesis and water loss.

Plants have evolved over time to adapt to their local environment and reduce transpiration(Figure **36.1.5**). Desert plant (xerophytes) and plants that grow on other plants (epiphytes) have limited access to water. Such plants usually have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (mesophytes). Aquatic plants (hydrophytes) also have their own set of anatomical and morphological leaf adaptations.

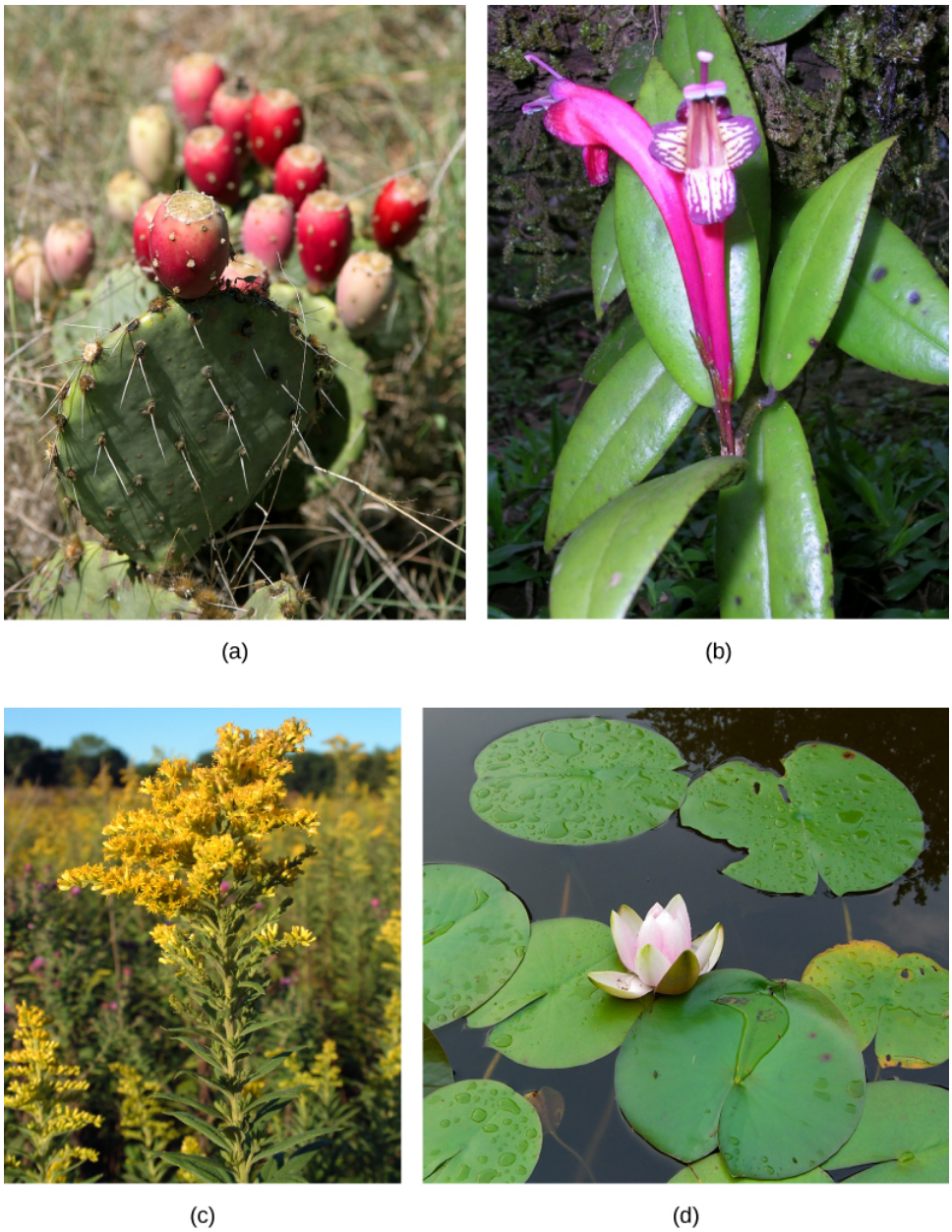


Figure **36.1.5**: Plants are suited to their local environment. (a) Xerophytes, like this prickly pear cactus (*Opuntia* sp.) and (b) epiphytes such as this tropical *Aeschynanthus perrottetii* have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. (b) *A. perottetii* leaves have a waxy cuticle that prevents water loss. (c) Goldenrod (*Solidago* sp.) is a mesophyte, well suited for moderate environments. (d) Hydrophytes, like this fragrant water lily (*Nymphaea odorata*), are adapted to thrive in aquatic environments. (credit a: modification of work by Jon Sullivan; credit b: modification of work by L. Shyamal/Wikimedia Commons; credit c: modification of work by Huw Williams; credit d: modification of work by Jason Hollinger)

Xerophytes and epiphytes often have a thick covering of trichomes or of stomata that are sunken below the leaf's surface. Trichomes are specialized hair-like epidermal cells that secrete oils and substances. These adaptations impede air flow across the stomatal pore and reduce transpiration. Multiple epidermal layers are also commonly found in these types of plants.

Transportation of Photosynthates in the Phloem

Plants need an energy source to grow. In seeds and bulbs, food is stored in polymers (such as starch) that are converted by metabolic processes into sucrose for newly developing plants. Once green shoots and leaves are growing, plants are able to produce

their own food by photosynthesizing. The products of photosynthesis are called photosynthates, which are usually in the form of simple sugars such as sucrose.

Structures that produce photosynthates for the growing plant are referred to as sources. Sugars produced in sources, such as leaves, need to be delivered to growing parts of the plant via the phloem in a process called translocation. The points of sugar delivery, such as roots, young shoots, and developing seeds, are called sinks. Seeds, tubers, and bulbs can be either a source or a sink, depending on the plant's stage of development and the season.

The products from the source are usually translocated to the nearest sink through the phloem. For example, the highest leaves will send photosynthates upward to the growing shoot tip, whereas lower leaves will direct photosynthates downward to the roots. Intermediate leaves will send products in both directions, unlike the flow in the xylem, which is always unidirectional (soil to leaf to atmosphere). The pattern of photosynthate flow changes as the plant grows and develops. Photosynthates are directed primarily to the roots early on, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to tubers for storage.

Translocation: Transport from Source to Sink

Photosynthates, such as sucrose, are produced in the mesophyll cells of photosynthesizing leaves. From there they are translocated through the phloem to where they are used or stored. Mesophyll cells are connected by cytoplasmic channels called plasmodesmata. Photosynthates move through these channels to reach phloem sieve-tube elements (STEs) in the vascular bundles. From the mesophyll cells, the photosynthates are loaded into the phloem STEs. The sucrose is actively transported against its concentration gradient (a process requiring ATP) into the phloem cells using the electrochemical potential of the proton gradient. This is coupled to the uptake of sucrose with a carrier protein called the sucrose-H^+ symporter.

Phloem STEs have reduced cytoplasmic contents, and are connected by a sieve plate with pores that allow for pressure-driven bulk flow, or translocation, of phloem sap. Companion cells are associated with STEs. They assist with metabolic activities and produce energy for the STEs (Figure **36.1.6**).

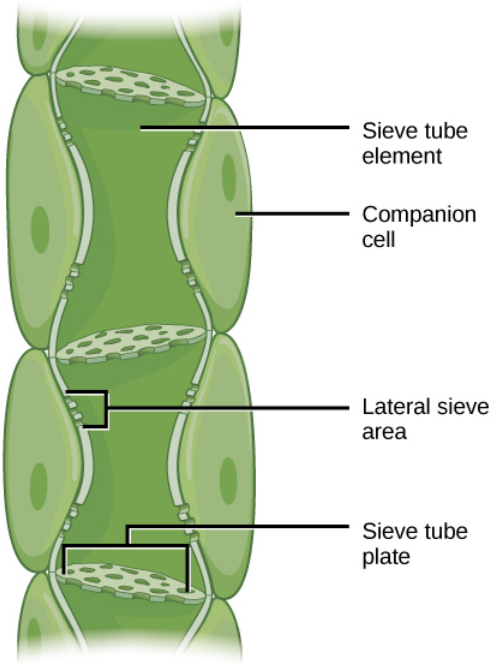


Figure **36.1.6**: Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells.

Once in the phloem, the photosynthates are translocated to the closest sink. Phloem sap is an aqueous solution that contains up to 30 percent sugar, minerals, amino acids, and plant growth regulators. The high percentage of sugar decreases Ψ_s, which decreases the total water potential and causes water to move by osmosis from the adjacent xylem into the phloem tubes, thereby increasing

pressure. This increase in total water potential causes the bulk flow of phloem from source to sink (Figure **36.1.7**). Sucrose concentration in the sink cells is lower than in the phloem STEs because the sink sucrose has been metabolized for growth, or converted to starch for storage or other polymers, such as cellulose, for structural integrity. Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Water diffuses from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.

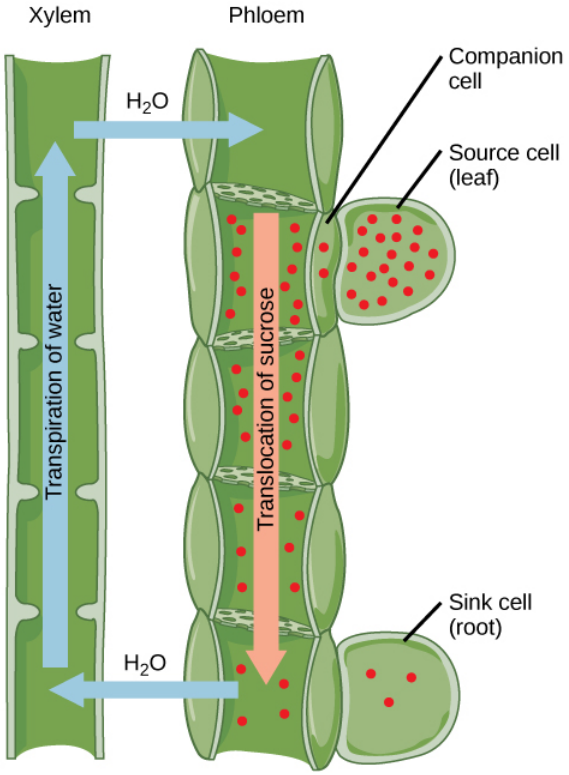


Figure **36.1.7**: Sucrose is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the sucrose-water mixture down toward the roots, where sucrose is unloaded. Transpiration causes water to return to the leaves through the xylem vessels.

Summary

Water potential (Ψ) is a measure of the difference in potential energy between a water sample and pure water. The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and matric potential. Water potential and transpiration influence how water is transported through the xylem in plants. These processes are regulated by stomatal opening and closing. Photosynthates (mainly sucrose) move from sources to sinks through the plant's phloem. Sucrose is actively loaded into the sieve-tube elements of the phloem. The increased solute concentration causes water to move by osmosis from the xylem into the phloem. The positive pressure that is produced pushes water and solutes down the pressure gradient. The sucrose is unloaded into the sink, and the water returns to the xylem vessels.

Art Connections

Figure **36.1.2**: Positive water potential is placed on the left side of the tube by increasing Ψ_p such that the water level rises on the right side. Could you equalize the water level on each side of the tube by adding solute, and if so, how?

Answer

Yes, you can equalize the water level by adding the solute to the left side of the tube such that water moves toward the left until the water levels are equal.

Figure 36.1.4: Which of the following statements is false?

A. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf.
B. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the phloem. Transpiration draws water from the leaf.
C. Water potential decreases from the roots to the top of the plant.
D. Water enters the plants through root hairs and exits through stoma.

Answer

B.

Glossary

cuticle
waxy covering on the outside of the leaf and stem that prevents the loss of water

megapascal (MPa)
pressure units that measure water potential

sink
growing parts of a plant, such as roots and young leaves, which require photosynthate

source
organ that produces photosynthate for a plant

translocation
mass transport of photosynthates from source to sink in vascular plants

transpiration
loss of water vapor to the atmosphere through stomata

water potential (Ψ_w)
the potential energy of a water solution per unit volume in relation to pure water at atmospheric pressure and ambient temperature

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36.2: Water and Mineral Absorption

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36.2.1: Movement of Water and Minerals in the Xylem

Learning Objectives

- Outline the movement of water and minerals in the xylem

Movement of Water and Minerals in the Xylem

Most plants obtain the water and minerals they need through their roots. The path taken is: soil -> roots -> stems -> leaves. The minerals (e.g., K+, Ca2+) travel dissolved in the water (often accompanied by various organic molecules supplied by root cells). Water and minerals enter the root by separate paths which eventually converge in the stele, or central vascular bundle in roots.

Transpiration is the loss of water from the plant through evaporation at the leaf surface. It is the main driver of water movement in the xylem. Transpiration is caused by the evaporation of water at the leaf, or atmosphere interface; it creates negative pressure (tension) equivalent to –2 MPa at the leaf surface. However, this value varies greatly depending on the vapor pressure deficit, which can be insignificant at high relative humidity (RH) and substantial at low RH. Water from the roots is pulled up by this tension. At night, when stomata close and transpiration stops, the water is held in the stem and leaf by the cohesion of water molecules to each other as well as the adhesion of water to the cell walls of the xylem vessels and tracheids. This is called the cohesion–tension theory of sap ascent.

The cohesion-tension theory explains how water moves up through the xylem. Inside the leaf at the cellular level, water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to the internal air space and the water on the surface of the cells evaporates into the air spaces. This decreases the thin film on the surface of the mesophyll cells. The decrease creates a greater tension on the water in the mesophyll cells, thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that form via a process called cavitation. The formation of gas bubbles in the xylem is detrimental since it interrupts the continuous stream of water from the base to the top of the plant, causing a break (embolism) in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water in a continuous column, increasing the number of cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them non-functional.

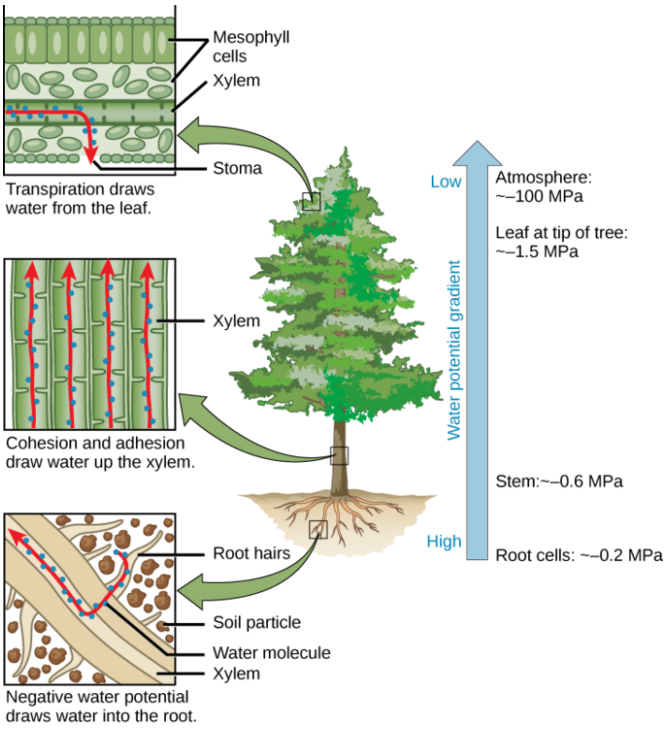


Figure **36.2.1.1**: Cohesion–Tension Theory of Sap Ascent: The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.

Control of Transpiration

Transpiration is a passive process: metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in energy between the water in the soil and the water in the atmosphere. However, transpiration is tightly controlled. The atmosphere to which the leaf is exposed drives transpiration, but it also causes massive water loss from the plant. Up to 90 percent of the water taken up by roots may be lost through transpiration.

Leaves are covered by a waxy cuticle on the outer surface that prevents the loss of water. Regulation of transpiration, therefore, is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells, which open and close in response to environmental cues such as light intensity and quality, leaf water status, and carbon dioxide concentrations. Stomata must open to allow air containing carbon dioxide and oxygen to diffuse into the leaf for photosynthesis and respiration. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between efficient photosynthesis and water loss.

Plants have evolved over time to adapt to their local environment and reduce transpiration. Desert plant (xerophytes) and plants that grow on other plants (epiphytes) have limited access to water. Such plants usually have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (mesophytes). Aquatic plants (hydrophytes) also have their own set of anatomical and morphological leaf adaptations.

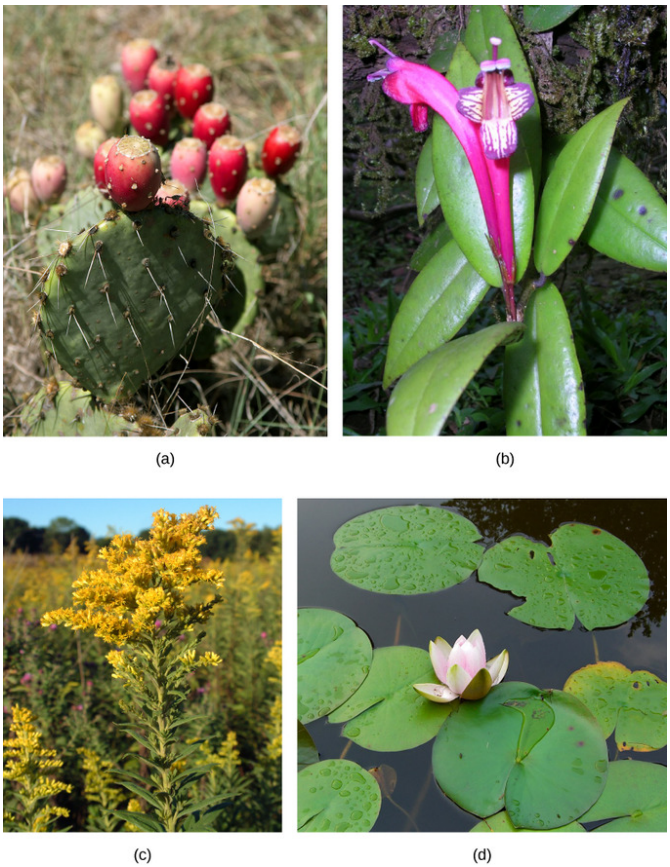


Figure **36.2.1.1**: Reducing Transpiration: Plants are suited to their local environment. (a) Xerophytes, like this prickly pear cactus (*Opuntia* sp.) and (b) epiphytes such as this tropical *Aeschynanthus perrottetii* have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. (b) *A. perrottetii* leaves have a waxy cuticle that prevents water loss. (c) Goldenrod (*Solidago* sp.) is a mesophyte, well suited for moderate environments. (d) Hydrophytes, like this fragrant water lily (*Nymphaea odorata*), are adapted to thrive in aquatic environments.

Xerophytes and epiphytes often have a thick covering of trichomes or stomata that are sunken below the leaf's surface. Trichomes are specialized hair-like epidermal cells that secrete oils and other substances. These adaptations impede air flow across the stomatal pore and reduce transpiration. Multiple epidermal layers are also commonly found in these types of plants.

Key Points

- The cohesion – tension theory of sap ascent explains how how water is pulled up from the roots to the top of the plant.
- Evaporation from mesophyll cells in the leaves produces a negative water potential gradient that causes water and minerals to move upwards from the roots through the xylem.
- Gas bubbles in the xylem can interrupt the flow of water in the plant, so they must be reduced through small perforations between vessel elements.
- Transpiration is controlled by the opening and closing of stomata in response to environmental cues.
- Stomata must open for photosynthesis and respiration, but when stomata are open, water vapor is lost to the external environment, increasing the rate of transpiration.
- Desert plants and plants with limited water access prevent transpiration and excess water loss by utilizing a thicker cuticle, trichomes, or multiple epidermal layers.

Key Terms

- **cohesion–tension theory of sap ascent**: explains the process of water flow upwards (against the force of gravity) through the xylem of plants
- **cavitation**: the formation, in a fluid, of vapor bubbles that can interrupt water flow through the plant
- **trichome**: a hair- or scale-like extension of the epidermis of a plant

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36.3: Xylem Transport

Most plants secure the water and minerals they need from their roots. The path taken is:

$$\text{soil} \rightarrow \text{roots} \rightarrow \text{stems} \rightarrow \text{leaves} \tag{36.3.1}$$

The minerals (e.g., K^+, Ca^{2+}) travel dissolved in the water (often accompanied by various organic molecules supplied by root cells), but less than 1% of the water reaching the leaves is used in photosynthesis and plant growth. Most of it is lost in transpiration, which serve two useful functions- it provides the force for lifting the water up the stems and it cools the leaves. Water and minerals enter the root by separate paths which eventually converge in the stele.

The Pathway of Water and Minerals

Soil water enters the root through its epidermis. It appears that water then travels in both the cytoplasm of root cells - called the symplast (i.e., it crosses the plasma membrane and then passes from cell to cell through plasmodesmata) and in the nonliving parts of the root - called the apoplast (i.e., in the spaces between the cells and in the cells walls themselves. This water has not crossed a plasma membrane. However, the inner boundary of the cortex, the endodermis, is impervious to water because of a band of lignified matrix called the casparian strip. Therefore, to enter the stele, apoplastic water must enter the symplasm of the endodermal cells. From here it can pass by plasmodesmata into the cells of the stele. Once inside the stele, water is again free to move between cells as well as through them. In young roots, water enters directly into the xylem vessels and/or tracheids. These are nonliving conduits so are part of the apoplast.

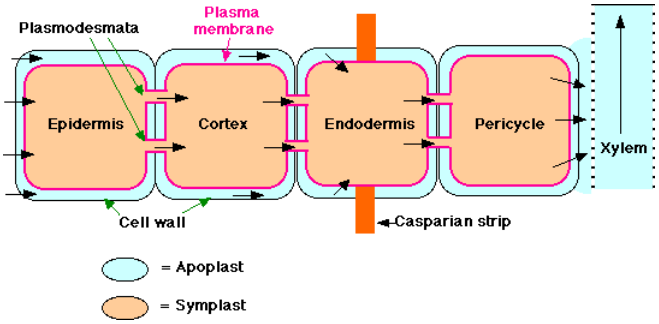


Figure 16.2.1.1: Pathway of water

Once in the xylem, water with the minerals that have been deposited in it (as well as occasional organic molecules supplied by the root tissue) move up in the vessels and tracheids. At any level, the water can leave the xylem and pass laterally to supply the needs of other tissues. At the leaves, the xylem passes into the petiole and then into the veins of the leaf. Water leaves the finest veins and enters the cells of the spongy and palisade layers. Here some of the water may be used in metabolism, but most is lost in transpiration.

Minerals enter the root by active transport into the symplast of epidermal cells and move toward and into the stele through the plasmodesmata connecting the cells. They enter the water in the xylem from the cells of the pericycle (as well as of parenchyma cells surrounding the xylem) through specialized transmembrane channels.

What Forces Water Through the Xylem?

Observations

- The mechanism is based on purely physical forces because the xylem vessels and tracheids are lifeless.
- Roots are not needed. This was demonstrated over a century ago by a German botanist who sawed down a 70-ft (21 meters) oak tree and placed the base of the trunk in a barrel of picric acid solution. The solution was drawn up the trunk, killing nearby tissues as it went.
- However, leaves are needed. When the acid reached the leaves and killed them, the upward movement of water ceased.
- Removing a band of **bark** from around the trunk - a process called **girdling** - does not interrupt the upward flow of water. Girdling removes only the phloem, not the xylem, and so the foliage does not wilt. (In due course, however, the roots - and thus the entire plant - will die because the roots cannot receive any of the food manufactured by the leaves.)

Transpiration-Pull

In 1895, the Irish plant physiologists H. H. Dixon and J. Joly proposed that water is pulled up the plant by **tension** (negative pressure) from above. As we have seen, water is continually being lost from leaves by transpiration. Dixon and Joly believed that the loss of water in the leaves exerts a pull on the water in the xylem ducts and draws more water into the leaf. But even the best vacuum pump can pull water up to a height of only 34 ft (10.4 m) or so. This is because a column of water that high exerts a pressure of ~15 lb/in^2 (103 kilopascals, kPa) just counterbalanced by the pressure of the atmosphere. How can water be drawn to the top of a sequoia (the tallest is 370 feet [113 meters] high)? Taking all factors into account, a pull of at least 270 lb/in^2 (~1.9 x 10^3 kPa) is probably needed.

The answer to the dilemma lies the **cohesion** of water molecules; that is the property of water molecules to cling to each through the hydrogen bonds they form. When ultrapure water is confined to tubes of very small bore, the force of cohesion between water molecules imparts great strength to the column of water. It has been reported that tensions as great as 3000 lb/in^2 (21 x 10^3 kPa) are needed to break the column, about the value needed to break steel wires of the same diameter. In a sense, the cohesion of water molecules gives them the physical properties of solid wires. Because of the critical role of cohesion, the transpiration-pull theory is also called the **cohesion theory**.

support for Cohesion theory

- If sap in the xylem is under tension, we would expect the column to snap apart if air is introduced into the xylem vessel by puncturing it. This is the case.
- If the water in all the xylem ducts is under tension, there should be a resulting inward pull (because of adhesion) on the walls of the ducts. This inward pull in the band of sapwood in an actively transpiring tree should, in turn, cause a **decrease** in the diameter of the trunk.

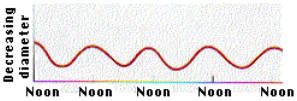


Figure 16.2.1.2 Transpiration in a monterey pine

- The graph shows the results of obtained by D. T. MacDougall when he made continuous measurements of the diameter of a Monterey pine. The diameter fluctuated on a daily basis reaching its **minimum** when the rate of transpiration reached its **maximum** (around noon)
- The rattan vine may climb as high as 150 ft (45.7 m) on the trees of the tropical rain forest in northeastern Australia to get its foliage into the sun. When the base of a vine is severed while immersed in a basin of water, water continues to be taken up. A vine less than 1 inch (2.5 cm) in diameter will "drink" water indefinitely at a rate of up to 12 ml/minute.

  If forced to take water from a sealed container, the vine does so without any decrease in rate, even though the resulting vacuum becomes so great that the remaining water begins to boil spontaneously. (The boiling temperature of water decreases as the air pressure over the water decreases, which is why it takes longer to boil an egg in Denver than in New Orleans.)

- Transpiration-pull enables some trees and shrubs to live in seawater. Seawater is markedly hypertonic to the cytoplasm in the roots of the red mangrove (*Rhizophora mangle*), and we might expect water to leave the cells resulting in a loss in turgor and wilting. In fact, the remarkably high tensions on the order of 500–800 lb/in^2 (~3 to 5 thousand kPa) in the xylem can pull water into the plant against this osmotic gradient. So mangroves literally desalt seawater to meet their needs.

Problems with the theory

When water is placed under a high vacuum, any dissolved gases come out of solution as bubbles (as we saw above with the rattan vine) - this is called **cavitation**. Any impurities in the water enhance the process. So measurements showing the high tensile strength of water in capillaries require water of high purity - not the case for sap in the xylem. So might cavitation break the column of water in the xylem and thus interrupt its flow? Probably not so long as the tension does not greatly exceed 270 lb/in^2 (~1.9 x 10^3 kPa).

By spinning branches in a centrifuge, it has been shown that water in the xylem avoids cavitation at negative pressures exceeding 225 lb/in^2 (~1.6 x 10^3 kPa). And the fact that sequoias can successfully lift water 358 ft (109 m) - which would require a tension of 270 lb/in^2 (~1.9 x 10^3 kPa) - indicates that cavitation is avoided even at that value. However, such heights may be approaching the

limit for xylem transport. Measurements close to the top of the tallest living sequoia (370 ft [=113 m] high) show that the high tensions needed to get water up there have resulted in smaller stomatal openings, causing lower concentrations of CO_2 in the needles, causing reduced photosynthesis, causing reduced growth (smaller cells and much smaller needles). (Reported by Koch, G. W. *et al.*, in *Nature*, 22 April 2004.) So the limits on water transport limit the ultimate height which trees can reach. The tallest tree ever measured, a Douglas fir, was 413 ft. (125.9 meters) high.

Root Pressure

When a tomato plant is carefully severed close to the base of the stem, sap oozes from the stump. The fluid comes out under pressure which is called root pressure. Root pressure is created by the osmotic pressure of xylem sap which is, in turn, created by dissolved minerals and sugars that have been actively transported into the apoplast of the stele.

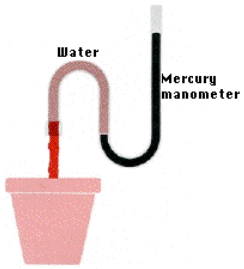


Figure 16.2.1.3: Root pressure

One important example is the sugar maple when, in very early spring, it hydrolyzes the starches stored in its roots into sugar. This causes water to pass by osmosis through the endodermis and into the xylem ducts. The continuous inflow forces the sap up the ducts.

Although root pressure plays a role in the transport of water in the xylem in some plants and in some seasons, it does not account for most water transport.

- Few plants develop root pressures greater than 30 lb/in^2 (207 kPa), and some develop no root pressure at all.
- The volume of fluid transported by root pressure is not enough to account for the measured movement of water in the xylem of most trees and vines.
- Those plants with a reasonably good flow of sap are apt to have the lowest root pressures and vice versa.
- The highest root pressures occur in the spring when the sap is strongly hypertonic to soil water, but the rate of transpiration is low. In summer, when transpiration is high and water is moving rapidly through the xylem, often no root pressure can be detected.

So although root pressure may play a significant role in water transport in certain species (e.g., the coconut palm) or at certain times, most plants meet their needs by transpiration-pull.

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36.4: Rate of Transpiration

Transpiration is the evaporation of water from plants. It occurs chiefly at the leaves while their stomata are open for the passage of CO_2 and O_2 during photosynthesis. But air that is not fully saturated with water vapor (100% relative humidity) will dry the surfaces of cells with which it comes in contact. So the photosynthesizing leaf loses substantial amount of water by evaporation. This transpired water must be replaced by the transport of more water from the soil to the leaves through the xylem of the roots and stem.

Transpiration is not simply a hazard of plant life. It is the "engine" that pulls water up from the roots to:

- supply photosynthesis (1%-2% of the total)
- bring minerals from the roots for biosynthesis within the leaf
- cool the leaf

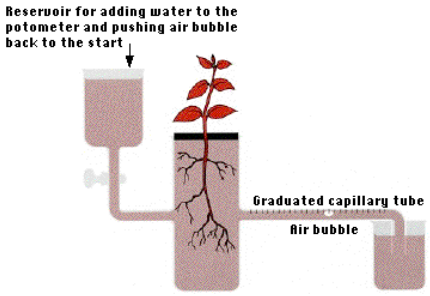


Figure 16.2.3.1 Potometer

Using a potometer (above), one can study the effect of various environmental factors on the rate of transpiration. As water is transpired or otherwise used by the plant, it is replaced from the reservoir on the right. This pushes the air bubble to the left providing a precise measure of the volume of water used.

Environmental factors that affect the rate of transpiration

1. Light

Plants transpire more rapidly in the light than in the dark. This is largely because light stimulates the opening of the stomata (mechanism). Light also speeds up transpiration by warming the leaf.

2. Temperature

Plants transpire more rapidly at higher temperatures because water evaporates more rapidly as the temperature rises. At 30°C, a leaf may transpire three times as fast as it does at 20°C.

3. Humidity

The rate of diffusion of any substance increases as the difference in concentration of the substances in the two regions increases.When the surrounding air is dry, diffusion of water out of the leaf goes on more rapidly.

4. Wind

When there is no breeze, the air surrounding a leaf becomes increasingly humid thus reducing the rate of transpiration. When a breeze is present, the humid air is carried away and replaced by drier air.

5. Soil water

A plant cannot continue to transpire rapidly if its water loss is not made up by replacement from the soil. When absorption of water by the roots fails to keep up with the rate of transpiration, loss of turgor occurs, and the stomata close. This immediately reduces the rate of transpiration (as well as of photosynthesis). If the loss of turgor extends to the rest of the leaf and stem, the plant **wilts**.

The volume of water lost in transpiration can be very high. It has been estimated that over the growing season, one acre of corn (maize) plants may transpire 400,000 gallons (1.5 million liters) of water. As liquid water, this would cover the field with a lake 15 inches (38 cm) deep. An acre of forest probably does even better.

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36.4.1: Stomatal Opening and Closing

Learning Objectives

- Relate the pattern of cell wall thickening in guard cells to their function.
- Explain the mechanism by which blue light triggers stomatal opening.
- Explain the mechanism by which water stress, signaled by abscisic acid, triggers stomatal closure.

Regulation of transpiration is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells (Figure **36.4.1.1**). Stomata must open to allow the gas exchange of carbon dioxide and oxygen for efficient photosynthesis (see Photorespiration), and light thus typically triggers stomatal opening. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between gas exchange and water loss. Water stress, high temperatures, and high carbon dioxide concentration causes stomata to close.

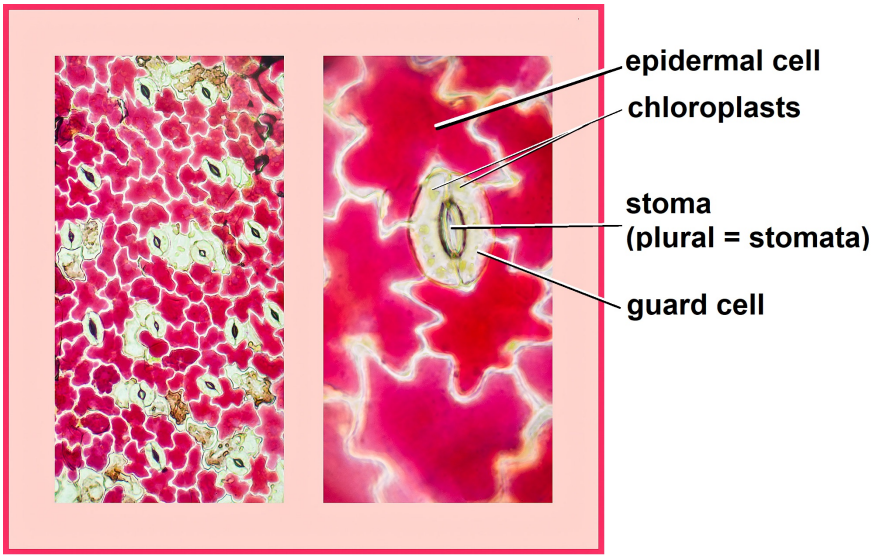


Figure **36.4.1.1**: Italian chicory leaf epidermis showing stomata. The epidermal cells are shaped like puzzle pieces. The stomata (singular = stoma) are pores in the epidermis. Each is bordered by two guard cells, which are filled with oval, green chloroplasts. Image by Umberto Salvagnin (CC-BY).

Stomatal Opening

Guard cell walls are radially thickened such that the thickenings are concentrated around the stoma (plural: stomata; Figure **36.4.1.2**). When turgor pressure increases in guard cells, the cells swell. However, the thickened inner walls near the stoma cannot expand, so they curve to accommodate the expanding outer walls. The curving of the guard cells opens the stoma.

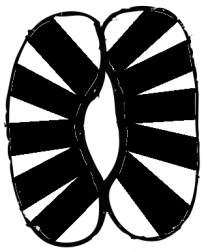


Figure **36.4.1.2**: The guard cells that surround the stoma have radial cell wall thickenings (represented by solid black lines). The portion of the guard cell adjacent to the stoma (ventral side) has a fully thickened cell wall. The outer portion (dorsal side) has alternating bands of thick and thin cell wall. Image modified from Vojtech.dostal (public domain).

How does light cause stomata to open? Phototropins detect blue light, causing a proton pumps to export protons (H^+). ATP, generated by the light reactions of photosynthesis, drives the pump. The cytosol usually more negative than the extracellular solution, and this difference in charge (**membrane potential**) increases as protons leave the cell. This increase in membrane potential is called **hyperpolarization**, and it causes potassium (K^+) to move down its electrochemical gradient into the cytosol. Protons also move down their electrochemical gradient back into the cytosol, bringing chloride (Cl^-) with them through **symport** channels. Meanwhile, starch is broken down, producing sucrose and malate. Nitrate (NO_3^-) also enters the cell. The solute potential resulting high concentrations of potassium, chloride, sucrose, malate, and nitrate in the cytosol drives the osmosis of water into the the guard cells. This increases turgor pressure, and the guard cells expand and bend, opening the stoma (Figure **36.4.1.3**).

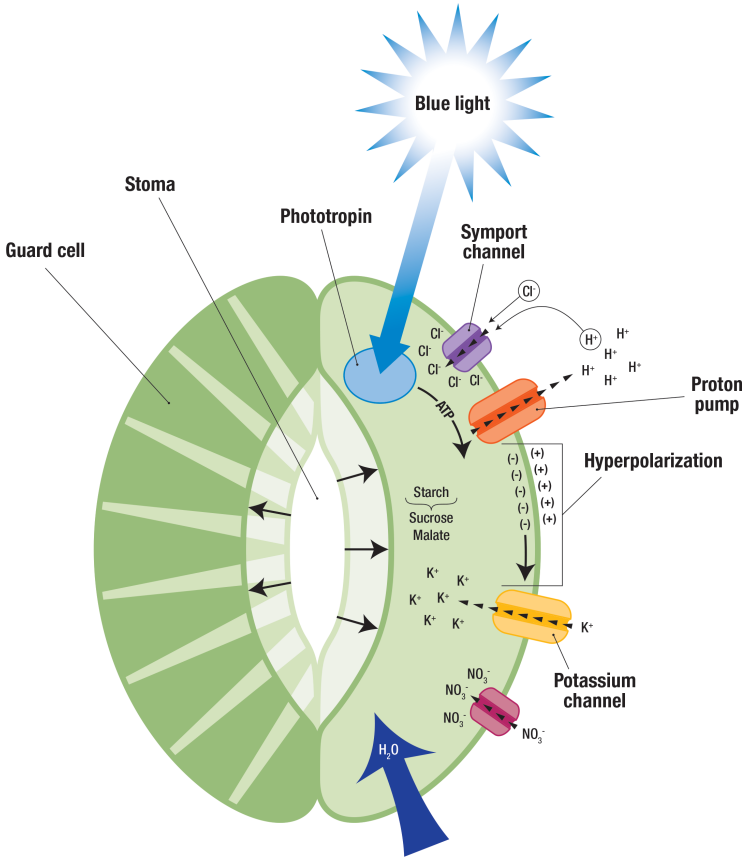


Figure **36.4.1.3**: Phototropins respond to blue light and signal to the proton pump to export protons. This active transport is fueled by the ATP produced in the light-dependent reactions of photosynthesis. This causes the cell to become hyperpolarized, stimulating an influx of potassium ions. At the same time, chloride is symported into the guard cell with protons as they reenter the cell. Nitrate (NO_3^-) also enters the cell. Starch breaks down, producing sucrose and malate. These, along with the influx of ions, increases the solute concentration inside of the guard cells, driving water into the cells. This increases turgor pressure and causes the guard cells to expand. Due to their radial cell wall thickenings, the guard cells curve when they expand, opening the stoma (plural: stomata). Image by Jen Valenzuela (CC-BY-NC).

Table **36.4.1.1** illustrates how osmotic pressure (which results in turgor pressure) increases with light availability during the day. When the osmotic pressure of the guard cells became greater than that of the surrounding cells, the stomata opened. In the evening, when the osmotic pressure of the guard cells dropped to nearly that of the surrounding cells, the stomata closed.

Table **36.4.1.1**: Osmotic pressure measured at different times of day in typical guard cells. The osmotic pressure within the other cells of the lower epidermis remained constant at ~1 MPa.

Time	Osmotic Pressure (MPa)
7 A.M.	1.46
11 A.M.	3.14
5 P.M.	1.88
12 Midnight	1.32

Stomatal Closure

When water is low, roots synthesize **abscisic acid** (ABA), which is transported through the xylem to the leaves. There, abscisic acid causes calcium channels to open. Calcium (Ca^{2+}) opens anion channels, and malate, chloride, and nitrate exit the cell. The membrane potential decreases (the difference in charge across the membrane becomes less pronounced) as anions leave the cell. Potassium exits the cell in response to this decrease in membrane potential (called **depolarization**). The loss of these solutes in the cytosol results in water leaving the cell and a decrease in turgor pressure. The guard cells regain their original shape, and the stoma closes (Figure **36.4.1.4**).

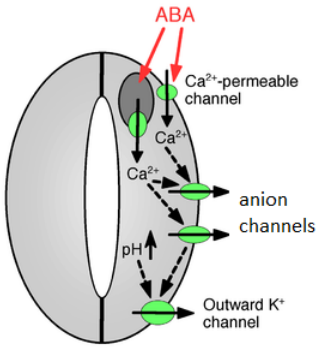


Figure **36.4.1.4**: Stomatal closure is triggered by abscisic acid (ABA), which causes calcium (Ca^{2+}) ions to enter the cell. These open anion channels. At this point, the cytoplasm is not as negatively charged as it was before. The change in charge opens potassium (K^{+}) channels, and potassium leaves the cell as well. Water leaves the cells, causing them to loose turgor pressure. The stoma then closes. Image modified from June Kwak (public domain).

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36.5: Water-Stress Responses

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36.5.1: Response to Water Stress

Learning Objectives

- Identify the locations of synthesis, transport, and actions of abscisic acid.
- Describe how ABA interacts with other plant hormones.

The plant hormone **abscisic acid** (ABA) was was once thought to be responsible for abscission; however, this is now known to be incorrect. Instead, ABA accumulates as a response to stressful environmental conditions, such as dehydration, cold temperatures, or shortened day lengths. Unlike animals, plants cannot flee from potentially harmful conditions like drought, freezing, exposure to salt water or salinated soil, and ABA plays in mediating adaptations of the plant to stress. Abscisic acid (Figure **36.5.1.1**) resembles the carotenoid zeaxanthin (Figure **36.5.1.2**), from which it is ultimately synthesized. It is produced in mature leaves and roots and transported through the vascular tissue.

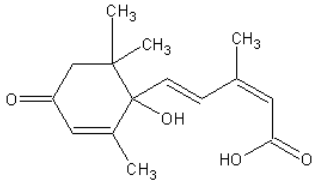


Figure **36.5.1.1**: Chemical structure of the plant hormone abscisic acid (ABA). Image by Socrtwo (public domain).

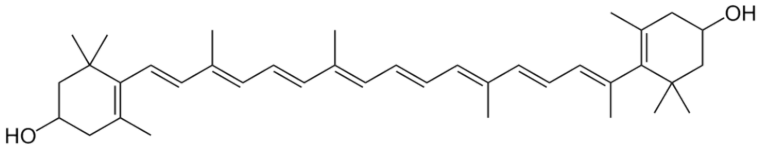


Figure **36.5.1.2**: The carotenoid zeaxanthin absorbs blue light and reflecting orange and red light. It is a precursor to abscisic acid. Image by Shaddack (public domain).

Maintaining Dormancy

Seed Maturation and Inhibition of Germination

Seeds are not only important agents of reproduction and dispersal, but they are also essential to the survival of annual and biennial plants. These angiosperms die after flowering and seed formation is complete. Abscisic acid is essential for seed maturation and also enforces a period of seed dormancy, by blocking germination and promoting the synthesis of storage proteins. It is important the seeds not germinate prematurely during unseasonably mild conditions prior to the onset of winter or a dry season. As the hormone gradually breaks down over winter, the seed is released from dormancy and germinates when conditions are favorable in spring. As discussed in the Environmental Responses chapter, other environmental cues such as exposure to a cold period, light, or water are often also needed to for germination to occur.

Interestingly, mangrove species with **viviparous germination**, meaning that seeds germinate while still attached to the parent plant have reduced levels of ABA during embryo formation, providing further evidence of ABA's role in maintain seed dormancy (Farnsworth and Farrant 1998, *Am J. Bot.)*. These mangroves are adapted to drop germinated seeds into surrounding water to be dispersed (Figure **36.5.1.3**).



Figure **36.5.1.3**: The elongated seedlings of the red mangrove, *Rhizophora mangle*, are still attached to the parent plant, illustrating viviparous germination. Image by M.elle F. Legendre (public domain).

Bud Dormancy

Another effect of ABA is to promote the development of winter buds; it mediates the conversion of the apical meristem into a dormant bud. The newly developing leaves growing above the meristem become converted into stiff bud scales that wrap the meristem closely and will protect it from mechanical damage and drying out during the winter. Abscisic acid in the bud also acts to enforce dormancy so if an unseasonably warm spell occurs before winter is over, the buds will not sprout prematurely. Only after a prolonged period of cold or the lengthening days of spring (photoperiodism) will bud dormancy be lifted.

Response to Water Stress

Stomatal Closure

Abscisic acid also regulates the short-term drought response. Recall that stomata are pores in the leaf and are surrounded by a pair of **guard cells**. Much of the water taken up by a plant is lost as water vapor exists stomata. Low soil moisture causes an increase in ABA, which causes stomata to close, reducing water loss. Note that stomatal closure also prevents exchange of oxygen and carbon dioxide, which is necessary for efficient photosynthesis (see Photorespiration and Phytosynthetic Pathways). The response to abscisic acid occurs *even if blue light is present*; that is, signaling from drought via ABA overrides the signaling from blue light to open stomata. See Transport for more details about stomatal opening and closure.

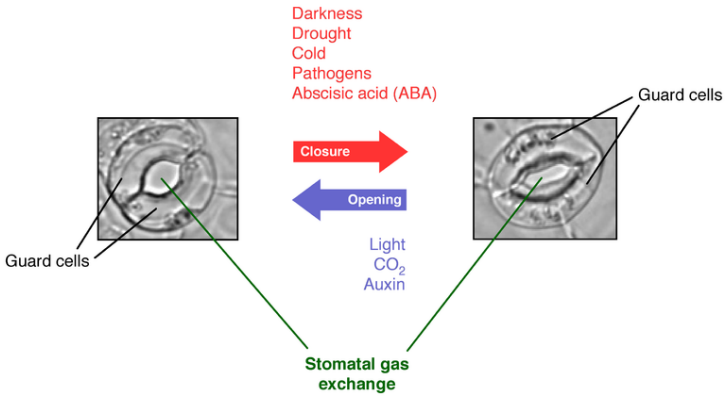


Figure **36.5.1.4**: Several factors mediate the opening and closure of stomata, which are surrounded by kidney-shaped guard cells. Stomatal gas exchange occurs through the stomata. Darkness, drought, cold, pathogens, and abscisic acid (ABA) mediate stomatal closure. Specifically, drought causes the releases of ABA, which signals stomata closure. Stomatal opening is triggered by light, carbon dioxide (CO_2), and auxin. Image by June Kwak, Pascal Mäser (public domain).

Cellular Protection from Dehydration

Abscisic acid turns on the expression of genes encoding proteins that protect cells - in seeds as well as in vegetative tissues - from damage when they become dehydrated.

Interactions with Other Hormones

At a cellular level, abscisic acid inhibits both cell division and cell expansion. It often opposes the growth-inducing effects of auxin and gibberellic acid. For example, abscisic acid prevents stem elongation probably by its inhibitory effect on gibberellic acid. In maintaining apical dominance, however, ABA synergizes with auxin. Abscisic acid moves up from the roots to the stem (opposite the flow of auxin) and suppresses the development of axillary buds. The result is inhibition of branching (maintaining apical dominance).

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36.6: Phloem Transport

Food and other organic substances (e.g., some plant hormones and even messenger RNAs) manufactured in the cells of the plant are transported in the **phloem**. Sugars (usually **sucrose**), amino acids and other organic molecules enter the sieve elements through plasmodesmata connecting them to adjacent **companion cells**. Once within the sieve elements, these molecules can be transported either up or down to any region of the plant moving at rates as high as 110 µm per second.

Two demonstrations:

- **Girdling**. Girdling is removing a band of bark from the circumference of the tree. Girdling removes the phloem, but not the xylem. If a tree is girdled in summer, it continues to live for a time. There is, however, no increase in the weight of the roots, and the bark just above the girdled region accumulates carbohydrates. Unless a special graft is made to bridge the gap, the tree eventually dies as its roots starve.



Figure 16.2.2.0: Girdling, also called ring barking or ring-barking, is the process of completely removing a strip of bark (consisting of Secondary Phloem tissue, cork cambium, and cork) around a tree's outer circumference, causing its death. Here girdling occurs by deliberate human action to give new habitats to species of dead woods (Lille, North of France, Parc de la Cidatelle (Bois de Boulogne). (CC-BY-SA-3.0; Lamiot).

- The pictures below are autoradiographs showing that the products of photosynthesis are transported in the phloem.

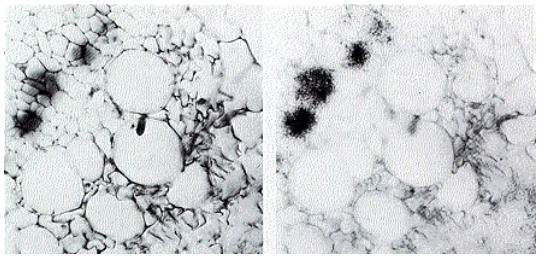


Figure 16.2.2.1 Products of photosynthesis transported in phloem courtesy of R. S. Gage and S. Aronoff

A cucumber leaf was supplied with radioactive water (^{3}HOH) and allowed to carry on photosynthesis for 30 minutes. Then slices were cut from the petiole of the leaf and covered with a photographic emulsion. Radioactive products of photosynthesis darkened the emulsion where it was in contact with the phloem (upper left in both photos), but not where it was in contact with the xylem vessels (center). In the photomicrograph on the left, the microscope is focused on the tissue in order to show the cells clearly; on the right, the microscope has been focused on the photographic emulsion.

Some fruits, such as the pumpkin, receive over 0.5 gram of food each day through the phloem. Because the fluid is fairly dilute, this requires a substantial flow. In fact, the use of radioactive tracers shows that substances can travel through as much as 100 cm of phloem in an hour.

Mechanism that drives translocation of food through the phloem

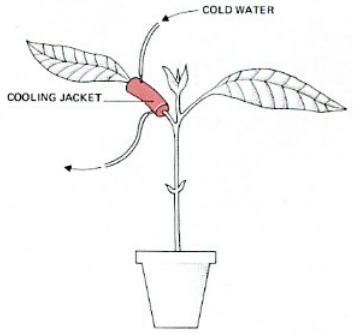


Figure 16.2.2.2 Chilling petiole

Translocation through the phloem is dependent on metabolic activity of the phloem cells (in contrast to transport in the xylem).

- Chilling its petiole slows the rate at which food is translocated out of the leaf (above).
- Oxygen lack also depresses it.
- Killing the phloem cells puts an end to it.

The Pressure-Flow Hypothesis

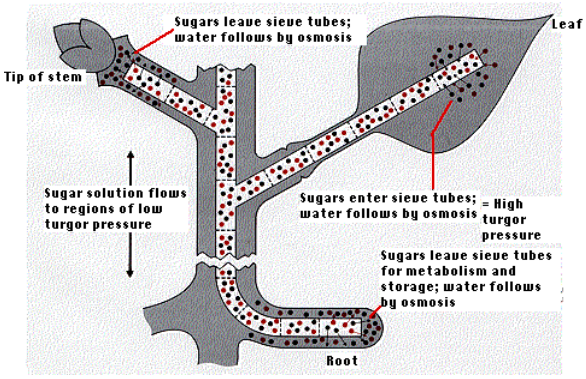


Figure 16.2.2.3 Pressure flow

The best-supported theory to explain the movement of food through the phloem is called the **pressure-flow hypothesis**.

- It proposes that water containing food molecules flows under pressure through the phloem.
- The pressure is created by the difference in water concentration of the solution in the phloem and the relatively pure water in the nearby xylem ducts.
- At their "source" - the leaves - sugars are pumped by active transport into the companion cells and sieve elements of the phloem.
- As sugars (and other products of photosynthesis) accumulate in the phloem, water enters by osmosis.

  In the figure, sugar molecules are represented in black, water molecules in red.)

- Turgor pressure builds up in the sieve elements (similar to the creation of root pressure).
- As the fluid is pushed down (and up) the phloem, sugars are removed by the cortex cells of both stem and root (the "**sinks**") and consumed or converted into starch.
- Starch is insoluble and exerts no osmotic effect.
- Therefore, the osmotic pressure of the contents of the phloem decreases.
- Finally, relatively pure water is left in the phloem, and this leaves by osmosis and/or is drawn back into nearby xylem vessels by the suction of transpiration-pull.

Thus it is the pressure gradient between "source" (leaves) and "sink" (shoot and roots) that drives the contents of the phloem up and down through the sieve elements.

Tests of the theory

1. The contents of the sieve elements must be under pressure.

This is difficult to measure because when a sieve element is punctured with a measuring probe, the holes in its end walls quickly plug up. However, aphids can insert their mouth parts without triggering this response.

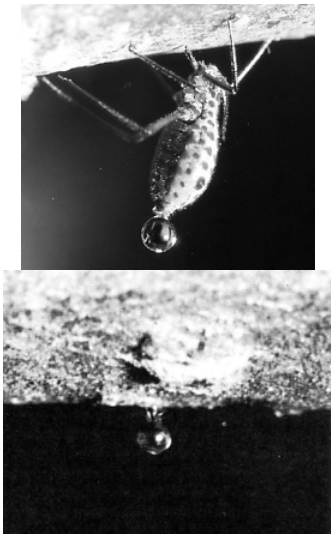


Figure 16.2.2.4 Pressure flow hypothesis in reality

Left: when it punctures a sieve element, sap enters the insect's mouth parts under pressure and some soon emerges at the other end (as a drop of honeydew that serves as food for ants and bees).

Right: honeydew will continue to exude from the mouthparts after the aphid has been cut away from them.

2. The osmotic pressure of the fluid in the phloem of the leaves must be greater than that in the phloem of the food-receiving organs such as the roots and fruits. Most measurements have shown this to be true.

Transport of Messenger RNA (mRNA) through the Phloem

Plant scientists at the Davis campus of the University of California (reported in the 13 July 2001 issue of **Science**) have demonstrated that messenger RNAs can also be transported long distances in the phloem. They grafted normal tomato scions onto mutant tomato stocks and found that mRNAs synthesized in the stock were transported into the scions. These mRNAs converted the phenotype of the scion into that of the stock.

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CHAPTER OVERVIEW

37: Plant Nutrition and Soils

37.1: Soils- The Substrates on Which Plants Depend

37.2: Plant Nutrients

37.3: Special Nutritional Strategies

37.4: Carbon-Nitrogen Balance and Global Change

37.5: Phytoremediation

37.5.1: Bioremediation

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37.1: Soils- The Substrates on Which Plants Depend

Skills to Develop

- Describe how soils are formed
- Explain soil composition
- Describe a soil profile

Plants obtain inorganic elements from the soil, which serves as a natural medium for land plants. Soil is the outer loose layer that covers the surface of Earth. Soil quality is a major determinant, along with climate, of plant distribution and growth. Soil quality depends not only on the chemical composition of the soil, but also the topography (regional surface features) and the presence of living organisms. In agriculture, the history of the soil, such as the cultivating practices and previous crops, modify the characteristics and fertility of that soil.

Soil develops very slowly over long periods of time, and its formation results from natural and environmental forces acting on mineral, rock, and organic compounds. Soils can be divided into two groups: organic soils are those that are formed from sedimentation and primarily composed of organic matter, while those that are formed from the weathering of rocks and are primarily composed of inorganic material are called mineral soils. Mineral soils are predominant in terrestrial ecosystems, where soils may be covered by water for part of the year or exposed to the atmosphere.

Soil Composition

Soil consists of these major components (Figure **37.1.1**):

- inorganic mineral matter, about 40 to 45 percent of the soil volume
- organic matter, about 5 percent of the soil volume
- water and air, about 50 percent of the soil volume

The amount of each of the four major components of soil depends on the amount of vegetation, soil compaction, and water present in the soil. A good healthy soil has sufficient air, water, minerals, and organic material to promote and sustain plant life.

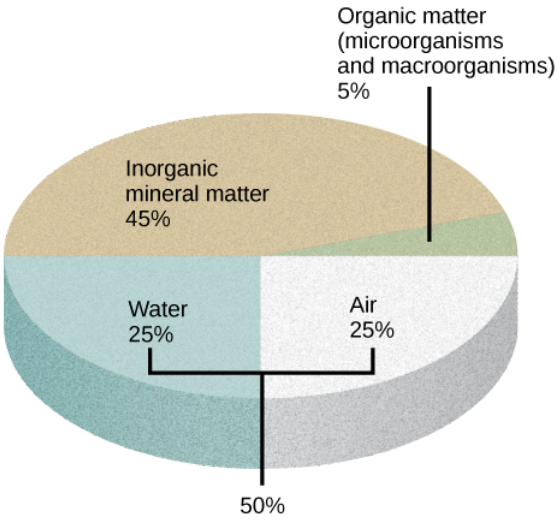


Figure **37.1.1**: The four major components of soil are shown: inorganic minerals, organic matter, water, and air.

Exercise 37.1.1

Soil compaction can result when soil is compressed by heavy machinery or even foot traffic. How might this compaction change the soil composition?

Answer

> The air content of the soil decreases.

The organic material of soil, called humus, is made up of microorganisms (dead and alive), and dead animals and plants in varying stages of decay. Humus improves soil structure and provides plants with water and minerals. The inorganic material of soil consists of rock, slowly broken down into smaller particles that vary in size. Soil particles that are 0.1 to 2 mm in diameter are sand. Soil particles between 0.002 and 0.1 mm are called silt, and even smaller particles, less than 0.002 mm in diameter, are called clay. Some soils have no dominant particle size and contain a mixture of sand, silt, and humus; these soils are called loams.

Soil Formation

Soil formation is the consequence of a combination of biological, physical, and chemical processes. Soil should ideally contain 50 percent solid material and 50 percent pore space. About one-half of the pore space should contain water, and the other half should contain air. The organic component of soil serves as a cementing agent, returns nutrients to the plant, allows soil to store moisture, makes soil tillable for farming, and provides energy for soil microorganisms. Most soil microorganisms—bacteria, algae, or fungi—are dormant in dry soil, but become active once moisture is available.

Soil distribution is not homogenous because its formation results in the production of layers; together, the vertical section of a soil is called the soil profile. Within the soil profile, soil scientists define zones called horizons. A horizon is a soil layer with distinct physical and chemical properties that differ from those of other layers. Five factors account for soil formation: parent material, climate, topography, biological factors, and time.

Parent Material

The organic and inorganic material in which soils form is the parent material. Mineral soils form directly from the weathering of bedrock, the solid rock that lies beneath the soil, and therefore, they have a similar composition to the original rock. Other soils form in materials that came from elsewhere, such as sand and glacial drift. Materials located in the depth of the soil are relatively unchanged compared with the deposited material. Sediments in rivers may have different characteristics, depending on whether the stream moves quickly or slowly. A fast-moving river could have sediments of rocks and sand, whereas a slow-moving river could have fine-textured material, such as clay.

Climate

Temperature, moisture, and wind cause different patterns of weathering and therefore affect soil characteristics. The presence of moisture and nutrients from weathering will also promote biological activity: a key component of a quality soil.

Topography

Regional surface features (familiarly called “the lay of the land”) can have a major influence on the characteristics and fertility of a soil. Topography affects water runoff, which strips away parent material and affects plant growth. Steeps soils are more prone to erosion and may be thinner than soils that are relatively flat or level.

Biological factors

The presence of living organisms greatly affects soil formation and structure. Animals and microorganisms can produce pores and crevices, and plant roots can penetrate into crevices to produce more fragmentation. Plant secretions promote the development of microorganisms around the root, in an area known as the rhizosphere. Additionally, leaves and other material that fall from plants decompose and contribute to soil composition.

Time

Time is an important factor in soil formation because soils develop over long periods. Soil formation is a dynamic process. Materials are deposited over time, decompose, and transform into other materials that can be used by living organisms or deposited onto the surface of the soil.

Physical Properties of the Soil

Soils are named and classified based on their horizons. The soil profile has four distinct layers: 1) O horizon; 2) A horizon; 3) B horizon, or subsoil; and 4) C horizon, or soil base (Figure **37.1.2**). The O horizon has freshly decomposing organic matter—humus—at its surface, with decomposed vegetation at its base. Humus enriches the soil with nutrients and enhances soil moisture retention. Topsoil—the top layer of soil—is usually two to three inches deep, but this depth can vary considerably. For instance, river deltas like the Mississippi River delta have deep layers of topsoil. Topsoil is rich in organic material; microbial processes occur there, and it is the "workhorse" of plant production. The A horizon consists of a mixture of organic material with inorganic products of weathering, and it is therefore the beginning of true mineral soil. This horizon is typically darkly colored because of the presence of organic matter. In this area, rainwater percolates through the soil and carries materials from the surface. The B horizon is an accumulation of mostly fine material that has moved downward, resulting in a dense layer in the soil. In some soils, the B horizon contains nodules or a layer of calcium carbonate. The C horizon, or soil base, includes the parent material, plus the organic and inorganic material that is broken down to form soil. The parent material may be either created in its natural place, or transported from elsewhere to its present location. Beneath the C horizon lies bedrock.

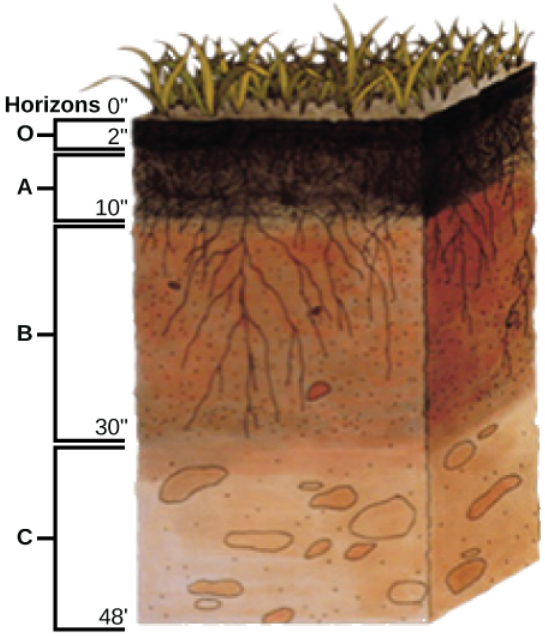


Figure **37.1.2**: This soil profile shows the different soil layers (O horizon, A horizon, B horizon, and C horizon) found in typical soils. (credit: modification of work by USDA)

Exercise 37.1.2

Which horizon is considered the topsoil, and which is considered the subsoil?

Answer

The A horizon is the topsoil, and the B horizon is subsoil.

Some soils may have additional layers, or lack one of these layers. The thickness of the layers is also variable, and depends on the factors that influence soil formation. In general, immature soils may have O, A, and C horizons, whereas mature soils may display all of these, plus additional layers (Figure **37.1.3**).

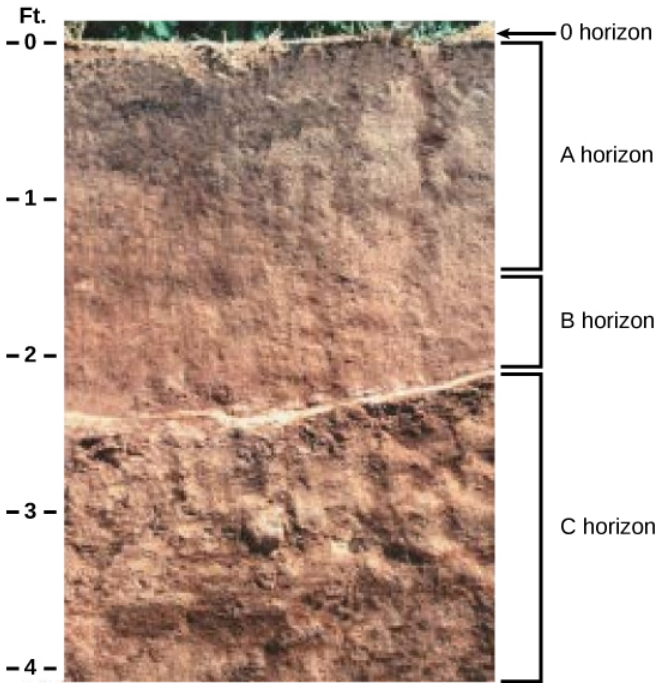


Figure **37.1.3**: The San Joaquin soil profile has an O horizon, A horizon, B horizon, and C horizon. (credit: modification of work by USDA)

Career Connections: Soil Scientist

A soil scientist studies the biological components, physical and chemical properties, distribution, formation, and morphology of soils. Soil scientists need to have a strong background in physical and life sciences, plus a foundation in mathematics. They may work for federal or state agencies, academia, or the private sector. Their work may involve collecting data, carrying out research, interpreting results, inspecting soils, conducting soil surveys, and recommending soil management programs.



Figure **37.1.4**: This soil scientist is studying the horizons and composition of soil at a research site. (credit: USDA)

Many soil scientists work both in an office and in the field. According to the United States Department of Agriculture (USDA): "a soil scientist needs good observation skills to analyze and determine the characteristics of different types of soils. Soil types are complex and the geographical areas a soil scientist may survey are varied. Aerial photos or various satellite images are often used to research the areas. Computer skills and geographic information systems (GIS) help the scientist to analyze the multiple facets of geomorphology, topography, vegetation, and climate to discover the patterns left on the landscape."[1] Soil scientists play a key role in understanding the soil's past, analyzing present conditions, and making recommendations for future soil-related practices.

Summary

Plants obtain mineral nutrients from the soil. Soil is the outer loose layer that covers the surface of Earth. Soil quality depends on the chemical composition of the soil, the topography, the presence of living organisms, the climate, and time. Agricultural practice and history may also modify the characteristics and fertility of soil. Soil consists of four major components: 1) inorganic mineral matter, 2) organic matter, 3) water and air, and 4) living matter. The organic material of soil is made of humus, which improves soil structure and provides water and minerals. Soil inorganic material consists of rock slowly broken down into smaller particles that vary in size, such as sand, silt, and loam.

Soil formation results from a combination of biological, physical, and chemical processes. Soil is not homogenous because its formation results in the production of layers called a soil profile. Factors that affect soil formation include: parent material, climate, topography, biological factors, and time. Soils are classified based on their horizons, soil particle size, and proportions. Most soils have four distinct horizons: O, A, B, and C.

Footnotes

1. 1 National Resources Conservation Service / United States Department of Agriculture. “Careers in Soil Science.” soils.usda.gov/education/facts/careers.html

Glossary

A horizon
consists of a mixture of organic material with inorganic products of weathering

B horizon
soil layer that is an accumulation of mostly fine material that has moved downward

bedrock
solid rock that lies beneath the soil

C horizon
layer of soil that contains the parent material, and the organic and inorganic material that is broken down to form soil; also known as the soil base

clay
soil particles that are less than 0.002 mm in diameter

horizon
soil layer with distinct physical and chemical properties, which differs from other layers depending on how and when it was formed

humus
organic material of soil; made up of microorganisms, dead animals and plants in varying stages of decay

loam
soil that has no dominant particle size

mineral soil
type of soil that is formed from the weathering of rocks and inorganic material; composed primarily of sand, silt, and clay

O horizon
layer of soil with humus at the surface and decomposed vegetation at the base

organic soil
type of soil that is formed from sedimentation; composed primarily of organic material

parent material
organic and inorganic material in which soils form

rhizosphere
area of soil affected by root secretions and microorganisms

sand
soil particles between 0.1–2 mm in diameter

silt

soil particles between 0.002 and 0.1 mm in diameter

soil profile

vertical section of a soil

soil

outer loose layer that covers the surface of Earth

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37.2: Plant Nutrients

Skills to Develop

- Describe how plants obtain nutrients
- List the elements and compounds required for proper plant nutrition
- Describe an essential nutrient

Plants are unique organisms that can absorb nutrients and water through their root system, as well as carbon dioxide from the atmosphere. Soil quality and climate are the major determinants of plant distribution and growth. The combination of soil nutrients, water, and carbon dioxide, along with sunlight, allows plants to grow.

The Chemical Composition of Plants

Since plants require nutrients in the form of elements such as carbon and potassium, it is important to understand the chemical composition of plants. The majority of volume in a plant cell is water; it typically comprises 80 to 90 percent of the plant's total weight. Soil is the water source for land plants, and can be an abundant source of water, even if it appears dry. Plant roots absorb water from the soil through root hairs and transport it up to the leaves through the xylem. As water vapor is lost from the leaves, the process of transpiration and the polarity of water molecules (which enables them to form hydrogen bonds) draws more water from the roots up through the plant to the leaves (Figure **37.2.1**). Plants need water to support cell structure, for metabolic functions, to carry nutrients, and for photosynthesis.

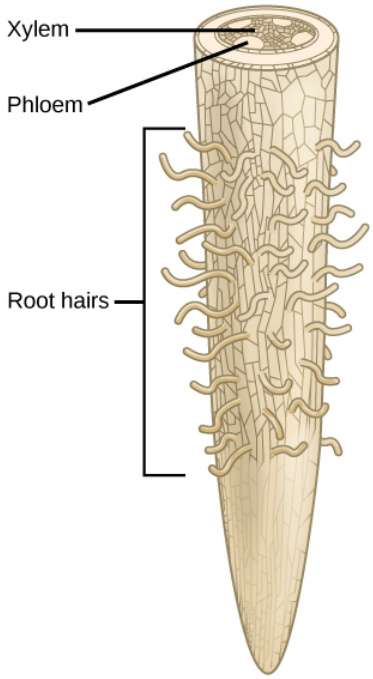


Figure **37.2.1**: Water is absorbed through the root hairs and moves up the xylem to the leaves.

Plant cells need essential substances, collectively called nutrients, to sustain life. Plant nutrients may be composed of either organic or inorganic compounds. An organic compound is a chemical compound that contains carbon, such as carbon dioxide obtained from the atmosphere. Carbon that was obtained from atmospheric CO_2 composes the majority of the dry mass within most plants. An inorganic compound does not contain carbon and is not part of, or produced by, a living organism. Inorganic substances, which form the majority of the soil solution, are commonly called minerals: those required by plants include nitrogen (N) and potassium (K) for structure and regulation.

Essential Nutrients

Plants require only light, water and about 20 elements to support all their biochemical needs: these 20 elements are called essential nutrients. For an element to be regarded as essential, three criteria are required: 1) a plant cannot complete its life cycle without the element; 2) no other element can perform the function of the element; and 3) the element is directly involved in plant nutrition.

Table 37.2.1: Essential elements for plant growth

Macronutrients	Micronutrients
Carbon (C)	Iron (Fe)
Hydrogen (H)	Manganese (Mn)
Oxygen (O)	Boron (B)
Nitrogen (N)	Molybdenum (Mo)
Phosphorus (P)	Copper (Cu)
Potassium (K)	Zinc (Zn)
Calcium (Ca)	Chlorine (Cl)
Magnesium (Mg)	Nickel (Ni)
Sulfur (S)	Cobalt (Co)
	Sodium (S)
	Silicon (Si)

Macronutrients and Micronutrients

The essential elements can be divided into two groups: macronutrients and micronutrients. Nutrients that plants require in larger amounts are called macronutrients. About half of the essential elements are considered macronutrients: carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, calcium, magnesium and sulfur. The first of these macronutrients, carbon (C), is required to form carbohydrates, proteins, nucleic acids, and many other compounds; it is therefore present in all macromolecules. On average, the dry weight (excluding water) of a cell is 50 percent carbon. As shown in Figure **37.2.2**, carbon is a key part of plant biomolecules.

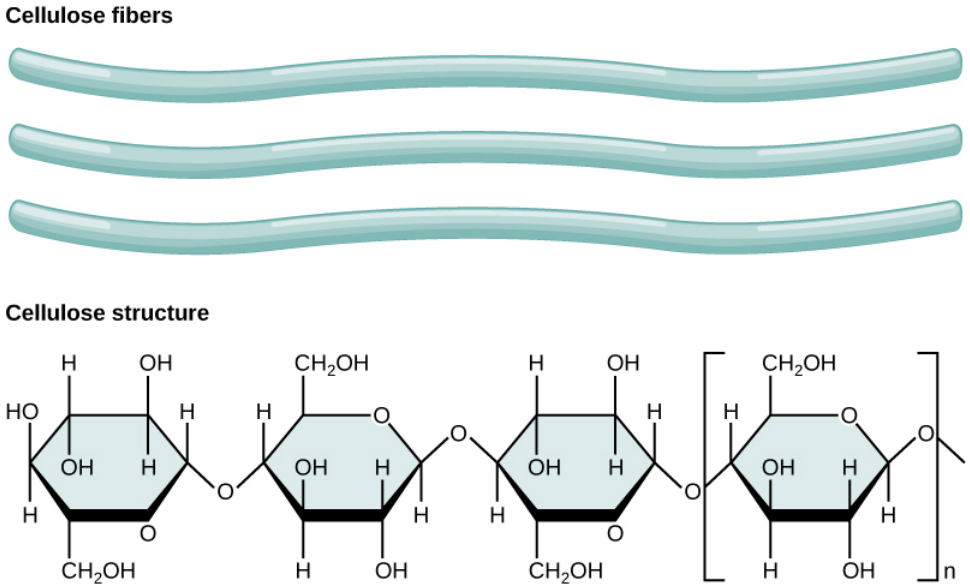


Figure **37.2.2**: Cellulose, the main structural component of the plant cell wall, makes up over thirty percent of plant matter. It is the most abundant organic compound on earth. Plants are able to make their own cellulose, but need carbon from the soil to do so.

The next most abundant element in plant cells is nitrogen (N); it is part of proteins and nucleic acids. Nitrogen is also used in the synthesis of some vitamins. Hydrogen and oxygen are macronutrients that are part of many organic compounds, and also form water. Oxygen is necessary for cellular respiration; plants use oxygen to store energy in the form of ATP. Phosphorus (P), another macromolecule, is necessary to synthesize nucleic acids and phospholipids. As part of ATP, phosphorus enables food energy to be converted into chemical energy through oxidative phosphorylation. Likewise, light energy is converted into chemical energy during photophosphorylation in photosynthesis, and into chemical energy to be extracted during respiration. Sulfur is part of certain amino acids, such as cysteine and methionine, and is present in several coenzymes. Sulfur also plays a role in photosynthesis as part of the electron transport chain, where hydrogen gradients play a key role in the conversion of light energy into ATP. Potassium (K) is important because of its role in regulating stomatal opening and closing. As the openings for gas exchange, stomata help maintain a healthy water balance; a potassium ion pump supports this process.

Magnesium (Mg) and calcium (Ca) are also important macronutrients. The role of calcium is twofold: to regulate nutrient transport, and to support many enzyme functions. Magnesium is important to the photosynthetic process. These minerals, along with the micronutrients, which are described below, also contribute to the plant's ionic balance.

In addition to macronutrients, organisms require various elements in small amounts. These micronutrients, or trace elements, are present in very small quantities. They include boron (B), chlorine (Cl), manganese (Mn), iron (Fe), zinc (Zn), copper (Cu), molybdenum (Mo), nickel (Ni), silicon (Si), and sodium (Na).

Deficiencies in any of these nutrients—particularly the macronutrients—can adversely affect plant growth (Figure **37.2.3**). Depending on the specific nutrient, a lack can cause stunted growth, slow growth, or chlorosis (yellowing of the leaves). Extreme deficiencies may result in leaves showing signs of cell death.



(a)



(b)



(c)



(d)

Figure **37.2.3**: Nutrient deficiency is evident in the symptoms these plants show. This (a) grape tomato suffers from blossom end rot caused by calcium deficiency. The yellowing in this (b) *Frangula alnus* results from magnesium deficiency. Inadequate magnesium also leads to (c) intervenal chlorosis, seen here in a sweetgum leaf. This (d) palm is affected by potassium deficiency. (credit c: modification of work by Jim Conrad; credit d: modification of work by Malcolm Manners)

Everyday Connection: Hydroponics

Hydroponics is a method of growing plants in a water-nutrient solution instead of soil. Since its advent, hydroponics has developed into a growing process that researchers often use. Scientists who are interested in studying plant nutrient deficiencies can use hydroponics to study the effects of different nutrient combinations under strictly controlled conditions. Hydroponics has also developed as a way to grow flowers, vegetables, and other crops in greenhouse environments. You might find hydroponically grown produce at your local grocery store. Today, many lettuces and tomatoes in your market have been hydroponically grown.

Summary

Plants can absorb inorganic nutrients and water through their root system, and carbon dioxide from the environment. The combination of organic compounds, along with water, carbon dioxide, and sunlight, produce the energy that allows plants to grow. Inorganic compounds form the majority of the soil solution. Plants access water though the soil. Water is absorbed by the plant root, transports nutrients throughout the plant, and maintains the structure of the plant. Essential elements are indispensable elements for plant growth. They are divided into macronutrients and micronutrients. The macronutrients plants require are carbon, nitrogen, hydrogen, oxygen, phosphorus, potassium, calcium, magnesium, and sulfur. Important micronutrients include iron, manganese, boron, molybdenum, copper, zinc, chlorine, nickel, cobalt, silicon and sodium.

Glossary

inorganic compound
: chemical compound that does not contain carbon; it is not part of or produced by a living organism

macronutrient
: nutrient that is required in large amounts for plant growth; carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur

micronutrient
: nutrient required in small amounts; also called trace element

organic compound
: chemical compound that contains carbon

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37.3: Special Nutritional Strategies

Skills to Develop

- Understand the nutritional adaptations of plants
- Describe mycorrhizae
- Explain nitrogen fixation

Plants obtain food in two different ways. Autotrophic plants can make their own food from inorganic raw materials, such as carbon dioxide and water, through photosynthesis in the presence of sunlight. Green plants are included in this group. Some plants, however, are heterotrophic: they are totally parasitic and lacking in chlorophyll. These plants, referred to as holo-parasitic plants, are unable to synthesize organic carbon and draw all of their nutrients from the host plant.

Plants may also enlist the help of microbial partners in nutrient acquisition. Particular species of bacteria and fungi have evolved along with certain plants to create a mutualistic symbiotic relationship with roots. This improves the nutrition of both the plant and the microbe. The formation of nodules in legume plants and mycorrhization can be considered among the nutritional adaptations of plants. However, these are not the only type of adaptations that we may find; many plants have other adaptations that allow them to thrive under specific conditions.

Nitrogen Fixation: Root and Bacteria Interactions

Nitrogen is an important macronutrient because it is part of nucleic acids and proteins. Atmospheric nitrogen, which is the diatomic molecule $\mathbf{N_2}$, or dinitrogen, is the largest pool of nitrogen in terrestrial ecosystems. However, plants cannot take advantage of this nitrogen because they do not have the necessary enzymes to convert it into biologically useful forms. However, nitrogen can be "fixed," which means that it can be converted to ammonia ($\mathbf{NH_3}$) through biological, physical, or chemical processes. As you have learned, biological nitrogen fixation (BNF) is the conversion of atmospheric nitrogen ($\mathbf{N_2}$) into ammonia ($\mathbf{NH_3}$), exclusively carried out by prokaryotes such as soil bacteria or cyanobacteria. Biological processes contribute 65 percent of the nitrogen used in agriculture. The following equation represents the process:

$$\mathbf{N_2 + 16\,ATP + 8\,e^- + 8\,H^+ \rightarrow 2\,NH_3 + 16\,ADP + 16\,P_i + H_2}$$

The most important source of BNF is the symbiotic interaction between soil bacteria and legume plants, including many crops important to humans (Figure **37.3.1**). The NH_3 resulting from fixation can be transported into plant tissue and incorporated into amino acids, which are then made into plant proteins. Some legume seeds, such as soybeans and peanuts, contain high levels of protein, and serve among the most important agricultural sources of protein in the world.



(a) (b) (c)

Figure **37.3.1**: Some common edible legumes—like (a) peanuts, (b) beans, and (c) chickpeas—are able to interact symbiotically with soil bacteria that fix nitrogen. (credit a: modification of work by Jules Clancy; credit b: modification of work by USDA)

Exercise 37.3.1

Farmers often rotate corn (a cereal crop) and soy beans (a legume) planting a field with each crop in alternate seasons. What advantage might this crop rotation confer?

Answer

Answer

Soybeans are able to fix nitrogen in their roots, which are not harvested at the end of the growing season. The belowground nitrogen can be used in the next season by the corn.

Farmers often rotate corn (a cereal crop) and soy beans (a legume), planting a field with each crop in alternate seasons. What advantage might this crop rotation confer?

Soil bacteria, collectively called rhizobia, symbiotically interact with legume roots to form specialized structures called nodules, in which nitrogen fixation takes place. This process entails the reduction of atmospheric nitrogen to ammonia, by means of the enzyme nitrogenase. Therefore, using rhizobia is a natural and environmentally friendly way to fertilize plants, as opposed to chemical fertilization that uses a nonrenewable resource, such as natural gas. Through symbiotic nitrogen fixation, the plant benefits from using an endless source of nitrogen from the atmosphere. The process simultaneously contributes to soil fertility because the plant root system leaves behind some of the biologically available nitrogen. As in any symbiosis, both organisms benefit from the interaction: the plant obtains ammonia, and bacteria obtain carbon compounds generated through photosynthesis, as well as a protected niche in which to grow (Figure **37.3.2**).



Figure **37.3.2**: Soybean roots contain (a) nitrogen-fixing nodules. Cells within the nodules are infected with *Bradyrhyzobium japonicum*, a rhizobia or "root-loving" bacterium. The bacteria are encased in (b) vesicles inside the cell, as can be seen in this transmission electron micrograph. (credit a: modification of work by USDA; credit b: modification of work by Louisa Howard, Dartmouth Electron Microscope Facility; scale-bar data from Matt Russell)

Mycorrhizae: The Symbiotic Relationship between Fungi and Roots

A nutrient depletion zone can develop when there is rapid soil solution uptake, low nutrient concentration, low diffusion rate, or low soil moisture. These conditions are very common; therefore, most plants rely on fungi to facilitate the uptake of minerals from the soil. Fungi form symbiotic associations called mycorrhizae with plant roots, in which the fungi actually are integrated into the physical structure of the root. The fungi colonize the living root tissue during active plant growth.

Through mycorrhization, the plant obtains mainly phosphate and other minerals, such as zinc and copper, from the soil. The fungus obtains nutrients, such as sugars, from the plant root (Figure **37.3.3**). Mycorrhizae help increase the surface area of the plant root system because hyphae, which are narrow, can spread beyond the nutrient depletion zone. Hyphae can grow into small soil pores that allow access to phosphorus that would otherwise be unavailable to the plant. The beneficial effect on the plant is best observed in poor soils. The benefit to fungi is that they can obtain up to 20 percent of the total carbon accessed by plants. Mycorrhizae functions as a physical barrier to pathogens. It also provides an induction of generalized host defense mechanisms, and sometimes involves production of antibiotic compounds by the fungi.



Figure **37.3.3**: Root tips proliferate in the presence of mycorrhizal infection, which appears as off-white fuzz in this image. (credit: modification of work by Nilsson et al., BMC Bioinformatics 2005)

There are two types of mycorrhizae: ectomycorrhizae and endomycorrhizae. Ectomycorrhizae form an extensive dense sheath around the roots, called a mantle. Hyphae from the fungi extend from the mantle into the soil, which increases the surface area for water and mineral absorption. This type of mycorrhizae is found in forest trees, especially conifers, birches, and oaks. Endomycorrhizae, also called arbuscular mycorrhizae, do not form a dense sheath over the root. Instead, the fungal mycelium is embedded within the root tissue. Endomycorrhizae are found in the roots of more than 80 percent of terrestrial plants.

Nutrients from Other Sources

Some plants cannot produce their own food and must obtain their nutrition from outside sources. This may occur with plants that are parasitic or saprophytic. Some plants are mutualistic symbionts, epiphytes, or insectivorous.

Plant Parasites

A parasitic plant depends on its host for survival. Some parasitic plants have no leaves. An example of this is the dodder (Figure **37.3.4**), which has a weak, cylindrical stem that coils around the host and forms suckers. From these suckers, cells invade the host stem and grow to connect with the vascular bundles of the host. The parasitic plant obtains water and nutrients through these connections. The plant is a total parasite (a holoparasite) because it is completely dependent on its host. Other parasitic plants (hemiparasites) are fully photosynthetic and only use the host for water and minerals. There are about 4,100 species of parasitic plants.



Figure **37.3.4**: The dodder is a holoparasite that penetrates the host's vascular tissue and diverts nutrients for its own growth. Note that the vines of the dodder, which has white flowers, are beige. The dodder has no chlorophyll and cannot produce its own food. (credit: "Lalithamba"/Flickr)

Saprophytes

A saprophyte is a plant that does not have chlorophyll and gets its food from dead matter, similar to bacteria and fungi (note that fungi are often called saprophytes, which is incorrect, because fungi are not plants). Plants like these use enzymes to convert organic food materials into simpler forms from which they can absorb nutrients (Figure **37.3.5**). Most saprophytes do not directly digest dead matter: instead, they parasitize fungi that digest dead matter, or are mycorrhizal, ultimately obtaining photosynthate from a fungus that derived photosynthate from its host. Saprophytic plants are uncommon; only a few species are described.



Figure **37.3.5**: Saprophytes, like this Dutchmen's pipe (*Monotropa hypopitys*), obtain their food from dead matter and do not have chlorophyll. (credit: modification of work by Iwona Erskine-Kellie)

Symbionts

A symbiont is a plant in a symbiotic relationship, with special adaptations such as mycorrhizae or nodule formation. Fungi also form symbiotic associations with cyanobacteria and green algae (called lichens). Lichens can sometimes be seen as colorful growths on the surface of rocks and trees (Figure **37.3.6**). The algal partner (phycobiont) makes food autotrophically, some of which it shares with the fungus; the fungal partner (mycobiont) absorbs water and minerals from the environment, which are made available to the green alga. If one partner was separated from the other, they would both die.



Figure **37.3.6**: Lichens, which often have symbiotic relationships with other plants, can sometimes be found growing on trees. (credit: "benketaro"/Flickr)

Epiphytes

An epiphyte is a plant that grows on other plants, but is not dependent upon the other plant for nutrition (Figure **37.3.7**). Epiphytes have two types of roots: clinging aerial roots, which absorb nutrients from humus that accumulates in the crevices of trees; and aerial roots, which absorb moisture from the atmosphere.



Figure **37.3.7**: These epiphyte plants grow in the main greenhouse of the *Jardin des Plantes* in Paris.

Insectivorous Plants

An insectivorous plant has specialized leaves to attract and digest insects. The Venus flytrap is popularly known for its insectivorous mode of nutrition, and has leaves that work as traps (Figure **37.3.8**). The minerals it obtains from prey compensate for those lacking in the boggy (low pH) soil of its native North Carolina coastal plains. There are three sensitive hairs in the center of each half of each leaf. The edges of each leaf are covered with long spines. Nectar secreted by the plant attracts flies to the leaf. When a fly touches the sensory hairs, the leaf immediately closes. Next, fluids and enzymes break down the prey and minerals are absorbed by the leaf. Since this plant is popular in the horticultural trade, it is threatened in its original habitat.



Figure **37.3.8**: A Venus flytrap has specialized leaves to trap insects. (credit: "Selena N. B. H."/Flickr)

Summary

Atmospheric nitrogen is the largest pool of available nitrogen in terrestrial ecosystems. However, plants cannot use this nitrogen because they do not have the necessary enzymes. Biological nitrogen fixation (BNF) is the conversion of atmospheric nitrogen to ammonia. The most important source of BNF is the symbiotic interaction between soil bacteria and legumes. The bacteria form nodules on the legume's roots in which nitrogen fixation takes place. Fungi form symbiotic associations (mycorrhizae) with plants, becoming integrated into the physical structure of the root. Through mycorrhization, the plant obtains minerals from the soil and the fungus obtains photosynthate from the plant root. Ectomycorrhizae form an extensive dense sheath around the root, while endomycorrhizae are embedded within the root tissue. Some plants—parasites, saprophytes, symbionts, epiphytes, and insectivores—have evolved adaptations to obtain their organic or mineral nutrition from various sources.

Glossary

epiphyte
plant that grows on other plants but is not dependent upon other plants for nutrition

insectivorous plant
plant that has specialized leaves to attract and digest insects

nitrogenase
enzyme that is responsible for the reduction of atmospheric nitrogen to ammonia

nodules
specialized structures that contain *Rhizobia* bacteria where nitrogen fixation takes place

parasitic plant
plant that is dependent on its host for survival

rhizobia
soil bacteria that symbiotically interact with legume roots to form nodules and fix nitrogen

saprophyte
plant that does not have chlorophyll and gets its food from dead matter

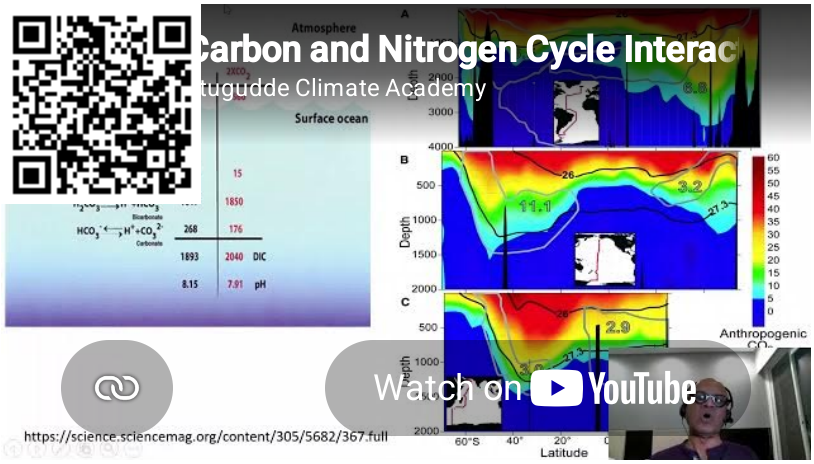
symbiont
plant in a symbiotic relationship with bacteria or fungi

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37.4: Carbon-Nitrogen Balance and Global Change

Nitrogen availability limits plant growth, and because of this interacts strongly with the carbon cycle. Humans are altering the carbon balance of the atmosphere by burning fossil fuels and nitrogen availability by producing and using fertilizers. There is a complex interplay of this simplified statement discussed in the video below.



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37.5: Phytoremediation

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37.5.1: Bioremediation

Bioremediation is a waste management technique that involves the use of organisms such as plants, bacteria, and fungi to remove or neutralize pollutants from a contaminated site. According to the United States EPA, bioremediation is a “treatment that uses naturally occurring organisms to break down hazardous substances into less toxic or non toxic substances”.

Bioremediation is widely used to treat human sewage and has also been used to remove agricultural chemicals (pesticides and fertilizers) that leach from soil into groundwater. Certain toxic metals, such as selenium and arsenic compounds, can also be removed from water by bioremediation. Mercury is an example of a toxic metal that can be removed from an environment by bioremediation. Mercury is an active ingredient of some pesticides and is also a byproduct of certain industries, such as battery production. Mercury is usually present in very low concentrations in natural environments but it is highly toxic because it accumulates in living tissues. Several species of bacteria can carry out the biotransformation of toxic mercury into nontoxic forms. These bacteria, such as *Pseudomonas aeruginosa*, can convert Hg^{2+} to Hg, which is less toxic to humans.

Probably one of the most useful and interesting examples of the use of prokaryotes for bioremediation purposes is the cleanup of oil spills. The importance of prokaryotes to petroleum bioremediation has been demonstrated in several oil spills in recent years, such as the Exxon Valdez spill in Alaska (1989) (Figure **37.5.1.1**), the Prestige oil spill in Spain (2002), the spill into the Mediterranean from a Lebanon power plant (2006,) and more recently, the BP oil spill in the Gulf of Mexico (2010). To clean up these spills, bioremediation is promoted by adding inorganic nutrients that help bacteria already present in the environment to grow. Hydrocarbon-degrading bacteria feed on the hydrocarbons in the oil droplet, breaking them into inorganic compounds. Some species, such as *Alcanivorax borkumensis*, produce surfactants that solubilize the oil, while other bacteria degrade the oil into carbon dioxide. In the case of oil spills in the ocean, ongoing, natural bioremediation tends to occur, inasmuch as there are oil-consuming bacteria in the ocean prior to the spill. Under ideal conditions, it has been reported that up to 80 percent of the nonvolatile components in oil can be degraded within 1 year of the spill. Researchers have genetically engineered other bacteria to consume petroleum products; indeed, the first patent application for a bioremediation application in the U.S. was for a genetically modified oil-eating bacterium.



(a) (b)

Figure **37.5.1.1**. (a) Cleaning up oil after the Valdez spill in Alaska, the workers hosed oil from beaches and then used a floating boom to corral the oil, which was finally skimmed from the water surface. Some species of bacteria are able to solubilize and degrade the oil. (b) One of the most catastrophic consequences of oil spills is the damage to fauna. (credit a: modification of work by NOAA; credit b: modification of work by GOLUBENKOV, NGO: Saving Taman)

There are a number of cost/efficiency advantages to bioremediation, which can be employed in areas that are inaccessible without excavation. For example, hydrocarbon spills (specifically, oil spills) or certain chlorinated solvents may contaminate groundwater, which can be easier to treat using bioremediation than more conventional approaches. This is typically much less expensive than excavation followed by disposal elsewhere, incineration, or other off-site treatment strategies. It also reduces or eliminates the need for “pump and treat”, a practice common at sites where hydrocarbons have contaminated clean groundwater. Using prokaryotes for bioremediation of hydrocarbons also has the advantage of breaking down contaminants at the molecular level, as opposed to simply chemically dispersing the contaminant.

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CHAPTER OVERVIEW

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38.4.1: Jasmonates

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38.1: Physical Defenses

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38.1.1: Plant Defenses Against Herbivores

Learning Objectives

- Identify plant defense responses to herbivores

Defense Responses Against Herbivores

Herbivores, both large and small, use plants as food and actively chew them. Plants have developed a variety of strategies to discourage or kill attackers.

Mechanical Defenses

The first line of defense in plants is an intact and impenetrable barrier composed of bark and a waxy cuticle. Both protect plants against herbivores. Other adaptations against herbivores include hard shells, thorns (modified branches), and spines (modified leaves). They discourage animals by causing physical damage or by inducing rashes and allergic reactions. Some Acacia tree species have developed mutualistic relationships with ant colonies: they offer the ants shelter in their hollow thorns in exchange for the ants' defense of the tree's leaves.



Figure **38.1.1.1**: Acacia collinsii: The large thorn-like stipules of Acacia collinsii are hollow and offer shelter for ants, which in return protect the plant against herbivores.



Figure **38.1.1.1**: Modified leaves on a cactus: The spines on cactus plants are modified leaves that act as a mechanical defense against predators.

Chemical Defenses

A plant's exterior protection can be compromised by mechanical damage, which may provide an entry point for pathogens. If the first line of defense is breached, the plant must resort to a different set of defense mechanisms, such as toxins and enzymes. Secondary metabolites are compounds that are not directly derived from photosynthesis and are not necessary for respiration or plant growth and development.

Many metabolites are toxic and can even be lethal to animals that ingest them. Some metabolites are alkaloids, which discourage predators with noxious odors (such as the volatile oils of mint and sage) or repellent tastes (like the bitterness of quinine). Other alkaloids affect herbivores by causing either excessive stimulation (caffeine is one example) or the lethargy associated with opioids. Some compounds become toxic after ingestion; for instance, glycol cyanide in the cassava root releases cyanide only upon ingestion by the herbivore. Foxgloves produce several deadly chemicals, namely cardiac and steroidal glycosides. Ingestion can cause nausea, vomiting, hallucinations, convulsions, or death.



Figure **38.1.1.1**: Foxgloves: Foxgloves produce several deadly chemicals, namely cardiac and steroidal glycosides. Ingestion can cause nausea, vomiting, hallucinations, convulsions, or death.

Timing

Mechanical wounding and predator attacks activate defense and protective mechanisms in the damaged tissue and elicit long-distancing signaling or activation of defense and protective mechanisms at sites farther from the injury location. Some defense reactions occur within minutes, while others may take several hours. In addition, long-distance signaling elicits a systemic response aimed at deterring predators. As tissue is damaged, jasmonates may promote the synthesis of compounds that are toxic to predators. Jasmonates also elicit the synthesis of volatile compounds that attract parasitoids: insects that spend their developing stages in or on another insect, eventually killing their host. The plant may activate abscission of injured tissue if it is damaged beyond repair.

Key Points

- Many plants have impenetrable barriers, such as bark and waxy cuticles, or adaptations, such as thorns and spines, to protect them from herbivores.
- If herbivores breach a plant's barriers, the plant can respond with secondary metabolites, which are often toxic compounds, such as glycol cyanide, that may harm the herbivore.
- When attacked by a predator, damaged plant tissue releases jasmonate hormones that promote the release of volatile compounds, attracting parasitoids, which use, and eventually kill, the predators as host insects.

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38.1.2: Plant Defenses Against Pathogens

Plants defend against pathogens with barriers, secondary metabolites, and antimicrobial compounds.

Learning Objectives

- Identify plant defense responses to pathogens

Defense Responses Against Pathogens

Pathogens are agents of disease. These infectious microorganisms, such as fungi, bacteria, and nematodes, live off of the plant and damage its tissues. Plants have developed a variety of strategies to discourage or kill attackers.

The first line of defense in plants is an intact and impenetrable barrier composed of bark and a waxy cuticle. Both protect plants against pathogens.

A plant's exterior protection can be compromised by mechanical damage, which may provide an entry point for pathogens. If the first line of defense is breached, the plant must resort to a different set of defense mechanisms, such as toxins and enzymes. Secondary metabolites are compounds that are not directly derived from photosynthesis and are not necessary for respiration or plant growth and development. Many metabolites are toxic and can even be lethal to animals that ingest them.

Additionally, plants have a variety of inducible defenses in the presence of pathogens. In addition to secondary metabolites, plants produce antimicrobial chemicals, antimicrobial proteins, and antimicrobial enzymes that are able to fight the pathogens. Plants can close stomata to prevent the pathogen from entering the plant. A hypersensitive response, in which the plant experiences rapid cell death to fight off the infection, can be initiated by the plant; or it may use endophyte assistance: the roots release chemicals that attract other beneficial bacteria to fight the infection.

Mechanical wounding and predator attacks activate defense and protective mechanisms in the damaged tissue and elicit long-distancing signaling or activation of defense and protective mechanisms at sites farther from the injury location. Some defense reactions occur within minutes, while others may take several hours.

Key Points

- Many plants have impenetrable barriers, such as bark and waxy cuticles, or adaptations, such as thorns and spines, to protect them from pathogens.
- If pathogens breach a plant's barriers, the plant can respond with secondary metabolites, which are often toxic compounds, such as glycol cyanide, that may harm the pathogen.
- Plants produce antimicrobial chemicals, antimicrobial proteins, and antimicrobial enzymes that are able to fight the pathogens.

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38.2: Chemical Defenses

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38.2.1: Plant Defenses Against Herbivores

Learning Objectives

- Identify plant defense responses to herbivores

Defense Responses Against Herbivores

Herbivores, both large and small, use plants as food and actively chew them. Plants have developed a variety of strategies to discourage or kill attackers.

Mechanical Defenses

The first line of defense in plants is an intact and impenetrable barrier composed of bark and a waxy cuticle. Both protect plants against herbivores. Other adaptations against herbivores include hard shells, thorns (modified branches), and spines (modified leaves). They discourage animals by causing physical damage or by inducing rashes and allergic reactions. Some Acacia tree species have developed mutualistic relationships with ant colonies: they offer the ants shelter in their hollow thorns in exchange for the ants' defense of the tree's leaves.



Figure **38.2.1.1**: Acacia collinsii: The large thorn-like stipules of Acacia collinsii are hollow and offer shelter for ants, which in return protect the plant against herbivores.



Figure **38.2.1.1**: Modified leaves on a cactus: The spines on cactus plants are modified leaves that act as a mechanical defense against predators.

Chemical Defenses

A plant's exterior protection can be compromised by mechanical damage, which may provide an entry point for pathogens. If the first line of defense is breached, the plant must resort to a different set of defense mechanisms, such as toxins and enzymes. Secondary metabolites are compounds that are not directly derived from photosynthesis and are not necessary for respiration or plant growth and development.

Many metabolites are toxic and can even be lethal to animals that ingest them. Some metabolites are alkaloids, which discourage predators with noxious odors (such as the volatile oils of mint and sage) or repellent tastes (like the bitterness of quinine). Other alkaloids affect herbivores by causing either excessive stimulation (caffeine is one example) or the lethargy associated with opioids. Some compounds become toxic after ingestion; for instance, glycol cyanide in the cassava root releases cyanide only upon ingestion by the herbivore. Foxgloves produce several deadly chemicals, namely cardiac and steroidal glycosides. Ingestion can cause nausea, vomiting, hallucinations, convulsions, or death.



Figure **38.2.1.1**: Foxgloves: Foxgloves produce several deadly chemicals, namely cardiac and steroidal glycosides. Ingestion can cause nausea, vomiting, hallucinations, convulsions, or death.

Timing

Mechanical wounding and predator attacks activate defense and protective mechanisms in the damaged tissue and elicit long-distancing signaling or activation of defense and protective mechanisms at sites farther from the injury location. Some defense reactions occur within minutes, while others may take several hours. In addition, long-distance signaling elicits a systemic response aimed at deterring predators. As tissue is damaged, jasmonates may promote the synthesis of compounds that are toxic to predators. Jasmonates also elicit the synthesis of volatile compounds that attract parasitoids: insects that spend their developing stages in or on another insect, eventually killing their host. The plant may activate abscission of injured tissue if it is damaged beyond repair.

Key Points

- Many plants have impenetrable barriers, such as bark and waxy cuticles, or adaptations, such as thorns and spines, to protect them from herbivores.
- If herbivores breach a plant's barriers, the plant can respond with secondary metabolites, which are often toxic compounds, such as glycol cyanide, that may harm the herbivore.
- When attacked by a predator, damaged plant tissue releases jasmonate hormones that promote the release of volatile compounds, attracting parasitoids, which use, and eventually kill, the predators as host insects.

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38.2.2: Plant Defenses Against Pathogens

Plants defend against pathogens with barriers, secondary metabolites, and antimicrobial compounds.

Learning Objectives

- Identify plant defense responses to pathogens

Defense Responses Against Pathogens

Pathogens are agents of disease. These infectious microorganisms, such as fungi, bacteria, and nematodes, live off of the plant and damage its tissues. Plants have developed a variety of strategies to discourage or kill attackers.

The first line of defense in plants is an intact and impenetrable barrier composed of bark and a waxy cuticle. Both protect plants against pathogens.

A plant's exterior protection can be compromised by mechanical damage, which may provide an entry point for pathogens. If the first line of defense is breached, the plant must resort to a different set of defense mechanisms, such as toxins and enzymes. Secondary metabolites are compounds that are not directly derived from photosynthesis and are not necessary for respiration or plant growth and development. Many metabolites are toxic and can even be lethal to animals that ingest them.

Additionally, plants have a variety of inducible defenses in the presence of pathogens. In addition to secondary metabolites, plants produce antimicrobial chemicals, antimicrobial proteins, and antimicrobial enzymes that are able to fight the pathogens. Plants can close stomata to prevent the pathogen from entering the plant. A hypersensitive response, in which the plant experiences rapid cell death to fight off the infection, can be initiated by the plant; or it may use endophyte assistance: the roots release chemicals that attract other beneficial bacteria to fight the infection.

Mechanical wounding and predator attacks activate defense and protective mechanisms in the damaged tissue and elicit long-distancing signaling or activation of defense and protective mechanisms at sites farther from the injury location. Some defense reactions occur within minutes, while others may take several hours.

Key Points

- Many plants have impenetrable barriers, such as bark and waxy cuticles, or adaptations, such as thorns and spines, to protect them from pathogens.
- If pathogens breach a plant's barriers, the plant can respond with secondary metabolites, which are often toxic compounds, such as glycol cyanide, that may harm the pathogen.
- Plants produce antimicrobial chemicals, antimicrobial proteins, and antimicrobial enzymes that are able to fight the pathogens.

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38.3: Animals That Protect Plants

Plants are food and there are myriad animals ranging from small insects to large mammals that eat them. There are also other animals that eat the ones eating the plants. In some cases when plants are attacked they emit chemicals which attract their protectors.

It has long been noted that plants respond to leaf devouring insect attacks by releasing volatile chemicals, a response that not only leads other plants to beef up their own leaf level of insect-repellents but that sometimes draws in specific insect predators and parasitizing wasps (Pare & Tumlinson, 1999). The timing and intensity of release can vary in accordance with a multiplicity of environmental factors, and blends of different odor-producing volatiles can be produced in response to different leaf-eaters, possibly summoning particular carnivorous insects specialized to feast on each kind of herbivore, making it a highly sophisticated response that has been considered, according to a 'behavioural ecological approach' that speaks in terms of plant 'decisions,' and a 'crying for help' within the larger ecological community (Dicke, 2009).

In other cases insects that prey on plant eating insects were purposefully introduced. Three of these include (Freedman, 1995)

- The cottony-cushion scale (Icyera purchasi) is a sap-sucking insect that was accidentally introduced to the United States, where it became a threat to citrus agriculture. Research in its native Australia discovered that the pest was naturally controlled by certain insect predators and parasites. In 1888, two of its predators, a lady beetle and a parasitic fly, were introduced to California. This allowed almost total control over this potentially disastrous pest. Unfortunately, this biological control was disrupted when DDT and other broad-spectrum insecticides were used to deal with other orchard pests beginning in the late 1940s.
- St. John's wort (Hypericum perforatum), a common weed, is toxic to cattle. It became a serious pest in pastures after it was introduced from Europe. In 1943, two leaf beetles that feed on this plant were released to North America, and this pest is no longer an important problem.
- The prickly pear cactus (Opuntia stricta) was imported to Australia from North America and grown as an ornamental plant and a "living fence." It escaped and became a serious weed in rangelands. This pest was controlled by the introduction of one of its herbivores, a moth whose larvae feed on the cactus.

Birds also are great consumers of insects (as well as themselves eating seeds and grain) but on balance they protect plants against insects which eat more. The Four Pests campaign was one of the first actions taken in the Great Leap Forward in China from 1958 to 1962. Four pests were targeted for elimination: rats, flies, mosquitoes, and sparrows. The extermination of sparrows resulted in severe ecological imbalance, being one of the causes of the Great Chinese Famine of 1959–1961. With no sparrows to eat them, locust populations ballooned, swarming the country and compounding ecological problems.

Below is a powerpoint video on this chapter



References

Dicke, M. (2009). Behavioural and community ecology of plants that cry for help. *Planet, Cell, and Environment*, *32*(6), 654–665. https://doi.org/10.1111/j.1365-3040.2008.01913.x

Freedman, B., R. Morash, and D. MacKinnon. 1993. Short-term changes in vegetation after the silvicultural spraying of glyphosate herbicide onto regenerating clear-cuts in Nova Scotia, Canada. Canadian Journal of Forest Research, 23: 2300-2311.

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38.4: Systemic Responses to Invaders

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38.4.1: Jasmonates

Learning Objectives

- Identify several signaling molecules beyond the five major plant hormones and describe their effects.
- Distinguish between the hypersensitive response and systemic acquired response.
- Explain the mechanisms by which signaling compounds aid in plant defense against pathogens and herbivores.

Recent research has discovered a number of compounds that also influence plant development. Their roles are less understood than the effects of the major hormones described so far.

Brassinosteroids

Brassinosteroids (Figure **38.4.1.1**) are synthesized primarily in young tissues are important to many developmental and physiological processes. In fact, many sources considere them the sixth major plant hormones. Unlike the hormones discussed previously, brassinosteroids do not travel far from their site of synthesis. Signals between these compounds and other hormones, notably auxin and GAs, amplifies their physiological effect. Apical dominance, seed germination, gravitropism, lateral root formation, differentiation of cells in the vascular tissue, and resistance to freezing are all positively influenced by brassinosteroids. Root growth and fruit dropping are inhibited by steroids.

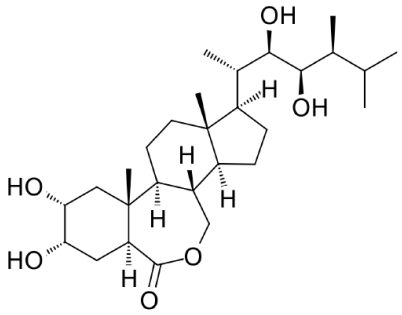


Figure **38.4.1.1**: Brassinolide, an example of a brassinosteroid. Image by Wostr (public domain).

Systemin

Systemin, named for the fact that it is distributed systemically (everywhere) in the plant body upon production, is a short polypeptide that activates plant responses to wounds from **herbivores** (animals that feed on plant parts). It causes the plant to produce **jasmonic acid** (see below).

Jasmonates

Jasmonates play a major role in defense responses to herbivory (Figure **38.4.1.2**). Their levels increase when a plant is wounded by an herbivore, resulting in an increase in toxic secondary metabolites. For example, **jasmonic acid** (Figure **38.4.1.3**) also induces transcription of protease inhibitors. Protease inhibitors both taste bad and prevent breakdown of proteins in the herbivore's gut, thus making the insect sick and deterring further herbivory. Jasmonates also contribute to the production of volatile compounds that attract natural enemies of herbivores. Chewing of tomato plants by caterpillars leads to an increase in jasmonic acid levels, which in turn triggers the release of volatile compounds that attract predators of the pest. Jasmonates also elicit the synthesis of volatile compounds that attract parasitoids, which are insects that spend their developing stages in or on another insect, and eventually kill their host.



Figure **38.4.1.2**: Jasmonic acid mediates plant defense against herbivores such as this tobacco hornworm (*Manduca sexta*). Image by Scot Nelson (public domain).

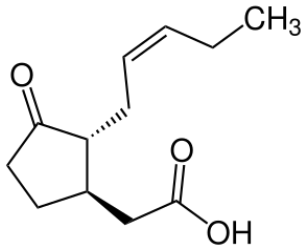


Figure **38.4.1.3**: The chemical structure of jasmonic acid. Image by Minutemen (public domain).

Jasmonates also work with systemin to mediate responses to drought, damage by ground-level ozone, and ultraviolet light.

Salicylic Acid

Salicylic acid resembles aspirin (Figure **38.4.1.4**) and is important for plant defense. It initiates the a systemic (whole body) response called the **systemic acquired response** (SAR) as a response to infection by parasites or pathogens. When a parasite or pathogen infects a cell, there is an specific, localized response called the **hypersensitive response** (HR). Following this very localized response, the plant initiates a systemic (whole body) response called the systemic acquired response (SAR). Salicylic acid is produced and converted to **methyl salicylate** (Figure **38.4.1.4**) inducing the SAR in response to the HR. The SAR activates transcription of general "**pathogenesis-resistance**" genes, which are *not* pathogen-specific (unlike in the hypersensitive response), but serve as general defense against pathogenic infection. The SAR is slower than the hypersensitive response, and also differs in that it is systemic instead of localized to the site of the infection.

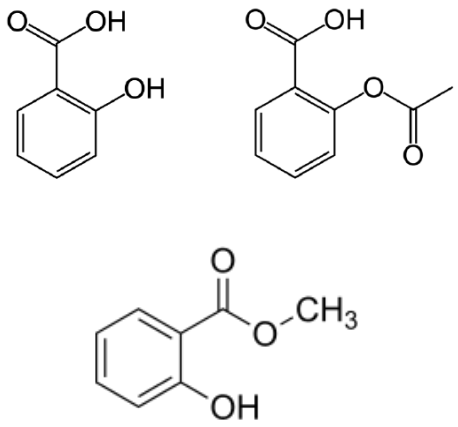


Figure **38.4.1.4**: Salicylic acid (left) resembles aspirin, or acetylsalicylic acid (right). In acetylsalicylic acid, an acetyl group ($COCH_3$) has replaced the hydrogen in the hydroxyl group (OH) of salicylic acid. Methyl salicylate (bottom) has a similar structure to salicylic acid, but a methyl group (CH_3) has replaced the hydrogen in the carboxyl group (COOH). Left image by Fvasconcellos (public domain), right image by Benjah-bmm27 (public domain), and bottom image by Emeldir (public domain).

Similar to jasmonic acid, salicylic acid can mediates defense against insect herbivores. It is directly toxic to some herbivores. Additionally, in response to herbivory, salicylic acid can be converted to methyl salicylate, which is released as a gas. This volatile compound can attract natural predators and parasites of the herbivores.

Some plants, such as skunk cabbage (Figure 38.4.1.5) and elephant yam, are adapted to flower while snow still covers the ground. Salicylic acid mediates their ability to produce heat to melt the snow around them. Such plants are thus called **thermogenic** ("heat producing").



Figure 38.4.1.5: Skunk-cabbage (*Symplocarpus foetidus*) is a thermogenic plant, producing heat that melts the snow surrounding it. This process is mediated by salicylic acid. Image by John Winkelman (CC-BY).

Oligosaccharins

Oligosaccharins are short chains of simple sugars that play a role in plant defense against bacterial and fungal infections. They act locally at the site of injury, and can also be transported to other tissues.

Strigolactones

Strigolactones (Figure 38.4.1.6) promote seed germination in some species and inhibit lateral apical development in the absence of auxins. Strigolactones also play a role in the establishment of mycorrhizae, a mutualistic association of plant roots and fungi.

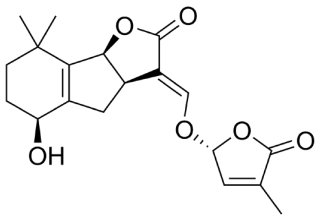


Figure 38.4.1.6: The chemical structure of (+)-strigol, a strigolactone.

Florigen

Florigen is a systemic signal that initiates flowering. It is also involved in the formation of storage organs and contributes to plant architecture. It is synthesized in leaves and transported to the shoot apical meristem (SAM) where it promotes flowering in response to daylength cues. At the molecular level, florigen is represented as a protein product encoded by the *FLOWERING LOCUS T* (*FT*) gene, which is highly conserved (occurs/has a similar genetic sequence in) across flowering plants.

Florigen is considered one of the important targets for crop improvement. Regulation of flowering time is an important target for plant breeding because the control of flowering to a favorable time provides successful grain production in a given cropping area. Flowering at unfavorable seasons causes loss of yield due to insufficient growth of photosynthetic organs or poor fertility due to heat or cold stress during reproduction. Thus, understanding florigen function can contribute to novel breeding techniques in crops to produce cultivars that can start their reproductive stage at optimal seasons.

Supplemental Reading

Filgueiras, C. C., Martins, A. D., Pereira, R. V., & Willett, D. S. (2019). The Ecology of Salicylic Acid Signaling: Primary, Secondary and Tertiary Effects with Applications in Agriculture. *International journal of molecular sciences*, *20* (23), 5851. https://doi.org/10.3390/ijms20235851

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- Tsuji H. (2017). Molecular function of florigen. *Breeding science*, *67* (4), 327–332. https://doi.org/10.1270/jsbbs.17026 (licensed CC BY)

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CHAPTER OVERVIEW

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39.1.1: Plant Responses to Light

39.1.2: Photoperiodism

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39.1: Responses to Light

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39.1.1: Plant Responses to Light

Learning Objectives

- Compare the ways plants respond to light

Plant Responses to Light

Plants have a number of sophisticated uses for light that go far beyond their ability to perform photosynthesis. Plants can differentiate and develop in response to light (known as photomorphogenesis), which allows plants to optimize their use of light and space. Plants use light to track time, which is known as photoperiodism. They can tell the time of day and time of year by sensing and using various wavelengths of sunlight. Light can also elicit a directional response in plants that allows them to grow toward, or even away from, light; this is known as phototropism.



Figure **39.1.1.1**: Phototropism of an orchid plant: This orchid plant placed next to a window grows toward the sunlight through the window. This is an example of positive phototropism.

The sensing of light in the environment is important to plants; it can be crucial for competition and survival. The response of plants to light is mediated by different photoreceptors: a protein covalently-bonded to a light-absorbing pigment called a chromophore; together, called a chromoprotein. The chromophore of the photoreceptor absorbs light of specific wavelengths, causing structural changes in the photoreceptor protein. The structural changes then elicit a cascade of signaling throughout the plant.

The red, far-red, and violet-blue regions of the visible light spectrum trigger structural development in plants. Sensory photoreceptors absorb light in these particular regions of the visible light spectrum because of the quality of light available in the daylight spectrum. In terrestrial habitats, light absorption by chlorophylls peaks in the blue and red regions of the spectrum. As light filters through the canopy and the blue and red wavelengths are absorbed, the spectrum shifts to the far-red end, shifting the plant community to those plants better adapted to respond to far-red light. Blue-light receptors allow plants to gauge the direction and abundance of sunlight, which is rich in blue–green emissions. Water absorbs red light, which makes the detection of blue light essential for algae and aquatic plants.

Key Points

- Plants grow and differentiate to optimize their space, using light in a process known as photomorphogenesis.
- Plants grow and move toward or away from light depending on their needs; this process is known as phototropism.
- Photoperiodism is illustrated by how plants flower and grow at certain times of the day or year through the use of photoreceptors that sense the wavelengths of sunlight available during the day (versus night) and throughout the seasons.
- The various wavelengths of light, red/far-red or blue regions of the visible light spectrum, trigger structural responses in plants suited for responding to those wavelengths.

Key Terms

- **photoreceptor**: a specialized protein that is able to detect and react to light
- **photoperiodism**: the growth, development and other responses of plants and animals according to the length of day and/or night
- **photomorphogenesis**: the regulatory effect of light on the growth, development and differentiation of plant cells, tissues and organs
- **phototropism**: the movement of a plant toward or away from light

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39.1.2: Photoperiodism

Learning Objectives

- Describe the mechanism of photoperiodism with respect to flowering.
- Distinguish among short-day, long-day, and day-neutral plants.
- Define circadian rhythms and provide examples in plants.

Detection of seasonal changes is crucial to plant survival. Although temperature and light intensity influence plant growth, they are not reliable indicators of season because they may vary from one year to the next. Day length is a better indicator of the time of year. Many angiosperms flower at about the same time every year. This occurs even though they may have started growing at different times. Their flowering is a response to the changing length of day and night as the season progresses. It helps promote cross pollination. The biological response to the timing and duration of day and night is called **photoperiodism**.

The Phytochrome System and the Red/Far-Red Response

Plants use the phytochrome system to sense the change of season, which can control flowering. The **phytochromes** are a family of photoreceptors. They are chromoproteins with a linear tetrapyrrole chromophore (a molecule that absorbs light), similar to the ringed tetrapyrrole light-absorbing head group of chlorophyll. A phytochrome is a homodimer: two identical protein molecules, each conjugated to a light-absorbing molecule (compare to rhodopsin). Plants make 5 phytochromes: **PhyA**, **PhyB**, as well as C, D, and E. There is some redundancy in function of the different phytochromes, but there also seem to be functions that are unique to one or another. The phytochromes also differ in their absorption spectrum; that is, which wavelengths (e.g., red vs. far-red) they absorb best. Phytochromes have two photo-interconvertible forms: Pr and Pfr. Pr absorbs red light (~667 nm) and is immediately converted to Pfr. Pfr absorbs far-red light (~730 nm) and is quickly converted back to Pr. Absorption of red or far-red light causes a massive change to the shape of the chromophore, altering the conformation and activity of the phytochrome protein to which it is bound. Pfr is the physiologically active form of the protein; therefore, exposure to red light yields physiological activity. Exposure to far-red light inhibits phytochrome activity. Together, the two forms represent the phytochrome system (Figure **39.1.2.1**).

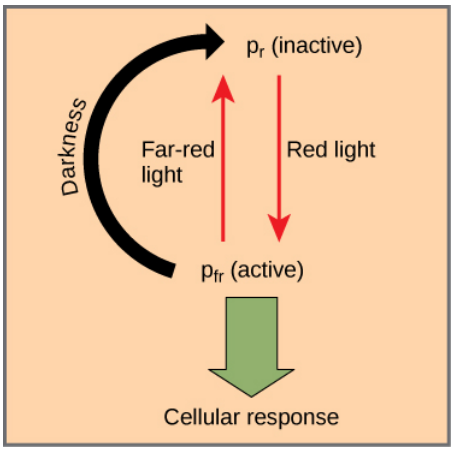


Figure **39.1.2.1**: The biologically inactive form of phytochrome (Pr) is converted to the biologically active form Pfr under illumination with red light. Far-red light and darkness convert the molecule back to the inactive form.

The phytochrome system acts as a biological light switch. It monitors the level, intensity, duration, and color of environmental light. The effect of red light is reversible by immediately shining far-red light on the sample, which converts the chromoprotein to the inactive Pr form. Additionally, Pfr can slowly revert to Pr in the dark, or break down over time. In all instances, the physiological response induced by red light is reversed. The active form of phytochrome (Pfr) can directly activate other molecules in the cytoplasm, or it can be transported to the nucleus, where it directly activates or represses specific gene expression.

Unfiltered sunlight is rich in red light but deficient in far-red light. Therefore, at dawn, all the phytochrome molecules in a leaf quickly convert to the active Pfr form, and remain in that form until sunset. In the dark, the Pfr form takes hours to slowly revert back to the Pr form. If the night is long (as in winter), all of the Pfr form reverts. If the night is short (as in summer), a considerable

amount of Pfr may remain at sunrise. By sensing the Pr/Pfr ratio at dawn, a plant can determine the length of the day/night cycle. In addition, leaves retain that information for several days, allowing a comparison between the length of the previous night and the preceding several nights. Shorter nights indicate springtime to the plant; when the nights become longer, autumn is approaching. This information, along with sensing temperature and water availability, allows plants to determine the time of the year and adjust their physiology accordingly.

In 1920 two employees of the U. S. Department of Agriculture, W. W. Garner and H. A. Allard, discovered a mutation in tobacco - a variety called Maryland Mammoth - that prevented the plant from flowering in the summer as normal tobacco plants do. Maryland Mammoth would not bloom until late December. Experimenting with artificial lighting in winter and artificial darkening in summer, they found that Maryland Mammoth was affected by photoperiod. Because it would flower only when exposed to short periods of light, they called it a **short-day** plant. Examples of other short-day plants include chrysanthemums, rice (*Oryza sativa*), poinsettias, morning glory (*Pharbitis nil*), and cocklebur (*Xanthium*).

Experiments with the cocklebur have shown that the term short-day is something of a misnomer; what the cocklebur needs is a sufficiently **long night** (Figure **39.1.2.2**). Short-day (long-night) plants flower in the late summer and early fall, when nights exceed a critical length (often eight or fewer hours). In short-day plants, the active form of phytochrome (Pfr) suppresses flowering. During long periods of darkness (long nights), Pfr is converted to Pr. With Pfr no longer present, flowering is not suppressed, and short-day plants flower. If a flash of light interrupts the dark period, Pr is converted back to Pfr, and flowering is suppressed.

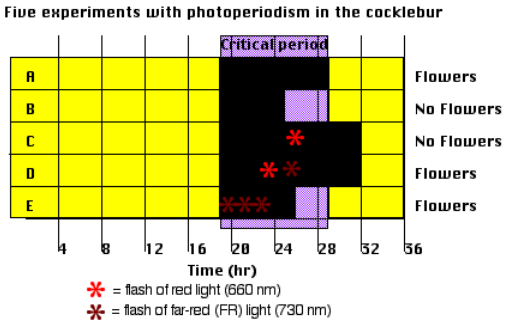


Figure **39.1.2.2**: Cockleburs (adapted to the latitude of Michigan) will flower only if they have been kept in the dark for at least 8.5 hours — the **critical period** (**A** and **B**). Interruption of an otherwise long night by light — **red** (**660 nm**) rays are particularly effective — prevents flowering (**C**). Unless it is followed by irradiation with **far-red** (**730 nm**) light (**D**). An intense exposure to far-red light at the start of the night reduces the dark requirement by two hours (**E**).

Long-day (short-night) plants flower during the spring, when darkness is less than a critical length (often eight to 15 hours). Examples include spinach, *Arabidopsis*, sugar beet, and the radish flower.

Flowering in **day-neutral** plants, such as the tomato, is not regulated by photoperiod.

Photoperiodism also explains why some plant species can be grown only in a certain latitude. Spinach, a long-day plant, cannot flower in the tropics because the days never get long enough (14 hours). Ragweed, a short-day plant, fails to thrive in northern Maine because by the time the days become short enough to initiate flowering, a killing frost in apt to occur before reproduction and the formation of seeds is completed.

Some plants do not neatly fit into the categories of short day, long day, or day neutral. In 1941, Marie Taylor Clark found that flowering in scarlet sage did not flower under daylengths longer than 16 hours, suggesting it was a short-day plant; however, days that were too short (6 hours) slowed flower development. Flower development was optimal with daylengths of 10 hours.

The leaves produce a chemical signal called **florigen** that is transmitted to the apical meristems to start their conversion into floral meristems. The chemical nature of florigen has been sought for decades. The most recent evidence suggests that at least one component is the protein encoded by the gene *FLOWERING LOCUS T* (***FT***). Due to florigen signaling, the entire plant will bloom even if only a part of one leaf is exposed to the correct photoperiod (Figure **39.1.2.3**).

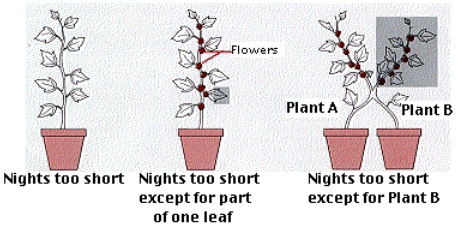


Figure **39.1.2.3**: The cocklebur needs at least 8.5 hours of darkness in order to flower. Grafting a cocklebur (**B**) that receives the required period of darkness to one (**A**) that does not causes flowering in both. Evidently the florigen signal passes from **B** to **A** through their connected vascular systems.

Career Connection: Horticulturist

The word “horticulturist” comes from the Latin words for garden (hortus) and culture (cultura). This career has been revolutionized by progress made in the understanding of plant responses to environmental stimuli. Growers of crops, fruit, vegetables, and flowers were previously constrained by having to time their sowing and harvesting according to the season. Now, horticulturists can manipulate plants to increase leaf, flower, or fruit production by understanding how environmental factors affect plant growth and development.

Greenhouse management is an essential component of a horticulturist’s education. To lengthen the night, plants are covered with a blackout shade cloth. Long-day plants are irradiated with red light in winter to promote early flowering. For example, fluorescent (cool white) light high in blue wavelengths encourages leafy growth and is excellent for starting seedlings. Incandescent lamps (standard light bulbs) are rich in red light, and promote flowering in some plants. The timing of fruit ripening can be increased or delayed by applying plant hormones. Recently, considerable progress has been made in the development of plant breeds that are suited to different climates and resistant to pests and transportation damage. Both crop yield and quality have increased as a result of practical applications of the knowledge of plant responses to external stimuli and hormones.

Horticulturists find employment in private and governmental laboratories, greenhouses, botanical gardens, and in the production or research fields (Figure **39.1.2.4**). They improve crops by applying their knowledge of genetics and plant physiology. To prepare for a horticulture career, students take classes in botany, plant physiology, plant pathology, landscape design, and plant breeding. To complement these traditional courses, horticulture majors add studies in economics, business, computer science, and communications.



Figure **39.1.2.4**: Horticulturalist Anderson Ifui (left) with Jack McGilchrist, the technical adviser for the Australian Volunteer Initiative (right), at Honiara Botanic gardens in the Solomon Islands in 2004. Image by Peter Davis/AusAID (CC-BY).

Circadian Rhythms

Circadian rhythms are changes based on a 24-hour cycle. For example, flowers might open every morning and close every evening or vice versa. In *Oxalis* and silk tree (*Albizia julibrissin*), leaflets expand during the day and retract at night. Circadian

rhythms may also involve physiological processes like photosynthetic rate or the the production of floral scent compounds.

Under constant conditions, circadian rhythms may drift out of phase with the environment (figure 39.1.2.5). However, when exposed to environmental changes (e.g., alternating day and night), the rhythms become **entrained**; that is, they now cycle synchronized with the cycle of day and night with a period of exactly 24 hours. Internal circadian clocks also adjust to changing photoperiods. Suppose a plant that flowers throughout the spring opens its flowers every morning. The sun rises earlier in the late spring compared to the early spring (photoperiod increases in late spring). As time passes and the plant detects the changing photoperiod (technically, plants measure the length of the night rather than daylength; see above), the circadian clock would adjust such that its flowers opened earlier. In *Arabidopsis*, the entrainment of circadian rhythms requires that light is detected by phytochromes (absorb red light) and cryptochromes (absorb blue light).



Figure 39.1.2.5: The leaves and leaflets of the silk tree (*Albizia julibrissin*) expand during the day (left) and retract and night (right). These diurnal (daily) movements are an example of circadian rhythms. Image is public domain.

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39.1.3: The Phytochrome System and Red Light Response

Learning Objectives

- Explain the response of the phytochrome system to red/far-red light

The phytochromes are a family of chromoproteins with a linear tetrapyrrole chromophore, similar to the ringed tetrapyrrole light-absorbing head group of chlorophyll. Phytochromes have two photo-interconvertible forms: Pr and Pfr. Pr absorbs red light (~667 nm) and is immediately converted to Pfr. Pfr absorbs far-red light (~730 nm) and is quickly converted back to Pr. Absorption of red or far-red light causes a massive change to the shape of the chromophore, altering the conformation and activity of the phytochrome protein to which it is bound. Pfr is the physiologically-active form of the protein; exposure to red light yields physiological activity in the plant. Exposure to far-red light converts the Pfr to the inactive Pr form, inhibiting phytochrome activity. Together, the two forms represent the phytochrome system.

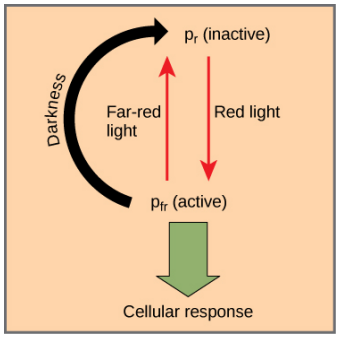


Figure **39.1.3.1**: Phytochrome system: The biologically-inactive form of phytochrome (Pr) is converted to the biologically-active form Pfr under illumination with red light. Far-red light and darkness convert the molecule back to the inactive form.

The phytochrome system acts as a biological light switch. It monitors the level, intensity, duration, and color of environmental light. The effect of red light is reversible by immediately shining far-red light on the sample, which converts the chromoprotein to the inactive Pr form. Additionally, Pfr can slowly revert to Pr in the dark or break down over time. In all instances, the physiological response induced by red light is reversed. The active form of phytochrome (Pfr) can directly activate other molecules in the cytoplasm, or it can be trafficked to the nucleus, where it directly activates or represses specific gene expression.

The Phytochrome System and Growth

Plants use the phytochrome system to grow away from shade and toward light. Unfiltered, full sunlight contains much more red light than far-red light. Any plant in the shade of another plant will be exposed to red-depleted, far-red-enriched light because the other plant has absorbed most of the other red light. The exposure to red light converts phytochrome in the shaded leaves to the Pr (inactive) form, which slows growth. The leaves in full sunlight are exposed to red light and have activated Pfr, which induces growth toward sunlit areas. Because competition for light is so fierce in a dense plant community, those plants who could grow toward light the fastest and most efficiently became the most successful.

The Phytochrome System in Seeds

In seeds, the phytochrome system is used to determine the presence or absence of light, rather than the quality. This is especially important in species with very small seeds and, therefore, food reserves. For example, if lettuce seedlings germinated a centimeter under the soil surface, the seedling would exhaust its food resources and die before reaching the surface. A seed will only germinate if exposed to light at the surface of the soil, causing Pr to be converted to Pfr, signaling the start of germination. In the dark, phytochrome is in the inactive Pr form so the seed will not germinate.

Photoperiodism

Plants also use the phytochrome system to adjust growth according to the seasons. Photoperiodism is a biological response to the timing and duration of dark and light periods. Since unfiltered sunlight is rich in red light, but deficient in far-red light, at dawn, all the phytochrome molecules in a leaf convert to the active Pfr form and remain in that form until sunset. Since Pfr reverts to Pr

during darkness, there will be no Pfr remaining at sunrise if the night is long (winter) and some Pfr remaining if the night is short (summer). The amount of Pfr present stimulates flowering, setting of winter buds, and vegetative growth according to the seasons.

In addition, the phytochrome system enables plants to compare the length of dark periods over several days. Shortening nights indicate springtime to the plant; lengthening nights indicate autumn. This information, along with sensing temperature and water availability, allows plants to determine the time of the year and adjust their physiology accordingly. Short-day (long-night) plants use this information to flower in the late summer and early fall when nights exceed a critical length (often eight or fewer hours). Long-day (short-night) plants flower during the spring when darkness is less than a critical length (often 8 to 15 hours). However, day-neutral plants do not regulate flowering by day length. Not all plants use the phyotochrome system to adjust their physiological responses to the seasons.

Key Points

- Exposure to red light converts the chromoprotein to the functional, active form (Pfr), while darkness or exposure to far-red light converts the chromophore to the inactive form (Pr).
- Plants grow toward sunlight because the red light from the sun converts the chromoprotein into the active form (Pfr), which triggers plant growth; plants in shade slow growth because the inactive form (Pr) is produced.
- If seeds sense light using the phytochrome system, they will germinate.
- Plants regulate photoperiodism by measuring the Pfr/Pr ratio at dawn, which then stimulates physiological processes such as flowering, setting winter buds, and vegetative growth.

Key Terms

- **phytochrome**: any of a class of pigments that control most photomorphogenic responses in higher plants
- **chromophore**: the group of atoms in a molecule in which the electronic transition responsible for a given spectral band is located
- **photoperiodism**: the growth, development and other responses of plants and animals according to the length of day and/or night

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39.1.4: Blue Light Response

Learning Objectives

- Differentiate among blue light responses of plants

Phototropism is the directional bending of a plant toward or away from a light source of blue wavelengths of light. Positive phototropism is growth toward a light source, while negative phototropism (also called skototropism) is growth away from light. Several proteins use blue light to control various physiological processes in the plant.



Figure **39.1.4.1**: Blue light response of azure bluets: Azure bluets (Houstonia caerulea) display a phototropic response by bending toward the light.

Phototropins and Physiological Responses

Phototropins are protein-based receptors responsible for mediating the phototropic response in plants. Like all plant photoreceptors, phototropins consist of a protein portion and a light-absorbing portion, called the chromophore, which senses blue wavelengths of light. Phototropins belong to a class of proteins called flavoproteins because the chromophore is a covalently-bound molecule of flavin.

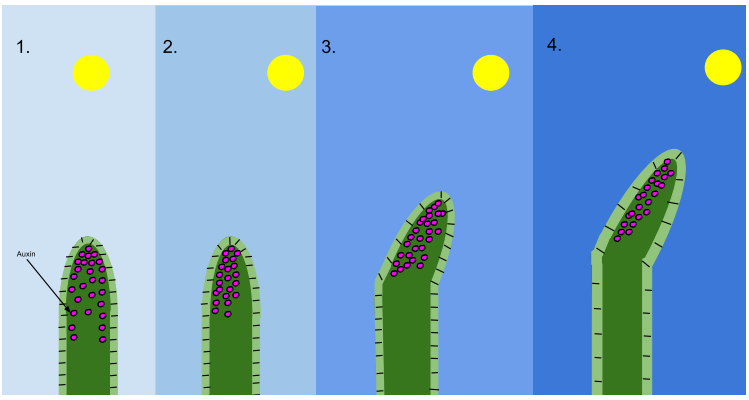
Phototropins control other physiological responses including leaf opening and closing, chloroplast movement, and the opening of stomata. However, of all responses controlled by phototropins, phototropism has been studied the longest and is the best understood.

Phototropism and Auxin

In 1880, Charles Darwin and his son Francis first described phototropism as the bending of seedlings toward light. Darwin observed that light was perceived by the the apical meristem (tip of the plant), but that the plant bent in response in a different part of the plant. The Darwins concluded that the signal had to travel from the apical meristem to the base of the plant, where it bent.

In 1913, Peter Boysen-Jensen conducted an experiment that demonstrated that a chemical signal produced in the plant tip was responsible for the plant's bending response at the base. He cut off the tip of a seedling, covered the cut section with a permeable layer of gelatin, and then replaced the tip. The seedling bent toward the light when illuminated even though the layer of gelatin was present. However, when impermeable mica flakes were inserted between the tip and the cut base, the seedling did not bend.

A refinement of Boysen-Jensen's experiment showed that the signal traveled on the shaded side of the seedling. When the mica plate was inserted on the illuminated side, the plant still bent toward the light. Therefore, the chemical signal from the sunlight, which is blue wavelengths of light, was a growth stimulant; the phototropic response involved faster cell elongation on the shaded side than on the illuminated side, causing the plant to bend. We now know that as light passes through a plant stem, it is diffracted and generates phototropin activation across the stem. Most activation occurs on the lit side, causing the plant hormones indole acetic acid (IAA) or auxin to accumulate on the shaded side. Stem cells elongate under the influence of IAA.



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Figure **39.1.4.1**: Phototropism and the distribution of auxin: Phototropism is the growth of plants in response to light. When the sun is positioned almost directly over the plant, the hormone auxin (pink dots) in the plant stem is evenly distributed. As the sun moves, the auxin is repositioned on the other side of the plant. This overload of auxin next to these cells causes them to start to grow or elongate, tipping the growth of the stem toward the light.

Cryptochromes

Cryptochromes are another class of blue-light absorbing photoreceptors. Their chromophores also contain a flavin-based chromophore. Cryptochromes set the plant's circadian rhythm (the 24-hour activity cycle) using blue light receptors. There is some evidence that cryptochromes work by sensing light-dependent redox reactions and that, together with phototropins, they mediate the phototropic response.

Key Points

- In addition to phototropism, phototropins sense blue light to control leaf opening and closing, chloroplast movement, and the opening of stomata.
- When phototropins are activated by blue light, the hormone auxin accumulates on the shaded side of the plant, triggering elongation of stem cells and phototropism.
- Cryptochromes sense blue light-dependent redox reactions to control the circadian rhythm of plants.

Key Terms

- **skototropism**: growth or movement away from light
- **phototropin**: any of a class of photoreceptor flavoproteins that mediate phototropism in higher plants
- **auxin**: a class of plant growth hormones that is responsible for elongation in phototropism and gravitropism and for other growth processes in the plant life cycle
- **cryptochrome**: any of several light-sensitive flavoproteins, in the protoreceptors of plants, that regulate germination, elongation, and photoperiodism

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39.2: Responses to Gravity

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39.2.1: Plant Responses to Gravity

Learning Objectives

- Describe the role of amyloplasts in gravitropism

Whether or not they germinate in the light or in total darkness, shoots usually sprout up from the ground, while roots grow downward into the ground. A plant laid on its side in the dark will send shoots upward when given enough time. Gravitropism ensures that roots grow into the soil and that shoots grow toward sunlight. Growth of the shoot apical tip upward is called negative gravitropism, whereas growth of the roots downward is called positive gravitropism.





Time-lapse of pea shoot and root growth: Time-lapse of a pea plant growing from seed, showing both the shoot and root system. The roots grown downward in the direction of gravity, which is positive gravitropism, and the shoot grows upward away from gravity, which is negative gravitropism.

The reason plants know which way to grow in response to gravity is due to amyloplasts in the plants. Amyloplasts (also known as statoliths) are specialized plastids that contain starch granules and settle downward in response to gravity. Amyloplasts are found

in shoots and in specialized cells of the root cap. When a plant is tilted, the statoliths drop to the new bottom cell wall. A few hours later, the shoot or root will show growth in the new vertical direction.



Figure **39.2.1.1**: Gravitropism: This is an image of an upright tree with high curvature at the base as a result of negative gravitropism. Despite being tilted, amyloplasts will cause the shoot to grow in a vertical direction.

The mechanism that mediates gravitropism is reasonably well understood. When amyloplasts settle to the bottom of the gravity-sensing cells in the root or shoot, they physically contact the endoplasmic reticulum (ER). This causes the release of calcium ions from inside the ER. This calcium signaling in the cells causes polar transport of the plant hormone indole acetic acid (IAA) to the bottom of the cell. In roots, a high concentration of IAA inhibits cell elongation. The effect slows growth on the lower side of the root while cells develop normally on the upper side. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion and causes the shoot to grow up. After the shoot or root begin to grow vertically, the amyloplasts return to their normal position. Other hypotheses, which involve the entire cell in the gravitropism effect, have been proposed to explain why some mutants that lack amyloplasts may still exhibit a weak gravitropic response.

Key Points

- Positive gravitropism occurs when roots grow into soil because they grow in the direction of gravity while negative gravitropism occurs when shoots grow up toward sunlight in the opposite direction of gravity.
- Amyloplasts settle at the bottom of the cells of the shoots and roots in response to gravity, causing calcium signaling and the release of indole acetic acid.
- Indole acetic acid inhibits cell elongation in the lower side of roots, but stimulates cell expansion in shoots, which causes shoots to grow upward.

Key Terms

- **amyloplast**: a non-pigmented organelle found in some plant cells that is responsible for the synthesis and storage of starch granules through the polymerization of glucose
- **statolith**: a specialized form of amyloplast involved in graviperception by plant roots and most invertebrates

- **gravitropism**: a plant's ability to change its growth in response to gravity

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39.3: Responses to Mechanical Stimuli

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39.3.1: Plant Responses to Wind and Touch

Learning Objectives

- Compare the ways plants respond to directional and non-directional stimuli

The shoot of a pea plant wraps around a trellis while a tree grows on an angle in response to strong prevailing winds. These are examples of how plants respond to touch or wind.

The movement of a plant subjected to constant directional pressure is called thigmotropism, from the Greek words thigma meaning “touch,” and tropism, implying “direction.” Tendrils are one example of this. A tendril is a specialized stem, leaf, or petiole with a threadlike shape that is used by climbing plants for support.The meristematic region of tendrils is very touch sensitive; light touch will evoke a quick coiling response. Cells in contact with a support surface contract, whereas cells on the opposite side of the support expand. Application of jasmonic acid is sufficient to trigger tendril coiling without a mechanical stimulus.



Figure **39.3.1.1**: Thigmotropism in a redvine: Tendrils of a redvine produce auxin in response to touching a support stick and then transfer the auxin to non-touching cells. The non-touching cells elongate faster to curl around the support stick.

A thigmonastic response is a touch response independent of the direction of stimulus. In the Venus flytrap, two modified leaves are joined at a hinge and lined with thin, fork-like tines along the outer edges. Tiny hairs are located inside the trap. When an insect brushes against these trigger hairs, touching two or more of them in succession, the leaves close quickly, trapping the prey. Glands on the leaf surface secrete enzymes that slowly digest the insect. The released nutrients are absorbed by the leaves, which reopen for the next meal.

Thigmomorphogenesis is a slow developmental change in the shape of a plant subjected to continuous mechanical stress. When trees bend in the wind, for example, growth is usually stunted and the trunk thickens. Strengthening tissue, especially xylem, is produced to add stiffness to resist the wind’s force. Researchers hypothesize that mechanical strain from wind, rain, or movement by other living things induces growth and differentiation to strengthen the tissues. Ethylene and jasmonate are likely involved in thigmomorphogenesis.

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Key Points

- When subjected to constant directional pressure, such as a trellis, plants move to grow around the object providing the pressure; this process is known as thigmotropism.
- Thigmonastic responses include opening and closing leaves, petals, or other parts of the plant as a reaction to touch.
- Through thigmomorphogenesis, plants change their growth in response to repeated mechanical stress from wind, rain, or other living things.

Key Terms

- **thigmotropism**: plant growth or motion in response to touch
- **thigmomorphogenesis**: the response by plants to mechanical sensation (touch) by altering their growth patterns
- **thigmonastic response**: a touch response independent of the direction of stimulus

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39.4: Responses to Water and Temperature

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39.4.1: Abscisic Acid

Learning Objectives

- Identify the locations of synthesis, transport, and actions of abscisic acid.
- Describe how ABA interacts with other plant hormones.

The plant hormone **abscisic acid** (ABA) was was once thought to be responsible for abscission; however, this is now known to be incorrect. Instead, ABA accumulates as a response to stressful environmental conditions, such as dehydration, cold temperatures, or shortened day lengths. Unlike animals, plants cannot flee from potentially harmful conditions like drought, freezing, exposure to salt water or salinated soil, and ABA plays in mediating adaptations of the plant to stress. Abscisic acid (Figure **39.4.1.1**) resembles the carotenoid zeaxanthin (Figure **39.4.1.2**), from which it is ultimately synthesized. It is produced in mature leaves and roots and transported through the vascular tissue.

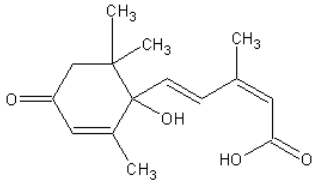


Figure **39.4.1.1**: Chemical structure of the plant hormone abscisic acid (ABA). Image by Socrtwo (public domain).

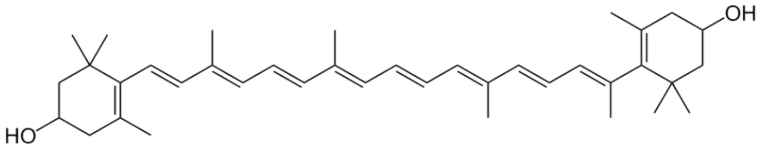


Figure **39.4.1.2**: The carotenoid zeaxanthin absorbs blue light and reflecting orange and red light. It is a precursor to abscisic acid. Image by Shaddack (public domain).

Maintaining Dormancy

Seed Maturation and Inhibition of Germination

Seeds are not only important agents of reproduction and dispersal, but they are also essential to the survival of annual and biennial plants. These angiosperms die after flowering and seed formation is complete. Abscisic acid is essential for seed maturation and also enforces a period of seed dormancy, by blocking germination and promoting the synthesis of storage proteins. It is important the seeds not germinate prematurely during unseasonably mild conditions prior to the onset of winter or a dry season. As the hormone gradually breaks down over winter, the seed is released from dormancy and germinates when conditions are favorable in spring. As discussed in the Environmental Responses chapter, other environmental cues such as exposure to a cold period, light, or water are often also needed to for germination to occur.

Interestingly, mangrove species with **viviparous germination**, meaning that seeds germinate while still attached to the parent plant have reduced levels of ABA during embryo formation, providing further evidence of ABA's role in maintain seed dormancy (Farnsworth and Farrant 1998, *Am J. Bot.)*. These mangroves are adapted to drop germinated seeds into surrounding water to be dispersed (Figure **39.4.1.3**).



Figure **39.4.1.3**: The elongated seedlings of the red mangrove, *Rhizophora mangle*, are still attached to the parent plant, illustrating viviparous germination. Image by M.elle F. Legendre (public domain).

Bud Dormancy

Another effect of ABA is to promote the development of winter buds; it mediates the conversion of the apical meristem into a dormant bud. The newly developing leaves growing above the meristem become converted into stiff bud scales that wrap the meristem closely and will protect it from mechanical damage and drying out during the winter. Abscisic acid in the bud also acts to enforce dormancy so if an unseasonably warm spell occurs before winter is over, the buds will not sprout prematurely. Only after a prolonged period of cold or the lengthening days of spring (photoperiodism) will bud dormancy be lifted.

Response to Water Stress

Stomatal Closure

Abscisic acid also regulates the short-term drought response. Recall that stomata are pores in the leaf and are surrounded by a pair of **guard cells**. Much of the water taken up by a plant is lost as water vapor exists stomata. Low soil moisture causes an increase in ABA, which causes stomata to close, reducing water loss. Note that stomatal closure also prevents exchange of oxygen and carbon dioxide, which is necessary for efficient photosynthesis (see Photorespiration and Phytosynthetic Pathways). The response to abscisic acid occurs *even if blue light is present*; that is, signaling from drought via ABA overrides the signaling from blue light to open stomata. See Transport for more details about stomatal opening and closure.

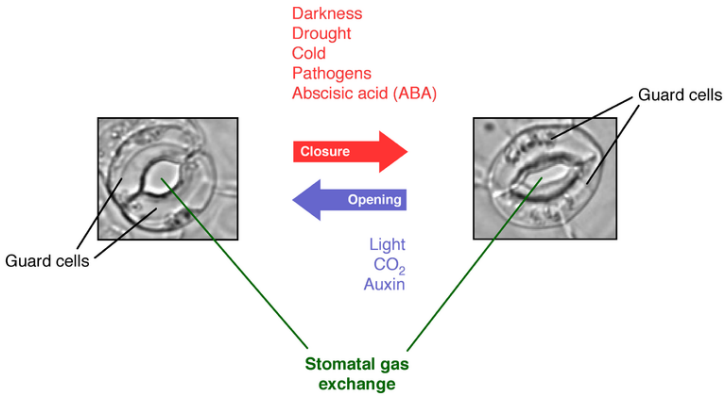


Figure **39.4.1.4**: Several factors mediate the opening and closure of stomata, which are surrounded by kidney-shaped guard cells. Stomatal gas exchange occurs through the stomata. Darkness, drought, cold, pathogens, and abscisic acid (ABA) mediate stomatal closure. Specifically, drought causes the releases of ABA, which signals stomata closure. Stomatal opening is triggered by light, carbon dioxide (CO_2), and auxin. Image by June Kwak, Pascal Mäser (public domain).

Cellular Protection from Dehydration

Abscisic acid turns on the expression of genes encoding proteins that protect cells - in seeds as well as in vegetative tissues - from damage when they become dehydrated.

Interactions with Other Hormones

At a cellular level, abscisic acid inhibits both cell division and cell expansion. It often opposes the growth-inducing effects of auxin and gibberellic acid. For example, abscisic acid prevents stem elongation probably by its inhibitory effect on gibberellic acid. In maintaining apical dominance, however, ABA synergizes with auxin. Abscisic acid moves up from the roots to the stem (opposite the flow of auxin) and suppresses the development of axillary buds. The result is inhibition of branching (maintaining apical dominance).

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39.5: Hormones and Sensory Systems

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39.5.1: Auxin

Learning Objectives

- Explain the mechanism of polar auxin transport.
- Identify locations of synthesis and actions of auxin.
- Define apical dominance and explain the role of auxin in maintaining it.
- Describe the commercial applications of auxin.
- Interpret and predict outcomes of experiments that demonstrate the action of auxin.

The term auxin is derived from the Greek word *auxein*, which means "to grow." While many synthetic auxins are used as herbicides, **indole-3-acetic acid** (**IAA**) is the only naturally occurring auxin that shows physiological activity (Figure **39.5.1.1**). Auxin is synthesized in apical meristems, young leaves, and developing seeds.

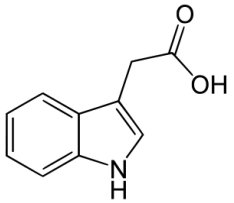


Figure **39.5.1.1**: Chemical structure of indole-3-acetic acid (IAA)

The Discovery of Auxin

Recall from the Tropisms section that the Boysen-Jensen experiment showed a chemical signal must be downward from the tip of the coleoptile tip along the shaded side, resulting in phototropism. Went extracted the chemical signal involved in the Boysen-Jensen experiment. He removed the tips of several coleoptiles of oat, *Avena sativa*, seedlings. He placed these on a block of agar for several hours. At the end of this time, the agar block itself was able to initiate resumption of growth of the decapitated coleoptile. The growth was vertical because the agar block was placed completely across the stump of the coleoptile and no light reached the plant from the side (Figure **39.5.1.2**). The unknown substance that had diffused from the agar block was named auxin. The amount of auxin in coleoptile tips was far too small to be purified and analyzed chemically. Therefore, a search was made for other sources of auxin activity.

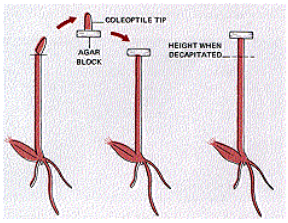


Figure **39.5.1.2**: Went's experiment showing that the coleoptile transferred a chemical signal (now know to be auxin) into an agar block. The agar block could then stimulate cell elongation in the absence of the coleoptile tip.

This search was aided by a technique called the *Avena* test developed by Went for determining the relative amount of auxin activity in a preparation. The material to be assayed is incorporated into an agar block, and the block is placed on one edge of a decapitated *Avena* coleoptile. As the auxin diffuses into that side of the coleoptile, it stimulates cell elongation and the coleoptile bends away from the block (Figure **39.5.1.3**). The degree of curvature, measured after 1.5 hours in the dark, is proportional to the amount of auxin activity (e.g., number of coleoptile tips used). The use of living tissue to determine the amount of a substance, such as in the *Avena* test, is called a **bioassay**.

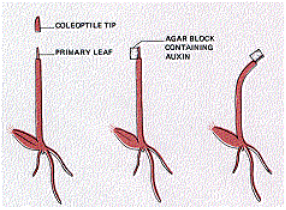


Figure **39.5.1.3**: In the *Avena* test, the coleoptile tip is removed. (The primary leaf pierces the coleoptile.) Plant tissue is then allowed to transfer the chemical signal (now know to be auxin) into an agar block. The agar block is then placed on one side of the coleoptile, resulting in bending in the absence of the coleoptile tip.

The *Avena* test soon revealed that substances with auxin activity occur widely in nature. One of the most potent was first isolated from human urine. It was **indole-3-acetic acid** (**IAA**) and turned out to be the auxin actually used by plants.

Auxin Transport

Auxin moves through the plant by two mechanisms, called polar and nonpolar transport.

Polar Transport

In contrast to the other major plant hormones, auxins can be transported in a specific direction (**polar transport**) through parenchyma cells. The cytoplasms of parenchyma cells are neutral (pH = 7), but the region outside the plasma membranes of adjacent cells (the **apoplast**) is acidic (pH = 5). When auxin is in the cytoplasm, it releases a proton and becomes an anion (IAA-). It cannot pass through hydrophobic portion of the plasma membrane as an anion, but it does pass through special auxin efflux transporters called **PIN proteins.** Eight different types of these transmembrane proteins have been identified so far. When IAA- enters the acidic environment of the apoplast, it is protonated, becoming IAAH. This uncharged molecule can then pass through the plasma membrane of adjacent cells through diffusion or via **influx transporters**. Once it enters the cytoplasm, it loses its proton, becoming IAA^- again. PIN proteins can be unevenly distributed around the cell (for example, only occurring on the bottom of the cell), which directs the flow of auxin (Figure **39.5.1.4**).

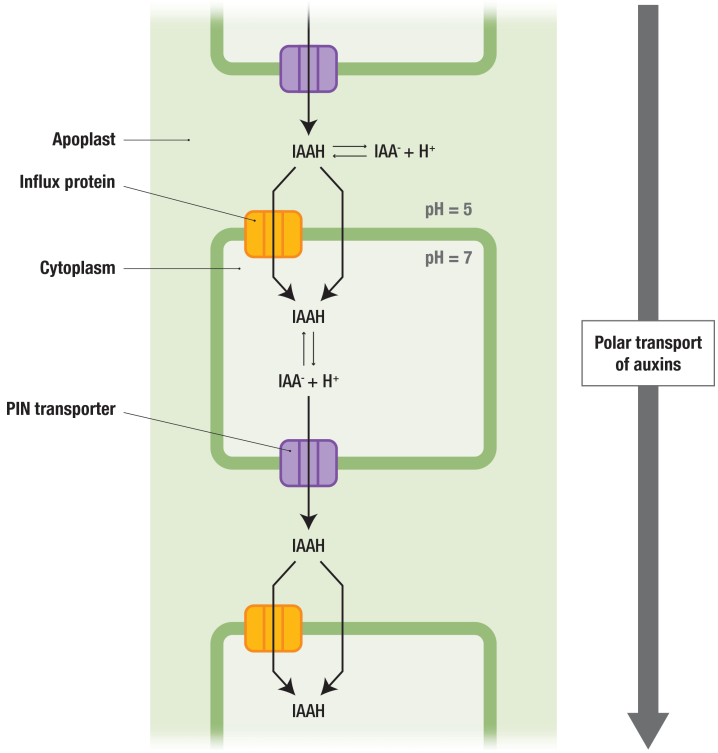


Figure 39.5.1.4: The polar transport of auxin. Auxin (IAAH) enters the cell through influx transporters (orange) or passes directly through the plasma membrane (not shown). In the cytoplasm (pH = 7), which has a higher pH than the apoplast (pH = 5), auxin dissociates to release a proton (H^+) and anion (IAA^-). It can no longer exit the cell through the way that it entered, but it can exit through PIN proteins (purple). In this example, PIN proteins are only on the lower side of the cell. Once IAA^- leaves the cell and enters the acidic apoplast, it binds to a proton becoming IAAH again. It then enters the next cells (below the first cell). This process continues, resulting in polar (unidirectional) transport. Image by Jen Valenzuela (CC-BY-NC).

Nonpolar Transport

Auxins can also be transported nondirectionally (**nonpolar transport**) through the phloem. It passes in the assimilate that translocates through the phloem from where it is synthesized (its "source", usually the shoot) to a "sink" (e.g., the root).

Actions of Auxin

Tropisms

Auxins are the main hormones responsible for phototropism and gravitropism. The auxin gradients that are required for these tropisms are facilitated by the movement of PIN proteins and the polar transport of auxin in response to environmental stimuli (light or gravity). Note that higher auxin concentration on one side of the stem typically causes that side of the stem to elongate; however, the effect is opposite in roots with higher auxin concentration inhibiting elongation (Figure 39.5.1.5).

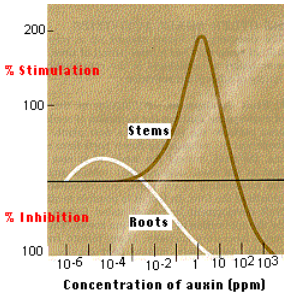


Figure 39.5.1.5: The graph (based on the work of K. V. Thimann) shows the effect of auxin concentration on root and stem growth. The x-axis shows the concentration of auxin in parts per million (ppm) on the log scale. The y-axis shows percent stimulation (positive) or inhibition (negative).The difference between the behavior of roots and stems lies in the difference in the sensitivity of their cells to auxin. Auxin concentrations high enough to stimulate stem growth (represented by a peak) inhibit root growth (represented by a dip).

Growth and Development

Embryo Development

Auxins play a role in embryo development. From the very first mitotic division of the zygote, gradients of auxin guide the patterning of the embryo into the parts that will become the organs of the plant, including the shoot apex, primary leaves, cotyledon(s), stem, and root.

Vascular Tissue Differentiation

They also control cell differentiation of vascular tissue.

Leaf Development and Arrangement

The formation of new leaves in the apical meristem is initiated by the accumulation of auxin. Already-developing leaves deplete the surrounding cells of auxin so that the new leaves do not form too close to them. In this way, the characteristic pattern of leaves in the plant is established. Auxin also controls the precise patterning of the epidermal cells of the developing leaf.

Root Initiation and Development

The localized accumulation of auxin in epidermal cells of the root initiates the formation of lateral or secondary roots. Auxin also stimulates the formation of **adventitious roots** in many species. Adventitious roots grow from stems or leaves rather than from the regular root system of the plant. Once a root is formed, a gradient of auxin concentration develops highest at the tip promoting the production of new cells at the meristem, and lowest in the region of differentiation, thus promoting the elongation and differentiation of root cells. The drop in auxin activity in the regions of elongation and differentiation is mediated by cytokinin — an auxin antagonist.

Shade Avoidance

Auxins stimulate cell elongation parts of the plants that have access to light as part of the shade-avoidance response (see Etiolation and Shade Avoidance).

Interactions with Other Growth-Regulating Hormones

Auxin is required for the function of other growth-regulating hormones such as **cytokinins**; cytokinins promote cell division, but only in the presence of auxin.

Apical Dominance

Apical dominance—the inhibition of **axillary bud** (lateral bud) formation—is triggered by downward transport of auxins produced in the apical meristem. Many plants grow primarily at a single apical meristem and have limited axillary branches (Figure 39.5.1.6). Growth of the shoot apical meristem (terminal shoot) usually inhibits the development of the lateral buds on the stem beneath. If the shoot apical meristem of a plant is removed, the inhibition is lifted, and axillary buds begin growth. However, if the apical meristem is removed and IAA applied to the stump, inhibition of the axillary buds is maintained (Figure 39.5.1.7). Gardeners exploit this principle by pruning the terminal shoot of ornamental shrubs, etc. The release of apical dominance enables lateral

branches to develop and the plant becomes bushier. The process usually must be repeated because one or two laterals will eventually outstrip the others and reimpose apical dominance.

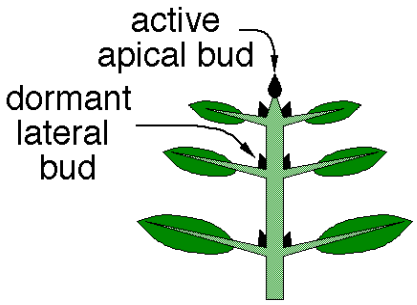


Figure **39.5.1.6**: The auxin produced by the shoot apical meristem (apical bud) inhibits the growth of the axillary (lateral) buds, maintaining apical dominance. Image by Doctor Smart (CC BY-SA).

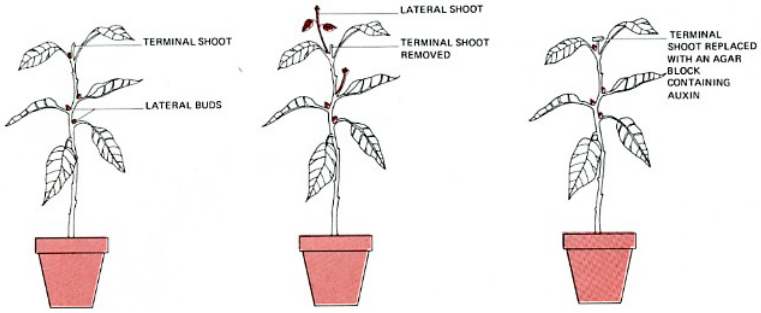


Figure **39.5.1.7**: The shoot apical meristem (terminal shoot) produces auxin and inhibits the growth of the axillary (lateral) buds, maintaining apical dominance (left). If the shoot apical meristem is removed, the axillary buds will growth into axillary (lateral) shoots (middle). If the shoot apical meristem is removed and replaced with an agar block containing axuin, apical dominance is maintained (right).

The common white potato also illustrates the principle of apical dominance. Note that a potato is a tuber, which is an underground stem modified for starch storage. As with an ordinary shoot, the potato has a terminal bud (containing the shoot apical meristem) or "eye" and several axillary (lateral) buds. After a long period of storage, the terminal bud usually sprouts but the other buds do not. However, if the potato is sliced into sections, one bud to a section, the axillary buds develop just as quickly as the terminal bud (Figure **39.5.1.8**).

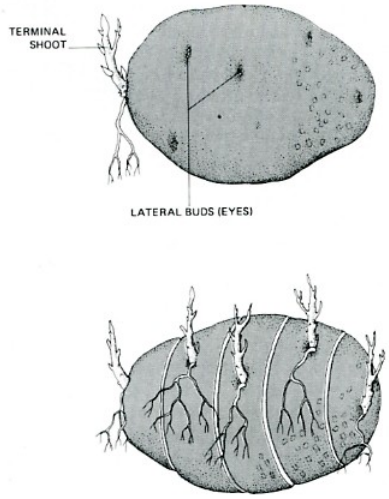


Figure **39.5.1.8**: The eyes of the potato illustrate apical dominance. Each eye of the potato is a bud. In the top image, the shoot apical meristem of the terminal shoot produces auxin that inhibits the growth of axillary (lateral) buds. In the bottom image, the potato is sliced into sections, apical dominance does not occur, and each axillary bud (lateral bud/eye) grows.

As will be discussed in the Abscisic Acid section, abscisic acid in the lateral buds inhibits production of auxin, and removal of the apical bud will release this inhibition of auxin, allowing the lateral buds to begin growing.

Flowering and Fruit Development

Auxins promote flowering and fruit setting and ripening. Pollination of the flowers of angiosperms initiates the formation of seeds. As the seeds mature, they release auxin to the surrounding flower parts, which develop into the fruit that covers the seeds.

Prevention of Abscission

Some plants drop leaves and fruits in response to changing seasons (based on temperatures, photoperiod, water, or other environmental conditions). This process is called **abscission**, and is regulated by interactions between **auxin** and **ethylene**. During the growing season, the young leaves and fruits produce high levels of auxin, which blocks activity of ethylene; they thus remain attached to the stem. As the seasons change, auxin levels decline and permit ethylene to initiate **senescence**, or aging (see Ethylene).

Figure **39.5.1.9** demonstrates the role of auxin in abscission. If the blade of the leaf is removed, as shown in the figure, the petiole remains attached to the stem for a few more days. The removal of the blade seems to be the trigger as an undamaged leaf at the same node of the stem remains on the plant much longer, in fact, the normal length of time. If, however, auxin is applied to the cut end of the petiole, abscission of the petiole is greatly delayed.

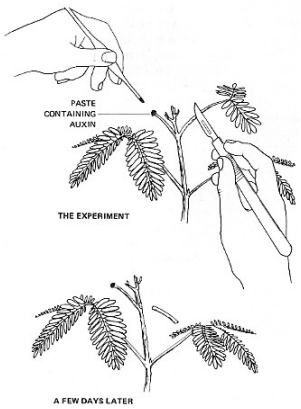


Figure **39.5.1.9**: This experiment shows that removal of the leaf blades from a *Mimosa* plant results in abscission of the petiole. Leaf blades produce auxin, which prevents abscission. When an auxin paste is applied to the petiole, abscission does not occur.

Mechanisms of Auxin Action

Auxin effects are mediated by two different pathways: immediate, direct effects on the cell and turning on of new patterns of gene expression. The arrival of auxin in the cytosol initiates such immediate responses as changes in the concentration of and movement of ions in and out of the cell and reduction in the redistribution of PIN proteins. At the cellular level, auxin generally increases the rate of cell division and longitudinal cell expansion. Some of the direct effects of auxin may be mediated by its binding to a cell-surface receptor designated **ABP1** ("Auxin-binding protein 1").

Many auxin effects are mediated by changes in the transcription of genes. Auxin enters the nucleus and binds to its receptor, a protein called **TIR1** ("transport inhibitor response protein 1") which now can bind to proteins responsible for attaching ubiquitin to one or another of several **Aux/IAA proteins**. This triggers the destruction of the Aux/IAA proteins by proteasomes. Aux/IAA proteins normally bind transcription factors called auxin response factors (**ARF**) **preventing** them from activating the promoters and other control sequences of genes that are turned on (or off) by auxin. Destruction of the Aux/IAA proteins **relieves** this inhibition, and gene transcription begins.

This mechanism is another of the many cases in biology where a pathway is turned on by inhibiting the inhibitor of that pathway (a double-negative is a positive). The presence in the cell of many different Aux/IAA proteins (29 in *Arabidopsis*), many different ARFs (23 in *Arabidopsis*) and several (~4) TIR1-like proteins provides a logical basis for mediating the different auxin effects that are described here, but how this is done remains to be discovered.

Commercial Applications of Auxins

Commercial use of auxins is widespread in for propagation in nurseries, crop production, and killing weeds. Horticulturists may propagate desirable plants by cutting pieces of stem and placing them base down in moist soil. Eventually adventitious roots grow

out at the base of the cutting. The process can often be hastened by treating the cuttings with a solution or powder containing a synthetic auxin.

Applying synthetic auxins to tomato plants in greenhouses promotes normal fruit development. Fruit growers often apply auxin sprays to cut down the loss of fruit from premature dropping. Additionally, outdoor application of auxin promotes synchronization of fruit setting and dropping to coordinate the harvesting season. Fruits such as seedless cucumbers can be induced to set fruit by treating unfertilized plant flowers with auxins.

Synthetic auxins are widely used as herbicides. Examples include **2,4-dichlorophenoxy acetic acid** (**2,4-D**) and **2,4,5-trichlorophenoxy acetic acid** (**2,4,5-T**), shown in Figure **39.5.1.10**. 2,4-D and its many variants are popular because they are **selective herbicides**, killing broad-leaved eudicots but not narrow-leaved monocots. (No one knows the basis of this selectivity). Why should a synthetic auxin kill the plant? It turns out that the auxin **influx transporter** works fine for 2,4-D, but that 2,4-D cannot leave the cell through the **efflux transporters**. Perhaps it is the resulting accumulation of 2,4-D within the cell that kills it. A mixture of 2,4,-D and 2,4,5-T was the "agent orange" used by the U.S. military to defoliate the forest in parts of South Vietnam. Because of health concerns, 2,4,5-T is no longer used in the U.S.

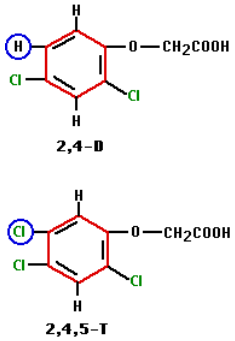


Figure **39.5.1.10**: Chemical structures of the synthetic auxins 2,4-D (top) and 2,4,5-T (bottom). As the formulas show, 2,4,5-T is 2,4-D with a third chlorine atom, instead of a hydrogen atom, at the #5 position in the benzene ring (circled and in blue).

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39.5.2: Cytokinins

Learning Objective

Identify the locations of synthesis, transport, and actions of cytokinins.

Cytokinins are plant hormones that promote **cytokinesis** (cell division) are derivatives of the purine adenine. (They are not to be confused with cytokines.) The effect of cytokinins was first reported when it was found that adding the liquid endosperm of coconuts to developing plant embryos in culture stimulated their growth. Without the cytokinins from the endosperm, plant cells would not divide by mitosis. Almost 200 naturally occurring or synthetic cytokinins are known to date. **Zeatin** is an example of naturally occurring cytokinin (Figure 39.5.2.1), and kinetin is an example of a synthetic cytokinin.

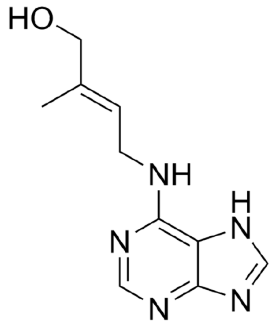


Figure 39.5.2.1: Zeatin, a naturally occurring cytokinin. Image by Edgar181 (public domain).

Cytokinins are synthesized in roots tips and other young structures where cell division is occurring such as embryos and fruits. They are also produced by wounded tissue. Cytokinins are transported through the xylem.

Actions of Cytokinins

One of the clearest examples of cytokinin stimulating cell division involves seed germination. The endosperm of monocot seeds, such as corn (maize), contains large stores of the precursor to the cytokinin zeatin. When the corn kernel germinates, zeatin moves from the endosperm to the root tip where it stimulates vigorous mitosis (Figure 39.5.2.2).



Figure 39.5.2.2: The root tips of these germinating wheat seedlings undergo rapid cell division induced by cytokinin. Image by Oksana Lastochkina (CC-BY).

Plant development is controlled by multiple hormones working together or balancing each other's effects. Cytokinins play an important role in plant development. They are involved in leaf formation, and they delay senescence in leaf tissues. Cytokinins also play a role in chloroplast development.

Cytokinins often counter the effects of auxin when regulating shoot and root development. Cytokinins inhibit apical dominance by stimulating axillary bud development, having the opposite effect as auxin. They inhibit the formation of lateral roots while auxin initiates lateral roots. When cytokinins are applied to a **callus** (mass of undifferentiated cells), shoots form. If auxin is applied, roots form. If the two hormones are applied in equal amounts, much the rate of cell division increases, but the callus does not produce distinct shoots and roots.

With respect to mediating roots gravitropism, however, the effect of cytokinin is similar to that of auxin. When a root is turned on its side, cytokinins accumulate on the lower side, inhibiting elongation there. As the upper surface of the root elongates, it bends downwards.

Mechanism of Cytokinin Action

Like auxins, cytokinin can cause changes in gene expression. To begin this process, a cytokinin binds to a receptor protein embedded in the plasma membrane of the cell. The internal portion of the receptor then attaches a phosphate group to a protein in the cytosol. This protein moves into the nucleus where it activates one or more nuclear transcription factors, which then bind to the promoters of genes. Transcription of these genes produces mRNAs that move out into the cytosol. Translation of these mRNAs produces the proteins that enable the cell to carry out its cytokine-induced function.

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39.5.3: Gibberellins

Learning Objectives

- Identify the locations of synthesis, transport, and actions of gibberellins.
- Interpret and predict the outcome of an experiment demonstrating the action of gibberellins.
- Describe the commercial applications of gibberellins.

During the 1930s Japanese scientists isolated a growth-promoting substance from cultures of a fungus that parasitizes rice plants. They called it gibberellin. **Gibberellins (GAs)** are a group of about 125 closely related plant hormones synthesized in the root and stem apical meristems, young leaves, and seed embryos. They are likely transported through the vascular tissue. One of the most active gibberellins - and one found as a natural hormone in the plants themselves - is **gibberellic acid** (**GA**; figure 39.5.3.1).

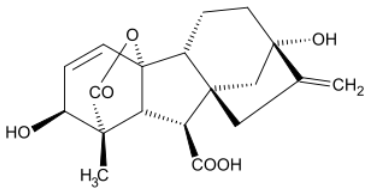


Figure 39.5.3.1: Chemical structure of the plant hormone gibberellic acid. Image by Minutemen (public domain).

Actions of Gibberellins

Several aspects of plant growth involve GAs, including stimulating shoot elongation, seed germination, and fruit and flower maturation. Other effects of GAs include gender expression (also see Ethylene) and the delay of senescence in leaves and fruit. Synthesis of gibberellins also helps grapevines climb up toward the light by causing meristems that would have developed into flowers to develop into **tendrils** instead.

Shoot elongation in this case results from both cell division and cell elongation. When applied in low concentrations to a bush or "dwarf" bean, the stem begins to grow rapidly. The length of the internodes becomes so great that the plant becomes indistinguishable from climbing or "pole" beans. GA seems to overcome the genetic limitations in many dwarf varieties.

Gibberellins break dormancy (a state of inhibited growth and development) in the seeds of plants that require exposure to cold or light to germinate. The seeds of some plant species rely on the imbibition (intake) of water to initiate germination. Intake of water activates gibberellins, which then signals to transcribe the gene encoding **amylase**, an enzyme that breaks down starches stored in the seed into simple sugars (note these final steps are identical to what occurs in phytochrome-regulated germination). Gibberellins also stimulate cell elongation of young roots during germination. When water is absent, germination in this pathway is blocked by a hormone called **abscisic acid,** which inhibits the activity of gibberellins. Thus gibberellins and abscisic acid act in opposition in regulating the the germination response.

Many plant species first produce a basal rosette of leaves. When daylength increase or the weather becomes cold, they **bolt,** producing a long stalk. Eventually, flowers and then fruits develop on this stalk. Gibberellins are responsible for inducing bolting (figure 39.5.3.2.



Figure 39.5.3.2: Arabidopsis thaliana plant as basal rosette (left). The plant on the right has bolted and started to flower. Gibberellins induce bolting. Left image by Quentin Groom (public domain), and right image by Frost Museum (CC-BY).

Mechanism of Gibberellin Action

Like auxins, gibberellins generally increase the rate of cell division and longitudinal cell expansion. Gibberellins also exert their effects by altering gene transcription through a mechanism similar to auxin in that a pathway is turned on by inhibiting the inhibitor of that pathway (a double-negative is a positive). First, Gibberellin enters the cell and binds to a soluble receptor protein called **GID1** ("gibberellin-insensitive dwarf mutant 1") which now can bind to a complex of proteins (**SCF**) responsible for attaching ubiquitin to one or another of several **DELLA proteins**. This triggers the destruction of the DELLA proteins by proteasomes. DELLA proteins normally bind gibberellin-dependent transcription factors, a prominent one is designated **PIF3/4**, **preventing** them from binding to the DNA of control sequences of genes that are turned on by gibberellin (also see Shade Avoidance and Etiolation).

The **dwarf** varieties of rice and wheat carry mutations related to GAs. In the case of rice, the mutation interfere with the synthesis of their gibberellins. The wheat mutation reduces is in the gene coding for a DELLA protein and reduce the plant's ability to respond to its own gibberellins. Dwarf varieties of sorghum and more recently maize (corn) also exist, but in these cases, the mutation interferes with auxin transport, not gibberellin activity.

Commercial Applications of Gibberellins

Gibberellin application assists with seedless grape production. Seedless grapes are obtained through standard breeding methods and contain inconspicuous seeds that fail to develop. Because GAs are produced by the seeds, and because fruit development and stem elongation are under GA control, these varieties of grapes would normally produce small fruit in compact clusters. Maturing grapes are routinely treated with GA to promote larger fruit size, as well as looser bunches (longer stems), which reduces the instance of mildew infection (Figure 39.5.3.3). Like auxins, GAs can be used commercially to induce fruit development in a variety of species.



Figure **39.5.3.3**: In grapes, application of gibberellic acid increases the size of fruit and loosens clustering. (credit: Bob Nichols, USDA)

Gibberellins have a few other commercial applications. They can be applied to artificially induce bolting and flowering, such that plants produce seeds earlier. Addition of gibberellic acid to the winter buds of peach trees helps break dormancy. In urban areas, GA antagonists are sometimes applied to trees under power lines to control growth and reduce the frequency of pruning.

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39.5.4: Ethylene

Learning Objectives

- Relate the chemical structure of ethylene to its mode of transport.
- Identify the locations of synthesis and actions of ethylene.
- Describe the commercial applications of ethylene.

Ethylene differs from other plant hormones in that it is a smaller and simpler molecule that is a volatile gas (Figure **39.5.4.1**). Hundreds of years ago, when gas street lamps were installed in city streets, trees that grew close to lamp posts developed twisted, thickened trunks and shed their leaves earlier than expected. These effects were caused by ethylene volatilizing from the lamps. Aging tissues, such as those that are wilting or ripening, and nodes of stems produce ethylene.

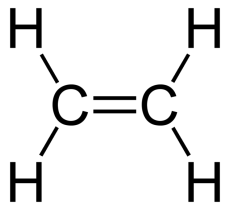


Figure **39.5.4.1**: The chemical structure of ethylene. Image by Benjah-bmm27 (public domain).

Actions of Ethylene

Ethylene has many functions, and its major functions are associated with **senescence**, or aging. This includes fruit ripening, flower wilting, and leaf and fruit **abscission**. Ethylene also promotes germination in some cereals and sprouting of bulbs and potatoes. It is responsible for drooping of leaves and sprouting of potato buds. In **monoecious** plants, ethylene promotes the production of female flowers where as gibberellic acid promotes male flower production. Ethylene mediates the **triple response**, which makes the shoots of seedlings that are buried under debris grow short and wide as well as bend horizontally. This makes it possible for the shoot to push through the debris. Ethylene causes stem elongation in rice and other plants that are submerged in water. It promotes the breakdown of abscisic acid (ABA) and thus relieves ABA's inhibition of gibberellic acid.

Fruit Ripening

As they approach maturity, many fruits (e.g., apples, oranges, avocados) release ethylene. During fruit ripening, ethylene stimulates the conversion of starch and acids to sugars. Some people store unripe fruit, such as avocados, in a sealed paper bag to accelerate ripening; the gas released by the first fruit to mature will speed up the maturation of the remaining fruit.

Abscission

Ethylene induces the abscission of leaves, fruits, and flower petals. When auxin levels decline, ethylene triggers senescence and ultimately programmed cell death at the site of leaf attachment to the stem. A special layer of cells — the **abscission layer** (abscission zone) — forms at the base of the petiole or fruit stalk (Figure **39.5.4.2**). In petioles of some plants, there are two parts of the abscission layer: the more distal separation layer and more proximal protective layer. Before abscission occurs, nutrients are absorbed into the stem so that they are not lost with the leaf. As the separation layer breaks down, the leaf breaks free at this point and leaf falls to the ground in a controlled manner without harming the rest of the plant. The protective layer, which was reinforced with suberin, serves as a seal.

Leaf abscission is particularly important for temperate deciduous trees in the autumn. This is a vital response to the onset of winter when ground water is frozen - and thus cannot support transpiration - and snow load would threaten to break any branches still in leaf.

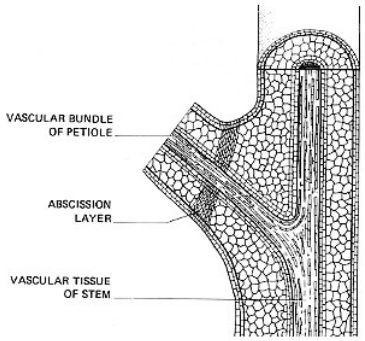


Figure **39.5.4.2**: The abscission layer forms at the base of a petiole (as shown) or fruit stalk, ultimately allowing leaves or fruits to fall from the stem. Vascular tissue passes through the center of the stem and petiole. The abscission layer is a dark band of cells at the base of the petiole.

In drought conditions, the immediate response is closing stomata (see Abscisic Acid). However, because closed stomata prevent gas exchange, plants will die if the stomata remain closed for too long. Thus if a drought persists for too long, the plant will begin sacrificing certain areas by allowing the leaves or stems to die in localized regions. This process may be regulated by ethylene, which can induce localized cell death under certain conditions.

Mechanism of Ethylene Action

At a cellular level, ethylene can inhibit or promote cell division. It sometimes inhibits cell expansion. In other circumstances, it stimulates lateral cell expansion. The presence of ethylene is detected by transmembrane receptors in the endoplasmic reticulum (ER) of cells. Binding of ethylene to these receptors unleashes a signaling cascade that leads to activation of transcription factors and the turning on of gene transcription.

Commercial Applications of Ethylene

Ethylene is widely used in agriculture. Commercial fruit growers can buy equipment to generate ethylene so that their harvest ripens quickly and uniformly. Horticulturalists inhibit leaf dropping in ornamental plants by removing ethylene from greenhouses using fans and ventilation.

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39.5.5: Abscisic Acid

Learning Objectives

- Identify the locations of synthesis, transport, and actions of abscisic acid.
- Describe how ABA interacts with other plant hormones.

The plant hormone **abscisic acid** (ABA) was was once thought to be responsible for abscission; however, this is now known to be incorrect. Instead, ABA accumulates as a response to stressful environmental conditions, such as dehydration, cold temperatures, or shortened day lengths. Unlike animals, plants cannot flee from potentially harmful conditions like drought, freezing, exposure to salt water or salinated soil, and ABA plays in mediating adaptations of the plant to stress. Abscisic acid (Figure **39.5.5.1**) resembles the carotenoid zeaxanthin (Figure **39.5.5.2**), from which it is ultimately synthesized. It is produced in mature leaves and roots and transported through the vascular tissue.

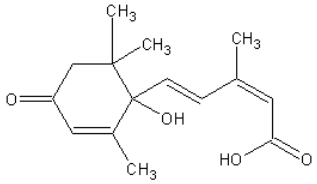


Figure **39.5.5.1**: Chemical structure of the plant hormone abscisic acid (ABA). Image by Socrtwo (public domain).

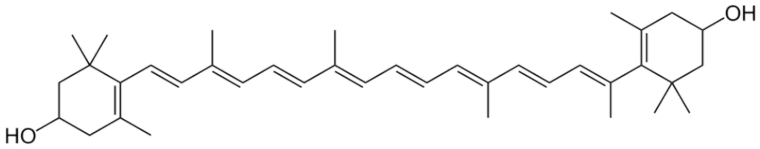


Figure **39.5.5.2**: The carotenoid zeaxanthin absorbs blue light and reflecting orange and red light. It is a precursor to abscisic acid. Image by Shaddack (public domain).

Maintaining Dormancy

Seed Maturation and Inhibition of Germination

Seeds are not only important agents of reproduction and dispersal, but they are also essential to the survival of annual and biennial plants. These angiosperms die after flowering and seed formation is complete. Abscisic acid is essential for seed maturation and also enforces a period of seed dormancy, by blocking germination and promoting the synthesis of storage proteins. It is important the seeds not germinate prematurely during unseasonably mild conditions prior to the onset of winter or a dry season. As the hormone gradually breaks down over winter, the seed is released from dormancy and germinates when conditions are favorable in spring. As discussed in the Environmental Responses chapter, other environmental cues such as exposure to a cold period, light, or water are often also needed to for germination to occur.

Interestingly, mangrove species with **viviparous germination**, meaning that seeds germinate while still attached to the parent plant have reduced levels of ABA during embryo formation, providing further evidence of ABA's role in maintain seed dormancy (Farnsworth and Farrant 1998, *Am J. Bot.)*. These mangroves are adapted to drop germinated seeds into surrounding water to be dispersed (Figure **39.5.5.3**).



Figure **39.5.5.3**: The elongated seedlings of the red mangrove, *Rhizophora mangle*, are still attached to the parent plant, illustrating viviparous germination. Image by M.elle F. Legendre (public domain).

Bud Dormancy

Another effect of ABA is to promote the development of winter buds; it mediates the conversion of the apical meristem into a dormant bud. The newly developing leaves growing above the meristem become converted into stiff bud scales that wrap the meristem closely and will protect it from mechanical damage and drying out during the winter. Abscisic acid in the bud also acts to enforce dormancy so if an unseasonably warm spell occurs before winter is over, the buds will not sprout prematurely. Only after a prolonged period of cold or the lengthening days of spring (photoperiodism) will bud dormancy be lifted.

Response to Water Stress

Stomatal Closure

Abscisic acid also regulates the short-term drought response. Recall that stomata are pores in the leaf and are surrounded by a pair of **guard cells**. Much of the water taken up by a plant is lost as water vapor exists stomata. Low soil moisture causes an increase in ABA, which causes stomata to close, reducing water loss. Note that stomatal closure also prevents exchange of oxygen and carbon dioxide, which is necessary for efficient photosynthesis (see Photorespiration and Phytosynthetic Pathways). The response to abscisic acid occurs *even if blue light is present*; that is, signaling from drought via ABA overrides the signaling from blue light to open stomata. See Transport for more details about stomatal opening and closure.

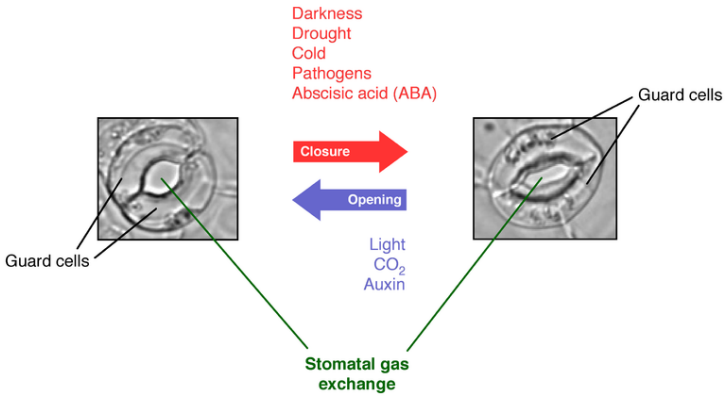


Figure **39.5.5.4**: Several factors mediate the opening and closure of stomata, which are surrounded by kidney-shaped guard cells. Stomatal gas exchange occurs through the stomata. Darkness, drought, cold, pathogens, and abscisic acid (ABA) mediate stomatal closure. Specifically, drought causes the releases of ABA, which signals stomata closure. Stomatal opening is triggered by light, carbon dioxide (CO_2), and auxin. Image by June Kwak, Pascal Mäser (public domain).

Cellular Protection from Dehydration

Abscisic acid turns on the expression of genes encoding proteins that protect cells - in seeds as well as in vegetative tissues - from damage when they become dehydrated.

Interactions with Other Hormones

At a cellular level, abscisic acid inhibits both cell division and cell expansion. It often opposes the growth-inducing effects of auxin and gibberellic acid. For example, abscisic acid prevents stem elongation probably by its inhibitory effect on gibberellic acid. In maintaining apical dominance, however, ABA synergizes with auxin. Abscisic acid moves up from the roots to the stem (opposite the flow of auxin) and suppresses the development of axillary buds. The result is inhibition of branching (maintaining apical dominance).

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39.5.6: Other Signaling Molecules

Learning Objectives

- Identify several signaling molecules beyond the five major plant hormones and describe their effects.
- Distinguish between the hypersensitive response and systemic acquired response.
- Explain the mechanisms by which signaling compounds aid in plant defense against pathogens and herbivores.

Recent research has discovered a number of compounds that also influence plant development. Their roles are less understood than the effects of the major hormones described so far.

Brassinosteroids

Brassinosteroids (Figure 39.5.6.1) are synthesized primarily in young tissues are important to many developmental and physiological processes. In fact, many sources considere them the sixth major plant hormones. Unlike the hormones discussed previously, brassinosteroids do not travel far from their site of synthesis. Signals between these compounds and other hormones, notably auxin and GAs, amplifies their physiological effect. Apical dominance, seed germination, gravitropism, lateral root formation, differentiation of cells in the vascular tissue, and resistance to freezing are all positively influenced by brassinosteroids. Root growth and fruit dropping are inhibited by steroids.

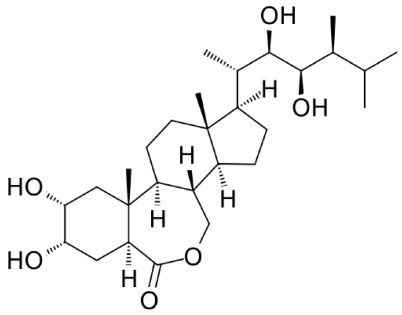


Figure 39.5.6.1: Brassinolide, an example of a brassinosteroid. Image by Wostr (public domain).

Systemin

Systemin, named for the fact that it is distributed systemically (everywhere) in the plant body upon production, is a short polypeptide that activates plant responses to wounds from **herbivores** (animals that feed on plant parts). It causes the plant to produce **jasmonic acid** (see below).

Jasmonates

Jasmonates play a major role in defense responses to herbivory (Figure 39.5.6.2). Their levels increase when a plant is wounded by an herbivore, resulting in an increase in toxic secondary metabolites. For example, **jasmonic acid** (Figure 39.5.6.3) also induces transcription of protease inhibitors. Protease inhibitors both taste bad and prevent breakdown of proteins in the herbivore's gut, thus making the insect sick and deterring further herbivory. Jasmonates also contribute to the production of volatile compounds that attract natural enemies of herbivores. Chewing of tomato plants by caterpillars leads to an increase in jasmonic acid levels, which in turn triggers the release of volatile compounds that attract predators of the pest. Jasmonates also elicit the synthesis of volatile compounds that attract parasitoids, which are insects that spend their developing stages in or on another insect, and eventually kill their host.



Figure **39.5.6.2**: Jasmonic acid mediates plant defense against herbivores such as this tobacco hornworm (*Manduca sexta*). Image by Scot Nelson (public domain).

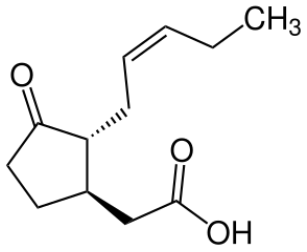


Figure **39.5.6.3**: The chemical structure of jasmonic acid. Image by Minutemen (public domain).

Jasmonates also work with systemin to mediate responses to drought, damage by ground-level ozone, and ultraviolet light.

Salicylic Acid

Salicylic acid resembles aspirin (Figure **39.5.6.4**) and is important for plant defense. It initiates the a systemic (whole body) response called the **systemic acquired response** (SAR) as a response to infection by parasites or pathogens. When a parasite or pathogen infects a cell, there is an specific, localized response called the **hypersensitive response** (HR). Following this very localized response, the plant initiates a systemic (whole body) response called the systemic acquired response (SAR). Salicylic acid is produced and converted to **methyl salicylate** (Figure **39.5.6.4**) inducing the SAR in response to the HR. The SAR activates transcription of general "**pathogenesis-resistance**" genes, which are *not* pathogen-specific (unlike in the hypersensitive response), but serve as general defense against pathogenic infection. The SAR is slower than the hypersensitive response, and also differs in that it is systemic instead of localized to the site of the infection.

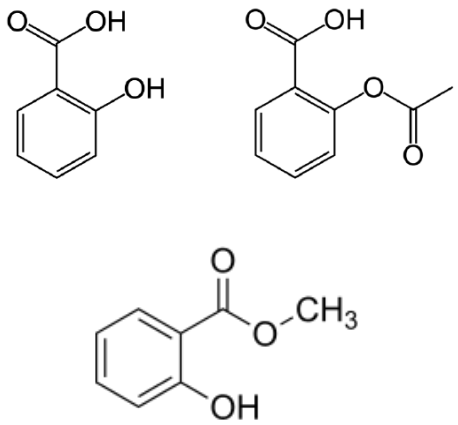


Figure **39.5.6.4**: Salicylic acid (left) resembles aspirin, or acetylsalicylic acid (right). In acetylsalicylic acid, an acetyl group ($COCH_3$) has replaced the hydrogen in the hydroxyl group (OH) of salicylic acid. Methyl salicylate (bottom) has a similar structure to salicylic acid, but a methyl group (CH_3) has replaced the hydrogen in the carboxyl group (COOH). Left image by Fvasconcellos (public domain), right image by Benjah-bmm27 (public domain), and bottom image by Emeldir (public domain).

Similar to jasmonic acid, salicylic acid can mediates defense against insect herbivores. It is directly toxic to some herbivores. Additionally, in response to herbivory, salicylic acid can be converted to methyl salicylate, which is released as a gas. This volatile compound can attract natural predators and parasites of the herbivores.

Some plants, such as skunk cabbage (Figure 39.5.6.5) and elephant yam, are adapted to flower while snow still covers the ground. Salicylic acid mediates their ability to produce heat to melt the snow around them. Such plants are thus called **thermogenic** ("heat producing").



Figure 39.5.6.5: Skunk-cabbage (*Symplocarpus foetidus*) is a thermogenic plant, producing heat that melts the snow surrounding it. This process is mediated by salicylic acid. Image by John Winkelman (CC-BY).

Oligosaccharins

Oligosaccharins are short chains of simple sugars that play a role in plant defense against bacterial and fungal infections. They act locally at the site of injury, and can also be transported to other tissues.

Strigolactones

Strigolactones (Figure 39.5.6.6) promote seed germination in some species and inhibit lateral apical development in the absence of auxins. Strigolactones also play a role in the establishment of mycorrhizae, a mutualistic association of plant roots and fungi.

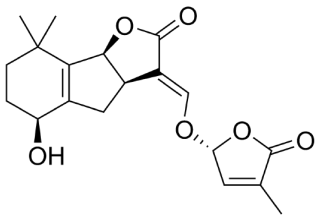


Figure 39.5.6.6: The chemical structure of (+)-strigol, a strigolactone.

Florigen

Florigen is a systemic signal that initiates flowering. It is also involved in the formation of storage organs and contributes to plant architecture. It is synthesized in leaves and transported to the shoot apical meristem (SAM) where it promotes flowering in response to daylength cues. At the molecular level, florigen is represented as a protein product encoded by the *FLOWERING LOCUS T* (*FT*) gene, which is highly conserved (occurs/has a similar genetic sequence in) across flowering plants.

Florigen is considered one of the important targets for crop improvement. Regulation of flowering time is an important target for plant breeding because the control of flowering to a favorable time provides successful grain production in a given cropping area. Flowering at unfavorable seasons causes loss of yield due to insufficient growth of photosynthetic organs or poor fertility due to heat or cold stress during reproduction. Thus, understanding florigen function can contribute to novel breeding techniques in crops to produce cultivars that can start their reproductive stage at optimal seasons.

Supplemental Reading

Filgueiras, C. C., Martins, A. D., Pereira, R. V., & Willett, D. S. (2019). The Ecology of Salicylic Acid Signaling: Primary, Secondary and Tertiary Effects with Applications in Agriculture. *International journal of molecular sciences*, *20* (23), 5851. https://doi.org/10.3390/ijms20235851

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CHAPTER OVERVIEW

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40.8: Plant Life Spans

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40.1: Reproductive Development

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40.1.1: Plant Growth

Growth in plants occurs chiefly at **meristems** where rapid **mitosis** provides new cells. As these cells differentiate, they provide new plant tissue.

Stem Growth

In **stems**, mitosis in the **apical meristem** of the shoot apex (also called the **terminal bud**) produces cells that enable the stem to grow longer and, periodically, cells that will give rise to leaves. The point on the stem where leaves develop is called a **node**. The region between a pair of adjacent nodes is called the **internode**. The internodes in the **terminal bud** are very short so that the developing leaves grow above the apical meristem that produced them and thus protect it. New meristems, the **lateral buds**, develop at the nodes, each just above the point where a leaf is attached. When the lateral buds develop, they produces new stem tissue, and thus **branches** are formed.

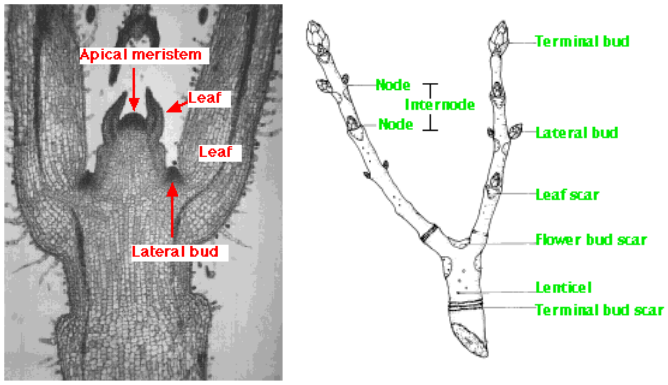


Figure 16.4.1.2 Horse chestnut

Under special circumstances (such as changes in photoperiod), the apical meristem is converted into a **flower bud**. This develops into a flower. The conversion of the apical meristem to a flower bud "uses up" the meristem so that no further growth of the stem can occur at that point. However, lateral buds behind the flower can develop into branches.

The drawing is of a typical woody dicot, the horse chestnut, as seen during the dormant season. The leaves have dropped off, leaving a **leaf scar**; the dots inside each leaf scar show where the vascular bundles (xylem and phloem) had entered the petiole of the leaf. A flower had been produced the season before, so that during the season just ended two branches had grown out on either side of the **flower bud scar**. **Lenticels** are openings that allow oxygen and carbon dioxide to diffuse between the living cells of the stem and the air.

The growth of roots in described in a separate page,

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40.2: Making Flowers

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40.2.1: Flowering

The flowering plants (angiosperms) go through a phase of **vegetative growth** producing more stems and leaves and a flowering phase where they produce the organs for sexual reproduction. In "**annuals**", like the snapdragon, the vegetative phase begins with germination of the seed. Flowering follows and ends with the senescence and death of the plant. In **biennials**, the vegetative phase takes up the first year; flowering followed by death occurs the second year. In **perennials**, flowering typically occurs year after year when conditions are appropriate.

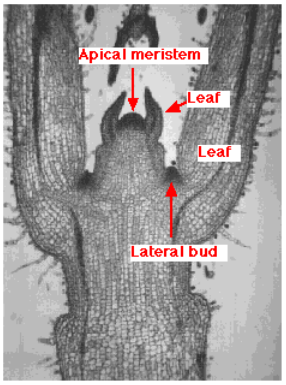


Figure 16.4.5.1 Meristem

Vegetative growth of the above-ground part of the plant — the **shoot** — occurs at the **apical meristem**. This is a mass of undifferentiated cells at the tip of the stem. Mitosis of these cells produces cells that differentiate to form more stem, leaves and **secondary meristems**. Also called **lateral buds**, these form in the axils of the leaves and will form branches.

The Signal to Flower

Flowering involves the conversion of the apical meristem into a **floral meristem**, from which all the parts of the flower will be produced. Signals that change the fate of the apical meristem include:

- maturity of the plant
- temperature
- the arrival of the plant hormone gibberellin
- for many plants, **photoperiod** - the relative length of day and night.

Temperature

Many annual plants (e.g., winter wheat) and biennial plants have their time of flowering delayed unless they have undergone a preceding period of wintertime cold. The change brought about by this prolonged exposure to the cold is called **vernalization**.

In the "model" plant *Arabidopsis thaliana*, vernalization works like this.

- A gene designated *Flowering Locus C* (*FLC*) encodes a transcription factor that blocks the expression of the genes needed for flowering.
- The level of FLC mRNA is high in the fall.
- But with the onset of cold temperatures, production of an antisense transcript of *FLC* (called *COOLAIR*) increasesas does, later, a sense transcript of part of the *FLC* gene.
- Both of these RNAs are non-coding; that is, they are not translated into protein.
- But they cooperate in suppressing the production of FLC mRNA and its translation into FLC protein.
- With the arrival of spring, there is no FLC protein remaining to suppress flowering so flowering can begin.

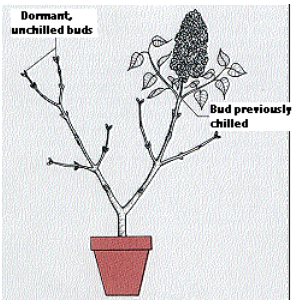


Figure 16.4.5.2 Lilac

The buds of many species of woody angiosperms found in temperate climates, such as apples and lilacs, also need a preceding period of cold weather before they can develop into flowers. So these plants cannot be grown successfully at lower latitudes because the winters never get cold enough (a few days at 0–10°C). This bud dormancy is localized. Prior chilling of one bud on a lilac stem enables it to flower while the other, nonchilled, buds on the stem remain dormant.

Photoperiod

Photoperiod is detected in the leaves. The cocklebur, drawn here, needs at least 8.5 hours of darkness in order to flower. Even if only a part of one leaf is exposed to the correct photoperiod, the entire plant will bloom (middle figure).

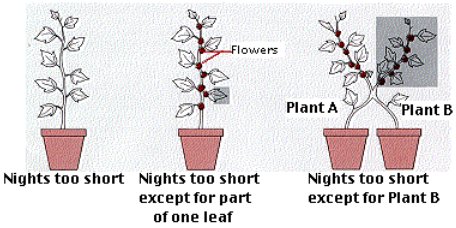


Figure 16.4.5.3 Photoperiod demonstration

The leaves produce a chemical signal called **florigen** that is transmitted to the apical meristems to start their conversion into floral meristems. The right-hand drawing shows that grafting a cocklebur (**B**) that receives the required period of darkness to one (**A**) that does not causes flowering in both. Evidently the florigen signal passes from **B** to **A** through their connected vascular systems.

The chemical nature of florigen has been sought for decades. The most recent evidence suggests that at least one component is the protein encoded by the gene *FLOWERING LOCUS T* (***FT***).

Converting the Apical Meristem to a Floral Meristem

In the nucleus of the meristem cells, the FT protein binds to the transcription factor **FD** and turns on the expression of genes needed for flowering, e.g., ***APETALA1*** and ***LEAFY***.

Structure of the Flower

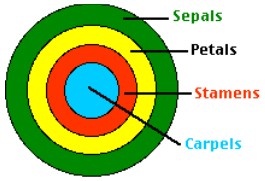


Figure 16.4.5.4 Floral meristem

The floral meristem differentiates into four concentric groups of cells that form the four parts of the flower.

1. The cells in whorl **1** develop into a whorl of **sepals**. These form at the lowest level. Collectively they make up the **calyx**.
2. Whorl **2** forms above the calyx, forming the **petals**. Collectively these make up the **corolla** of the flower (the part that most ornamentals are grown for).
3. Whorl **3** develops into the **stamens**, the **male** reproductive organs.
4. The innermost whorl, **4**, forms **carpels**, the female reproductive organs. Carpels often fuse to form a single structure, which some botanists call the **pistil**.

What triggers the various parts of the floral meristem to enter one or another of these four developmental pathways?

The ABC Model of Flower Development

Genetic analysis of mutants especially those found in the dicots ***Arabidopsis thaliana*** and in the snapdragon (***Antirrhinum***) support the ABC model of flowering. This model postulates a group of genes that encode the transcription factors needed to turn on the genes for sepal, petal, etc. development. The "master switches" fall into 3 groups: **A**, **B**, and **C**.

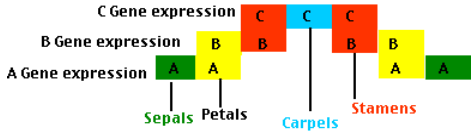


Figure 16.4.5.5 ABC Model

These are the rules:

- Cells in which only **A genes** are expressed develop into **sepals**. This occurs at the lowest level of the floral meristem.
- Cells in which both **A and B genes** are expressed develop into **petals**. This occurs at the next higher level.
- Expression of **B and C genes** turns on the developmental program to form **stamens**.
- Expression of **C genes** alone turns on the development of **carpels** in the innermost band of cells.

Examples of A, B and C group genes involved in flowering - these have been identified in ***Arabidopsis thaliana***

A group	***APETALA1*** (***AP1***) and ***APETALA2*** (***AP2***)
B group	***APETALA3*** (***AP3***) and ***PISTILLATA*** (***PI***)
C group	***AGAMOUS*** (***AG***)

The transcription factor **LEAFY** plays a major role in turning on the A, B, and C group genes in the appropriate locations.

- The LEAFY protein **alone** turns on ***AP1*** in whorls **1** and **2**.
- LEAFY plus a protein encoded by the gene ***UFO*** (for "unusual floral organs") turn on ***AP3*** in whorls **2** and **3**.
- LEAFY and a second, still unidentified, protein turn on ***AG*** in whorls **3** and **4**.

If LEAFY protein alone is sufficient to turn on *AP1*, why isn't *AP1* expressed in all four whorls?

The answer: **AGAMOUS** blocks the expression of ***AP1***, so any cell expressing AGAMOUS cannot express AP1. In fact, the antagonism is reciprocal: AP2 in whorls 1 and 2 (A group) inhibits AGAMOUS so the gene expression in whorls 3 and 4 remains distinct from that in whorls 1 and 2.

The proteins encoded by ***APETALA3*** and ***PISTILLATA*** (Group B) form a heterodimer that binds to

- the **APETALA1** protein to form **petals**
- the **AGAMOUS** protein to form **stamens**

Aided by a fourth transcription factor encoded by the gene *SEPALLATA3*, these quaternary complexes bind to specific sequences of DNA turning on the expression of the various genes needed to form whorls 2 and 3. Further research may reveal similar behavior for the other genes.

SEPALLATA3 (*SEP3*) is one of four *SEP* genes in Arabidopsis. If all but *SEP4* are inactivated, a flower with only sepals is formed (hence the name). If all four are inactivated, no flowers are formed at all.

So formation of a flower requires a **cascade of sequential gene activity** that gradually converts a mass of undifferentiated cells (the apical meristem) into the parts of a flower. The genes encode transcription factors that act as master switches, turning on (or off) downstream genes that ultimately make each part of the flower in its appropriate location. This same strategy of genetic control of developmental pathways is seen in animal development.

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40.3: Structure and Evolution of Flowers

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40.3.1: Sexual Reproduction in Angiosperms

Learning Objectives

- Outline the components of a flower and their function

The lifecycle of angiosperms follows the alternation of generations. In the angiosperm, the haploid gametophyte alternates with the diploid sporophyte during the sexual reproduction process of angiosperms. Flowers contain the plant's reproductive structures.

Flower Structure

A typical flower has four main parts, or whorls: the calyx, corolla, androecium, and gynoecium. The outermost whorl of the flower has green, leafy structures known as sepals, which are collectively called the calyx, and help to protect the unopened bud. The second whorl is comprised of petals, usually brightly colored, collectively called the corolla. The number of sepals and petals varies depending on whether the plant is a monocot or dicot. Together, the calyx and corolla are known as the perianth. The third whorl contains the male reproductive structures and is known as the androecium. The androecium has stamens with anthers that contain the microsporangia. The innermost group of structures in the flower is the gynoecium, or the female reproductive component(s). The carpel is the individual unit of the gynoecium and has a stigma, style, and ovary. A flower may have one or multiple carpels.

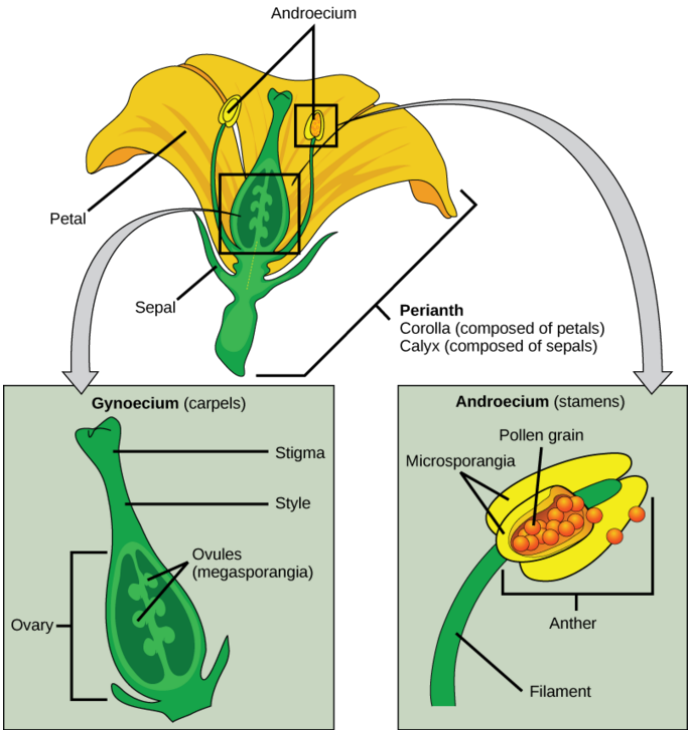


Figure **40.3.1.1**: Structures of the flower: The four main parts of the flower are the calyx, corolla, androecium, and gynoecium. The androecium is the sum of all the male reproductive organs, and the gynoecium is the sum of the female reproductive organs.

If all four whorls are present, the flower is described as complete. If any of the four parts is missing, the flower is known as incomplete. Flowers that contain both an androecium and a gynoecium are called perfect, androgynous, or hermaphrodites. There are two types of incomplete flowers: staminate flowers contain only an androecium; and carpellate flowers have only a gynoecium.



Figure **40.3.1.1**: Staminate and carpellate flowers: The corn plant has both staminate (male) and carpellate (female) flowers. Staminate flowers, which are clustered in the tassel at the tip of the stem, produce pollen grains. Carpellate flower are clustered in the immature ears. Each strand of silk is a stigma. The corn kernels are seeds that develop on the ear after fertilization. Also shown is the lower stem and root.

If both male and female flowers are borne on the same plant (e.g., corn or peas), the species is called monoecious (meaning “one home”). Species with male and female flowers borne on separate plants (e.g., *C. papaya* or *Cannabis*)are termed dioecious, or “two homes.” The ovary, which may contain one or multiple ovules, may be placed above other flower parts (referred to as superior); or it may be placed below the other flower parts (referred to as inferior).

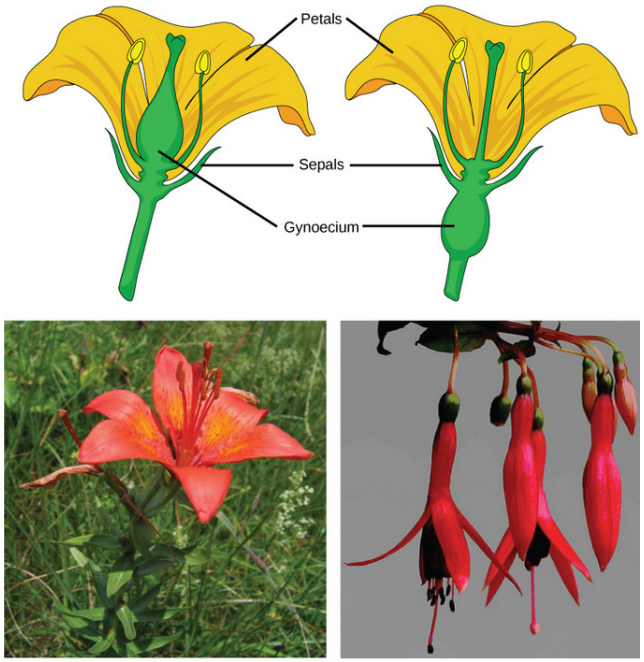


Figure **40.3.1.1**: Superior and inferior flowers: The (a) lily is a superior flower, which has the ovary above the other flower parts. (b) Fuchsia is an inferior flower, which has the ovary beneath other flower parts.

Male Gametophyte

The male gametophyte develops and reaches maturity in an immature anther. In a plant's male reproductive organs, development of pollen takes place in a structure known as the microsporangium. The microsporangia, usually bi-lobed, are pollen sacs in which the microspores develop into pollen grains.

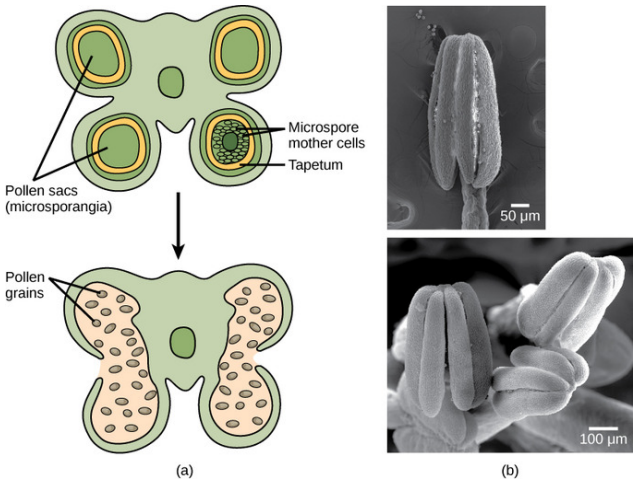


Figure **40.3.1.1**: Microsporangium: Shown is (a) a cross section of an anther at two developmental stages. The immature anther (top) contains four microsporangia, or pollen sacs. Each microsporangium contains hundreds of microspore mother cells that will each give rise to four pollen grains. The tapetum supports the development and maturation of the pollen grains. Upon maturation of the pollen (bottom), the pollen sac walls split open and the pollen grains (male gametophytes) are released. (b) In these scanning electron micrographs, pollen sacs are ready to burst, releasing their grains.

Within the microsporangium, the microspore mother cell divides by meiosis to give rise to four microspores, each of which will ultimately form a pollen grain. An inner layer of cells, known as the tapetum, provides nutrition to the developing microspores, contributing key components to the pollen wall. Mature pollen grains contain two cells: a generative cell and a pollen tube cell. The generative cell is contained within the larger pollen tube cell. Upon germination, the tube cell forms the pollen tube through which the generative cell migrates to enter the ovary. During its transit inside the pollen tube, the generative cell divides to form two male gametes. Upon maturity, the microsporangia burst, releasing the pollen grains from the anther.

Each pollen grain has two coverings: the exine (thicker, outer layer) and the intine. The exine contains sporopollenin, a complex waterproofing substance supplied by the tapetal cells. Sporopollenin allows the pollen to survive under unfavorable conditions and to be carried by wind, water, or biological agents without undergoing damage.

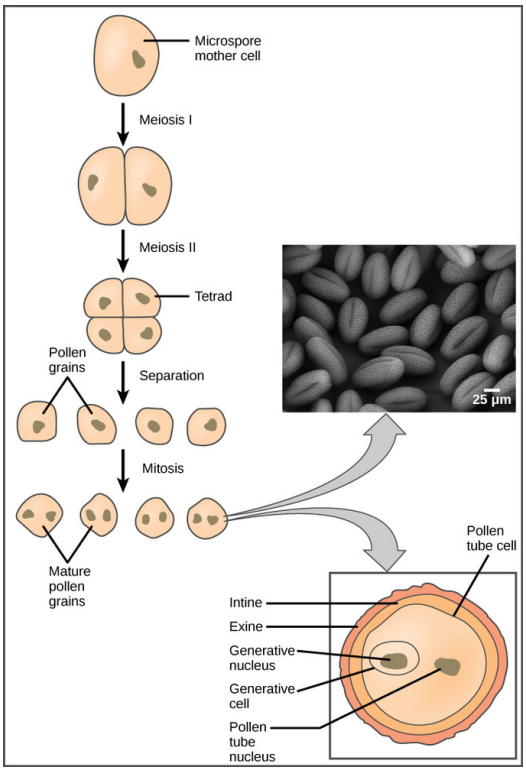


Figure 40.3.1.1: Pollen grain structure: Pollen develops from the microspore mother cells. The mature pollen grain is composed of two cells: the pollen tube cell and the generative cell, which is inside the tube cell. The pollen grain has two coverings: an inner layer (intine) and an outer layer (exine). The inset scanning electron micrograph shows *Arabidopsis lyrata* pollen grains.

Female Gametophyte (Embryo Sac)

The overall development of the female gametophyte has two distinct phases. First, in the process of megasporogenesis, a single cell in the diploid megasporangium undergoes meiosis to produce four megaspores, only one of which survives. During the second phase, megagametogenesis, the surviving haploid megaspore undergoes mitosis to produce an eight-nucleate, seven-cell female gametophyte, also known as the megagametophyte, or embryo sac. The polar nuclei move to the equator and fuse, forming a single, diploid central cell. This central cell later fuses with a sperm to form the triploid endosperm. Three nuclei position themselves on the end of the embryo sac opposite the micropyle and develop into the antipodal cells, which later degenerate. The nucleus closest to the micropyle becomes the female gamete, or egg cell, and the two adjacent nuclei develop into synergid cells. The synergids help guide the pollen tube for successful fertilization, after which they disintegrate. Once fertilization is complete, the resulting diploid zygote develops into the embryo; the fertilized ovule forms the other tissues of the seed.

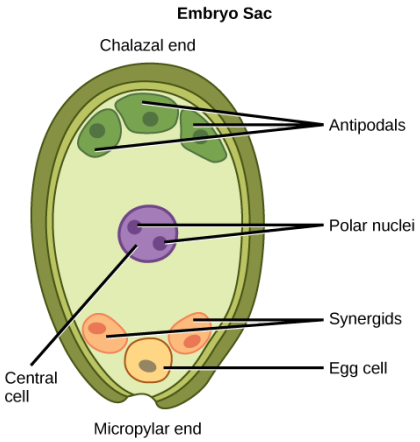


Figure 40.3.1.1: Embryo sac: As shown in this diagram of the embryo sac in angiosperms, the ovule is covered by integuments and has an opening called a micropyle. Inside the embryo sac are three antipodal cells, two synergids, a central cell, and the egg cell.

A double-layered integument protects the megasporangium and, later, the embryo sac. The integument will develop into the seed coat after fertilization, protecting the entire seed. The ovule wall will become part of the fruit. The integuments, while protecting the megasporangium, do not enclose it completely, but leave an opening called the micropyle. The micropyle allows the pollen tube to enter the female gametophyte for fertilization.

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Key Points

- A typical flower has four main parts, or whorls: the calyx (sepals), corolla (petals), androecium (male reproductive structure), and gynoecium (female reproductive structure).
- Angiosperms that contain both male and female gametophytes within the same flower are called complete and are considered to be androgynous or hermaphroditic.
- Angiosperms that contain only male or only female gametophytes are considered to be incomplete and are either staminate (contain only male structures) or carpellate (contain only female structures) flowers.
- Microspores develop in the microsporangium and form mature pollen grains (male gametophytes), which are then used to fertilize female gametophytes.
- During megasporogenesis, four megaspores are produced with one surviving; during megagametogenesism, the surviving megaspore undergoes mitosis to form an embryo sac (female gametophyte).
- The sperm, guided by the synergid cells, migrates to the ovary to complete fertilization; the diploid zygote develops into the embryo, while the fertilized ovule forms the other tissues of the seed.

Key Terms

- **perianth**: the calyx (sepals) and the corolla (petals)
- **androecium**: the set of a flower's stamens (male reproductive organs)
- **gynoecium**: the set of a flower's pistils (female reproductive organs)

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40.4: Pollination and Fertilization

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40.4.1: Pollination and Fertilization

Learning Objectives

- Determine the differences between self-pollination and cross-pollination, and describe how plants have developed ways to avoid self-pollination

Pollination: An Introduction

In angiosperms, pollination is defined as the placement or transfer of pollen from the anther to the stigma of the same or a different flower. In gymnosperms, pollination involves pollen transfer from the male cone to the female cone. Upon transfer, the pollen germinates to form the pollen tube and the sperm that fertilize the egg.

Self-Pollination and Cross-Pollination

Pollination takes two forms: self-pollination and cross-pollination. Self-pollination occurs when the pollen from the anther is deposited on the stigma of the same flower or another flower on the same plant. Cross-pollination is the transfer of pollen from the anther of one flower to the stigma of another flower on a different individual of the same species. Self-pollination occurs in flowers where the stamen and carpel mature at the same time and are positioned so that the pollen can land on the flower's stigma. This method of pollination does not require an investment from the plant to provide nectar and pollen as food for pollinators. These types of pollination have been studied since the time of Gregor Mendel. Mendel successfully carried out self-pollination and cross-pollination in garden peas while studying how characteristics were passed on from one generation to the next. Today's crops are a result of plant breeding, which employs artificial selection to produce the present-day cultivars. An example is modern corn, which is a result of thousands of years of breeding that began with its ancestor, teosinte. The teosinte that the ancient Mesoamericans originally began cultivating had tiny seeds, vastly different from today's relatively giant ears of corn. Interestingly, though these two plants appear to be entirely different, the genetic difference between them is minuscule.



Figure **40.4.1.1**: Teosinte: Teosinte (left) is the ancestor of modern corn (far-right). Although they are morphologically dissimilar, genetically they are not so different.

Genetic Diversity

Living species are designed to ensure survival of their progeny; those that fail become extinct. Genetic diversity is, therefore, required so that in changing environmental or stress conditions, some of the progeny can survive. Self-pollination leads to the production of plants with less genetic diversity since genetic material from the same plant is used to form gametes and, eventually, the zygote. In contrast, cross-pollination leads to greater genetic diversity because the male and female gametophytes are derived from different plants. Because cross-pollination allows for more genetic diversity, plants have developed many ways to avoid self-pollination. In some species, the pollen and the ovary mature at different times. These flowers make self-pollination nearly impossible. By the time pollen matures and has been shed, the stigma of this flower is mature and can only be pollinated by pollen

from another flower. Some flowers have developed physical features that prevent self-pollination. The primrose employs this technique. Primroses have evolved two flower types with differences in anther and stigma length: the pin-eyed flower and the thrum-eyed flower. In the pin-eyed flower, anthers are positioned at the pollen tube's halfway point, and in the thrum-eyed flower, the stigma is found at this same location. This allows insects to easily cross-pollinate while seeking nectar at the pollen tube. This phenomenon is also known as heterostyly. Many plants, such as cucumbers, have male and female flowers located on different parts of the plant, thus making self-pollination difficult. In other species, the male and female flowers are borne on different plants, making them dioecious. All of these are barriers to self-pollination; therefore, the plants depend on pollinators to transfer pollen. The majority of pollinators are biotic agents such as insects (bees, flies, and butterflies), bats, birds, and other animals. Other plant species are pollinated by abiotic agents, such as wind and water.



Figure **40.4.1.1**: Pollinators: To maximize their avoidance of self-pollination, plants have evolved relationships with animals, such as bees, to ensure cross-pollination between members of the same species.

Key Points

- Pollination, the transfer of pollen from flower-to-flower in angiosperms or cone -to-cone in gymnosperms, takes place through self-pollination or cross-pollination.
- Cross-pollination is the most advantageous of the two types of pollination since it provides species with greater genetic diversity.
- Maturation of pollen and ovaries at different times and heterostyly are methods plants have developed to avoid self-pollination.
- The placement of male and female flowers on separate plants or different parts of the plant are also barriers to self-pollination.

Key Terms

- **pollination**: the transfer of pollen from an anther to a stigma that is carried out by insects, birds, bats, and the wind
- **heterostyly**: the condition of having unequal male (anther) and female (stigma) reproductive organs
- **cross-pollination**: fertilization by the transfer of pollen from an anther of one plant to a stigma of another
- **self-pollination**: pollination of a flower by its own pollen in a flower that has both stamens and a pistil

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40.4.1: Pollination by Bats, Birds, Wind, and Water

Learning Objectives

- Differentiate among the non-insect methods of pollination

Non-Insect Methods of Pollination

Plants have developed specialized adaptations to take advantage of non-insect forms of pollination. These methods include pollination by bats, birds, wind, and water.

Pollination by Bats

In the tropics and deserts, bats are often the pollinators of nocturnal flowers such as agave, guava, and morning glory. The flowers are usually large and white or pale-colored so that they can be distinguished from their dark surroundings at night. The flowers have a strong, fruity, or musky fragrance and produce large amounts of nectar. They are naturally-large and wide-mouthed to accommodate the head of the bat. As the bats seek the nectar, their faces and heads become covered with pollen, which is then transferred to the next flower.

Pollination by Birds

Many species of small birds, such as hummingbirds and sun birds, are pollinators for plants such as orchids and other wildflowers. Flowers visited by birds are usually sturdy and are oriented in a way to allow the birds to stay near the flower without getting their wings entangled in the nearby flowers. The flower typically has a curved, tubular shape, which allows access for the bird's beak. Brightly-colored, odorless flowers that are open during the day are pollinated by birds. As a bird seeks energy-rich nectar, pollen is deposited on the bird's head and neck and is then transferred to the next flower it visits. Botanists determine the range of extinct plants by collecting and identifying pollen from 200-year-old bird specimens from the same site.



Figure **40.4.1.1**: Pollination by birds: Hummingbirds have adaptations that allow them to reach the nectar of certain tubular flowers, thereby, aiding them in the process of pollination.

Pollination by Wind

Most species of conifers and many angiosperms, such as grasses, maples, and oaks, are pollinated by wind. Pine cones are brown and unscented, while the flowers of wind-pollinated angiosperm species are usually green, small, may have small or no petals, and produce large amounts of pollen. Unlike the typical insect-pollinated flowers, flowers adapted to pollination by wind do not produce nectar or scent. In wind-pollinated species, the microsporangia hang out of the flower, and, as the wind blows, the lightweight pollen is carried with it. The flowers usually emerge early in the spring before the leaves so that the leaves do not block the movement of the wind. The pollen is deposited on the exposed feathery stigma of the flower.



Figure 40.4.1.1: Wind pollination: These male (a) and female (b) catkins from the goat willow tree (*Salix caprea*) have structures that are light and feathery to better disperse and catch the wind-blown pollen.

Pollination by Water

Some weeds, such as Australian sea grass and pond weeds, are pollinated by water. The pollen floats on water. When it comes into contact with the flower, it is deposited inside the flower.

Pollination by Deception

Orchids are highly-valued flowers, with many rare varieties. They grow in a range of specific habitats, mainly in the tropics of Asia, South America, and Central America. At least 25,000 species of orchids have been identified.

Flowers often attract pollinators with food rewards, in the form of nectar. However, some species of orchid are an exception to this standard; they have evolved different ways to attract the desired pollinators. They use a method known as food deception, in which bright colors and perfumes are offered, but no food. *Anacamptis morio*, commonly known as the green-winged orchid, bears bright purple flowers and emits a strong scent. The bumblebee, its main pollinator, is attracted to the flower because of the strong scent, which usually indicates food for a bee. In the process, the bee picks up the pollen to be transported to another flower.

Other orchids use sexual deception. *Chiloglottis trapeziformis* emits a compound that smells the same as the pheromone emitted by a female wasp to attract male wasps. The male wasp is attracted to the scent, lands on the orchid flower, and, in the process, transfers pollen. Some orchids, like the Australian hammer orchid, use scent as well as visual trickery in yet another sexual deception strategy to attract wasps. The flower of this orchid mimics the appearance of a female wasp and emits a pheromone. The male wasp tries to mate with what appears to be a female wasp, but instead picks up pollen, which it then transfers to the next counterfeit mate.



Figure 40.4.1.1: Pollination by deception in orchids: Certain orchids use food deception or sexual deception to attract pollinators. Shown here is a bee orchid (*Ophrys apifera*).

Key Points

- Flowers that are pollinated by bats bloom at night, tending to be large, wide-mouthed, and pale-colored; they may also give off strong scents.
- Flowers that are pollinated by small birds usually have curved, tubular shapes; birds carry the pollen off on their heads and neck to the next flower they visit.
- Wind-pollinated flowers do not produce scents or nectar; instead, they tend to have small or no petals and to produce large amounts of lightweight pollen.
- Some species of flowers release pollen that can float on water; pollination occurs when the pollen reaches another plant of the same species.
- Some flowers deceive pollinators through food or sexual deception; the pollinators become attracted to the flowers with false promises of food and mating opportunities.

Key Terms

- **food deception**: a trickery method employed by some species of orchids in which only bright colors and perfume are offered to their pollinators with no food reward

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40.4.1: Pollination by Insects

Learning Objectives

- Explain how pollination by insects aids plant reproduction

Bees

Bees are perhaps the most important pollinator of many garden plants and most commercial fruit trees. The most common species of bees are bumblebees and honeybees. Since bees cannot see the color red, bee-pollinated flowers usually have shades of blue, yellow, or other colors. Bees collect energy -rich pollen or nectar for their survival and energy needs. They visit flowers that are open during the day, are brightly colored, have a strong aroma or scent, and have a tubular shape, typically with the presence of a nectar guide. A nectar guide includes regions on the flower petals that are visible only to bees, which help guide bees to the center of the flower, thus making the pollination process more efficient. The pollen sticks to the bees' fuzzy hair; when the bee visits another flower, some of the pollen is transferred to the second flower. Recently, there have been many reports about the declining population of honeybees. Many flowers will remain unpollinated, failing to bear seeds if honeybees disappear. The impact on commercial fruit growers could be devastating.



Figure **40.4.1.1**: Pollination by insects: Insects, such as bees, are important agents of pollination. Bees are probably the most important species of pollinators for commercial and garden plant species.

Flies

Many flies are attracted to flowers that have a decaying smell or an odor of rotting flesh. These flowers, which produce nectar, usually have dull colors, such as brown or purple. They are found on the corpse flower or voodoo lily (*Amorphophallus*), dragon arum (*Dracunculus*), and carrion flower *(Stapleia, Rafflesia*). The nectar provides energy while the pollen provides protein. Wasps are also important insect pollinators, pollinating many species of figs.

Butterflies and Moths

Butterflies, such as the monarch, pollinate many garden flowers and wildflowers, which are usually found in clusters. These flowers are brightly colored, have a strong fragrance, are open during the day, and have nectar guides. The pollen is picked up and carried on the butterfly's limbs. Moths, on the other hand, pollinate flowers during the late afternoon and night. The flowers pollinated by moths are pale or white and are flat, enabling the moths to land. One well-studied example of a moth-pollinated plant is the yucca plant, which is pollinated by the yucca moth. The shape of the flower and moth have adapted in a way to allow successful pollination. The moth deposits pollen on the sticky stigma for fertilization to occur later. The female moth also deposits eggs into the ovary. As the eggs develop into larvae, they obtain food from the flower and developing seeds. Thus, both the insect and flower benefit from each other in this symbiotic relationship. The corn earworm moth and *Gaura* plant have a similar relationship.



Figure **40.4.1.1**: Moths as pollinators: A corn earworm (a moth) sips nectar from a night-blooming Gaura plant. Both the moth and plant benefit from each other as they have formed a symbiotic relationship; the plant is pollinated while the moth is able to obtain food.

Key Points

- Adaptations such as bright colors, strong fragrances, special shapes, and nectar guides are used to attract suitable pollinators.
- Important insect pollinators include bees, flies, wasps, butterflies, and moths.
- Bees and butterflies are attracted to brightly-colored flowers that have a strong scent and are open during the day, whereas moths are attracted to white flowers that are open at night.
- Flies are attracted to dull brown and purple flowers that have an odor of decaying meat.
- Nectar guides, which are only visible to certain insects, facilitate pollination by guiding bees to the pollen at the center of flowers.
- Insects and flowers both benefit from their specialized symbiotic relationships; plants are pollinated while insects obtain valuable sources of food.

Key Terms

- **nectar guide**: markings or patterns seen in flowers of some angiosperm species that guide pollinators to nectar or pollen

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40.5: Embryo Development

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40.5.1: Embryogenesis

Learning Objectives

- Explain the steps of embryogensis in eudicots.
- Compare embryogenesis in eudicots versus monocots.

The Seed Plants chapter discussed the fertilization of the egg within the ovule. The zygote ultimately divides to produce the mature embryo, the ovule develops into a seed, and the ovary that contained one or more ovules develops into a fruit. A typical seed contains a seed coat, cotyledons, endosperm, and a single embryo. The development of the embryo occurs through a process called **embryogenesis**.

Embryogenesis in Eudicots

After fertilization in eudicots, the zygote (Figure $40.5.1.1-I$) divides to form two cells: the upper **apical cell** and the lower **basal cell** . The division of the basal cell gives rise to the suspensor, which attaches the embryo to the **micropyle** (the pore through which the pollen tube original entered). The suspensor provides a route for nutrition to be transported from the mother plant to the growing embryo. The apical cell also divides, initially producing a **proembryo** (figure $40.5.1.1-II$).

As the proembryo continues to divide, it takes a spherical form, called the **globular stage** (Figures $40.5.1.1-III$ and $40.5.1.2a$). The globular is the first stage that is considered the **embryo proper**. Next, cotyledons arise from the embryo proper, forming the **heart stage** (Figures $40.5.1.1-IV$ and $40.5.1.2-4$). **Cotyledons** are embryonic leaf-life structures that function in food storage, food absorption and/or photosynthesis. As the cotyledons elongate, and the base of the embryo thickens, it results a torpedo. (This stage is called the **torpedo stage;** Figures $40.5.1.1-V$ and $40.5.1.2c$). Cell division is concentrated at the **shoot apical meristem**, located at the shoot tip in between the cotyledons, and the **root apical meristem** at the most basal (bottom) part of the embryo. Most of the suspensor deteriorates during the torpedo stage.

The final stage of embryogenesis results in the **mature embryo** (Figures $40.5.1.1-VI$ and $40.5.1.2d$). The mature embryo includes an embryonic root called the **radicle**. The embryo becomes dormant at this point, halting metabolic activity and cell division. At this point, the seed is ready for dispersal. Growth resumes when the seed germinates and the embryo develops into a seedling.

In some eudicots, the **endosperm** (triploid tissue that was formed when a sperm fertilized the two polar nuclei) cells divide, and endosperm fills a substantial portion of the mature seed. The endosperm stores nutrients. In other (non-endospermic) eudicots, such as *Capsella bursa-pastoris*, the endosperm develops initially, but is then digested, and the nutrients are moved into the two cotyledons (Figure $40.5.1.2$). After germination, the developing seedling relies on these food reserves stored in the endosperm or cotyledons until the first set of leaves begin photosynthesis.

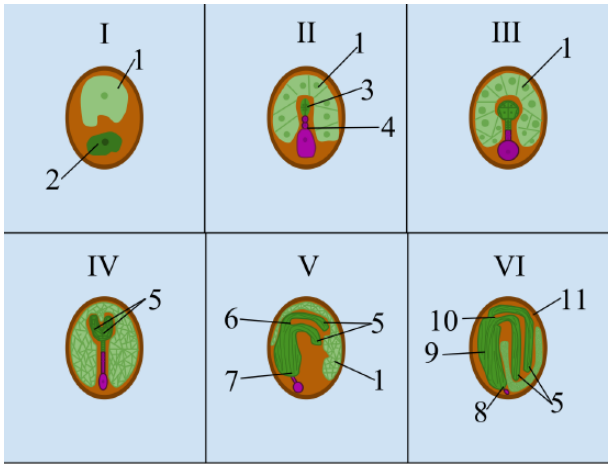


Figure **40.5.1.1**: The stages of embryogenesis in eudicots. I. The developing seed contains the triploid endosperm (1) and the diploid zygote (2). II. The zygote divides, forming the proembryo (3), which is anchored to the micropyle by suspensor (4), which has a large basal cell. The endosperm has also divided. III. The embryo proper is in the globular stage, now a spherical mass of cells. IV. The embryo proper is heart stage. The heart shape results from the two cotyledons (5). V. The embryo proper is in the torpedo stage, which is cylindrical with a rounded base. The shoot apical meristem (6) is between the cotyledons, and the root apical meristem (7) is on the opposite end, anchored to the suspensor. VI. The mature embryo includes the radicle (8), the **hypocotyl** (9) is the stem-like axis below the cotyledons. The **epicotyl** (10) is the stem-like axis above the cotyledons. The integument of the ovule has developed into the seed coat (11), which surrounds the seed. Image by TheLAW14 (CC-BY-SA).

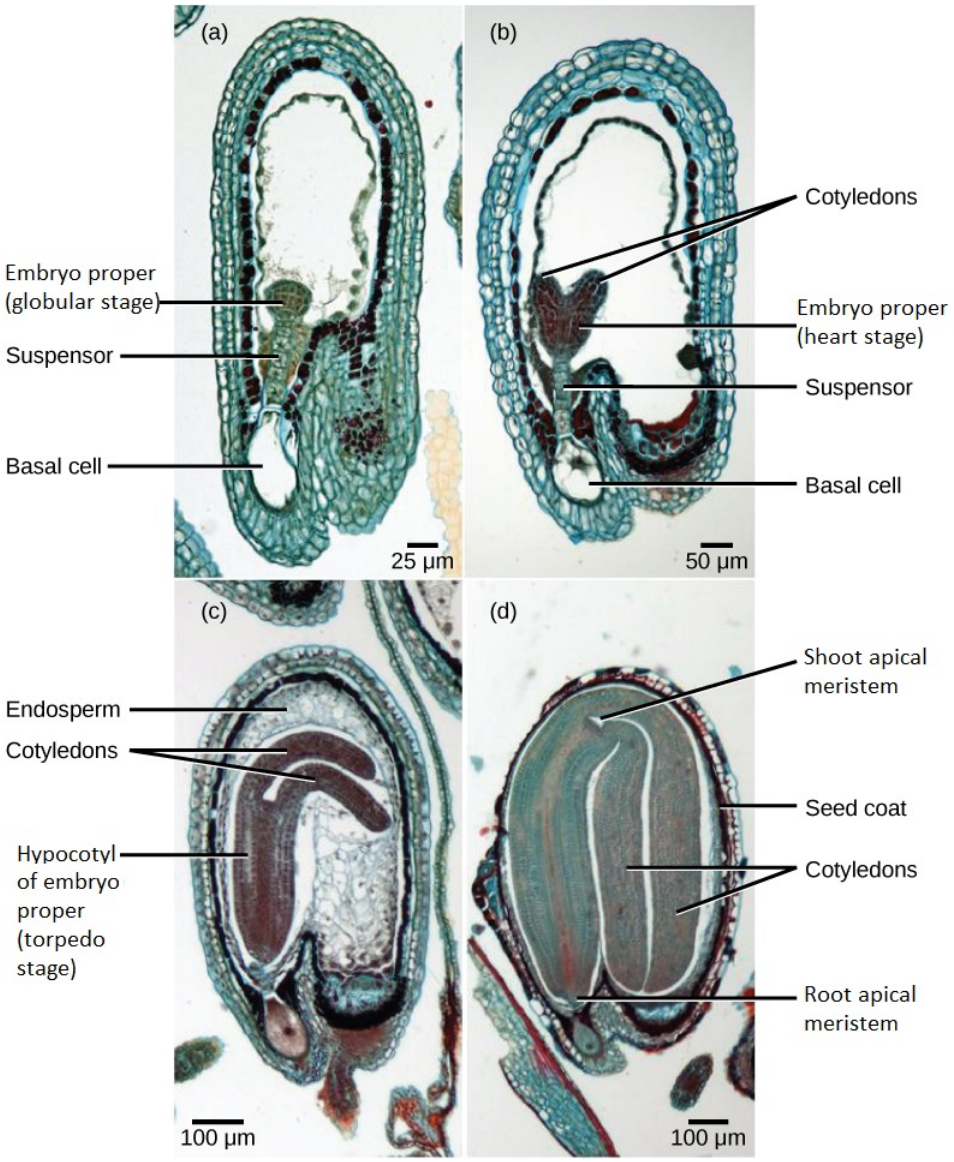


Figure **40.5.1.2**: Selected stages of embryogenesis in the ovule of shepherd's purse (*Capsella bursa-pastoris*). After fertilization, the zygote divides to form an apical cell and basal cell. The apical cell divides to first produce a proembryo, and then form the embryo proper. The basal cell also divides, giving rise to the suspensor. The embryo proper is initially in the globular stage (a), which is a spherical mass of cells seen growing inside the oval-shaped ovule. As the cotyledons emerge the embryo proper enters the heart stage (b), which resembles a heart due to the two cotyledons. The base of the embryo widens to form a cylindrical hypocotyl, and the cotyledons start to bend in the torpedo stage (c). Cells inside the embryo grow in vertical columns. Finally, the mature embryo fills the seed and becomes dormant (d). The seed coat now surrounds the ovule. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell; labels modified by Melissa Ha)

Embryogenesis in Monocots

The process of embryogenesis in monocots is similar to that of eudicots, but as there is only a single cotyledon, no heart stage occurs. Instead, the embryo proper of the monocot becomes cylindrical at this point in development. The shoot apical meristem, while still present at the shoot tip, is not in between cotyledons in the monocot (because there is only a single cotyledon).

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40.5.2: Mature Embryos and Seed Structure

Learning Objectives

- Locate the major seed structures and identify the function of each.
- Compare eudicot and monocot seeds.

Eudicot Seeds

The seed is protected by a **seed coat** that is formed from the integument of the ovule (Figure 40.5.2.1). The seed coat is further divided into an outer coat known as the **testa** and inner coat known as the **tegmen**. The **hilum** is a scar on the outside of the seed where it was attached to the endocarp (inner layer of the fruit wall). The **micropyle** is a small round structure next to the hilum where the pollen tube entered.

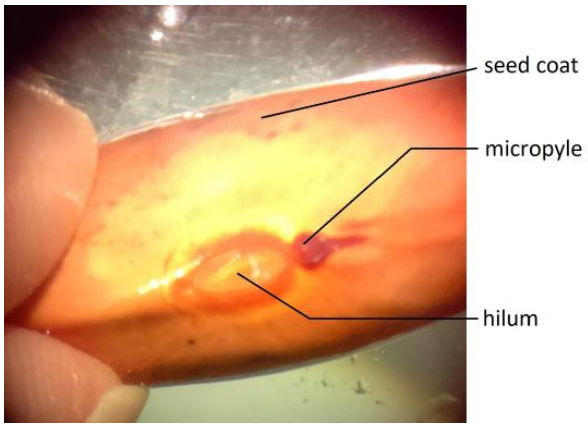


Figure 40.5.2.1: The external structures of a bean seed, an example of a eudicot (7X). The seed coat surrounds the seed. There is a round micropyle, where the pollen tube originally entered the ovule. The oval hilum is a scar from where the ovule was attached to the ovary. Image by Melissa Ha (CC-BY).

The **embryonic axis** (root-shoot axis) runs the length of the embryo. On end of the embryonic axis is the **plumule**, the young shoot apex, which includes the shoot apical meristem and developing leaves (**leaf primordia**). At the other end of the embryonic axis is the **radicle** (embryonic root). In some species, the radicle is not apparent in the embryo (in which case the distal end of the root is simply the root tip). The embryonic axis does not include the **cotyledons**. The portion of the embryo between the cotyledon attachment point and the radicle is known as the **hypocotyl** (hypocotyl means “below the cotyledons”). The portion of the embryonic axis between the cotyledon attachment and the shoot tip is the **epicotyl** (epicotyl means "above the cotyledons; Figures 40.5.2.2 – 3)). Some embryos lack a visible epicotyl because the cotyledons are attached to the embryonic axis at the shoot tip.

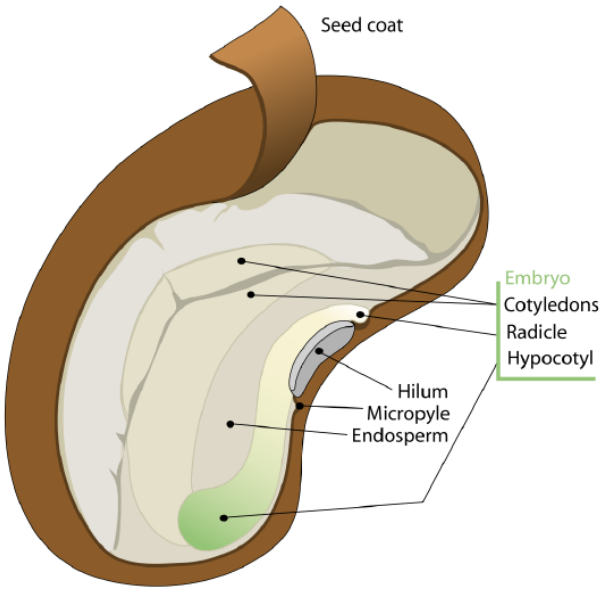


Figure 40.5.2.2: Diagram of a mature embryo from a bean seed, an example of a eudicot. The **seed coat** is a protective layer surrounding the seed. The two **cotyledons** form the bulk of the embryo. The stem-like axis below the cotyledons in the **hypocotyl**. At the tip of the hypocotyl is the **radicle** (the embryonic root). The **hilum** is an oval scar on the outside of the seed, and the **micropyle** is the small round structure adjacent to it. Image by LadyofHats (public domain).

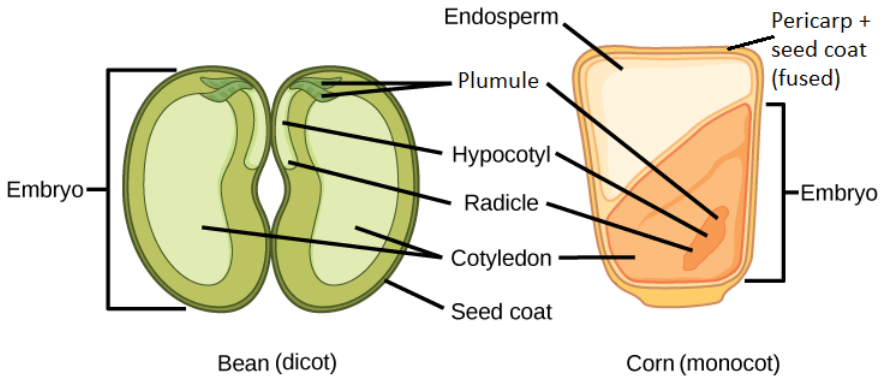


Figure 40.5.2.3: The structures of bean (eudicot) and corn (monocot) seeds. Eudicots (left) have two cotyledons. Monocots (right) have one cotyledon, called the **scutellum**, which channels nutrition to the growing embryo. Both monocot and eudicot embryos have a **plumule** (which contains developing leaves and the shoot apical meristem), a **hypocotyl** (embryonic stem below the cotyledons), and a **radicle** that forms the root. The embryonic axis comprises everything between the plumule and the radicle, not including the cotyledon(s). The corn "seed" is technically a caryopsis, a one-seeded fruit in which the pericarp (fruit wall) is fused with the seed coat.

The two cotyledons in the eudicot seed are connected to the rest of the embryo via vascular tissue (xylem and phloem). In **endospermic dicots**, the food reserves are stored in the endosperm. During germination, the two cotyledons therefore act as absorptive organs to take up the enzymatically released food reserves. Tobacco (*Nicotiana tabaccum*), tomato (*Solanum lycopersicum*), and pepper (*Capsicum annuum*) are examples of endospermic dicots. In **non-endospermic dicots**, the triploid endosperm develops normally following double fertilization, but the endosperm food reserves are quickly remobilized and moved into the developing cotyledon for storage. The two halves of a peanut seed (*Arachis hypogaea*; Figure 40.5.2.4) or a bean (*Phaseolus*; Figures 40.5.2.2 – 3) and the split peas (*Pisum sativum*; Figure 40.5.2.5) of split pea soup are individual cotyledons loaded with food reserves.

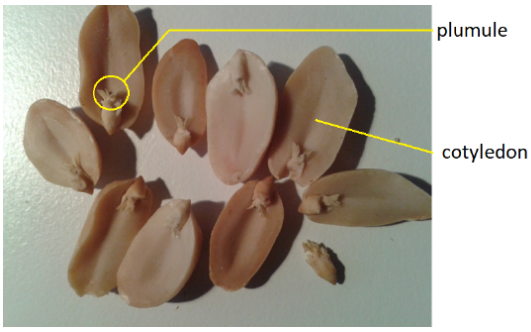


Figure 40.5.2.4: Each half of a peanut represents a cotyledon, which is rich with nutrients. The plumule, which contains tiny embryonic leaves, is found between the cotyledons. Image labeled from Jesusorizales (CC-BY-SA).



Figure 40.5.2.5: Like the peanut, each half of a pea represents a nutrient-filled cotyledon. The black coloration in the cotyledon is due to iodine staining the starch in the cotyledons. Most of the pea seed is filled with two cotyledons. The tiny embryonic axis consists of the plumule at the top and the descending hypocotyl. The radicle is at the tip of the hypocotyl. The seed coat surrounds the entire seed. Image by Melissa Ha (CC-BY).

Because seeds have food reserves to fuel germination, they also are a nutritious food source for people. Studying the nutrient content of seed crops such as beans can be used to increase the nutritive value of the plant using biotechnology. Maria Elena Zavala (Figure 40.5.2.6) is working to combat world hunger by manipulating plants to improve their nutritional qualities. For example, her research with beans is looking at how genetic engineering can be used to make the bean proteins more digestible and nutritious.



Figure 40.5.2.6: Maria Elena Zavala was the first Mexican-American woman to earn a PhD in botany in the United States. Her research includes manipulating plant genes as a way to improve plant productivity and address world hunger. Image by Lee Choo (CC BY-SA 4.0)

Monocot Seeds

The seeds of the most complex monocot family, Poaceae (the grass family), which includes corn and wheat, are highly specialized. The testa and tegmen of the seed coat are fused. The fruit is a **caryopsis** (grain), a one-seeded fruit in which the fruit wall (**pericarp**) is fused to the seed coat. Thus, not only are the two layers of the seed coat fused, but the seed coat is fused to the pericarp.

The single cotyledon is called a **scutellum**; the scutellum also has vascular connections to the rest of the embryo. The large inner layer of the endosperm that stores nutrients is called the **starchy endosperm**. The thin outer layer of the endosperm, which is a single layer of cells, is called the **aleurone**. Upon germination, enzymes are secreted by the aleurone. The enzymes degrade the stored carbohydrates, proteins and lipids, the products of which are absorbed by the scutellum and transported via a vasculature strand to the developing embryo. Therefore, the scutellum can be seen to be an absorptive organ, not a storage organ.

The root tip is protected by a sheath-like structure called the **coleorhiza**. Similarly, the **coleoptile** ensheaths the plumule at the shoot tip (Figure **40.5.2.7 – 10**).

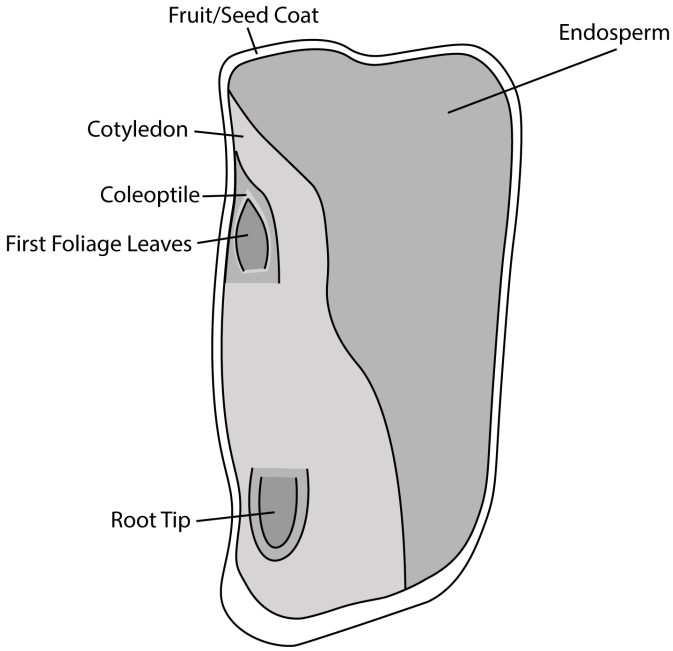


Figure **40.5.2.7**: Diagram of a corn kernel, an example of a "complex" monocot. The single cotyledon is called the scutellum. The outer layer is the pericarp (fruit wall) fused with the seed coat. The endosperm fills much of the seed and stores starch. It actually consists of a thin outer layer (aleurone) and a thick inner layer (starchy endosperm). The young shoot (plumule) consists of the shoot apical meristem surrounded by young leaves (first foliage leaves). It is surrounded by a sheath called the coleoptile. The young root (radicle) is surrounded by a sheath called the coleorhiza (not labeled). Image by Sarah Greenwood (CC-BY-SA).

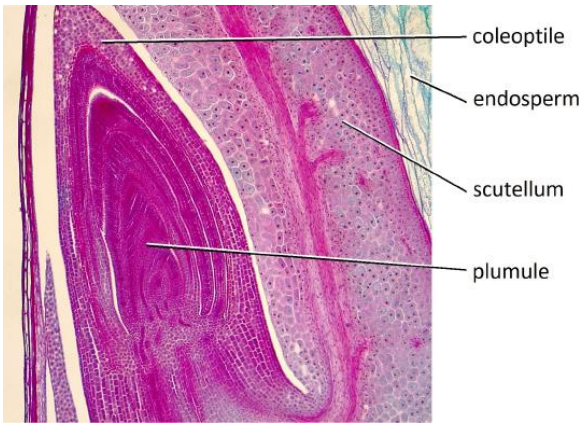


Figure **40.5.2.8**: Longitudinal section of a the upper portion of a corn embryo, a monocot (40X). The **coleoptile** is the sheath that surrounds the **plumule**, which consists of the shoot apical meristem and layers of developing leaves. The **scutellum** is the single cotyledon. A small portion of the **endosperm** is visible in this view. Image by Melissa Ha (CC-BY).

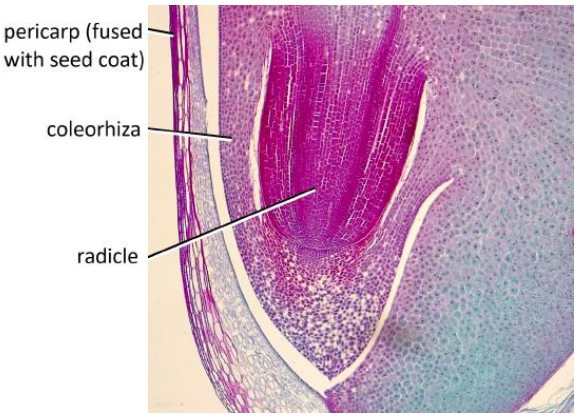


Figure 40.5.2.9: Longitudinal section of a the lower portion of a corn embryo, a monocot (40X). The outer layer is the **pericarp** fused with the **seed coat**. The **coleorhiza** surrounds the **radicle**, which is the embryonic root. Image by Melissa Ha (CC-BY).

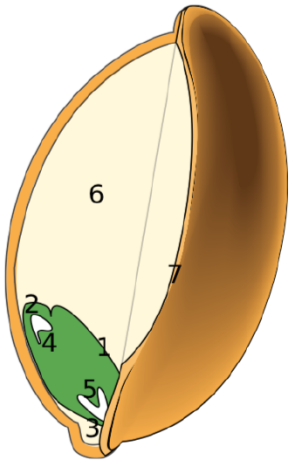


Figure 40.5.2.10: A grass seed (monocot). The scutellum (1) is the modified cotyledon of complex monocots such as grass. The coleoptile (2) is the sheath covering the young shoot tip (plumule, 4). The coleorhiza (3) is the sheath covering the young root (radicle, 5). The endosperm (6) fills much of the seed and nourishes the seedling upon germination. The seed coat (7) surrounds the seed and protects it.

Other Variations

Seeds are diverse. Pine (*Pinus*, a gymnosperm and thus neither a monocot nor eudicot) has multiple (five or more) cotyledons. Some plants like orchids (Orchidaceae, a monocot) do not have developed embryo and even endosperm in seeds; their germination depends on a presence of symbiotic (mycorrhizal) fungus.

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40.5.3: Double Fertilization in Plants

Learning Objectives

- Describe the process of double fertilization in plants

Double Fertilization

After pollen is deposited on the stigma, it must germinate and grow through the style to reach the ovule. The microspores, or the pollen, contain two cells: the pollen tube cell and the generative cell. The pollen tube cell grows into a pollen tube through which the generative cell travels. The germination of the pollen tube requires water, oxygen, and certain chemical signals. As it travels through the style to reach the embryo sac, the pollen tube's growth is supported by the tissues of the style. During this process, if the generative cell has not already split into two cells, it now divides to form two sperm cells. The pollen tube is guided by the chemicals secreted by the synergids present in the embryo sac; it enters the ovule sac through the micropyle. Of the two sperm cells, one sperm fertilizes the egg cell, forming a diploid zygote; the other sperm fuses with the two polar nuclei, forming a triploid cell that develops into the endosperm. Together, these two fertilization events in angiosperms are known as double fertilization. After fertilization is complete, no other sperm can enter. The fertilized ovule forms the seed, whereas the tissues of the ovary become the fruit, usually enveloping the seed.

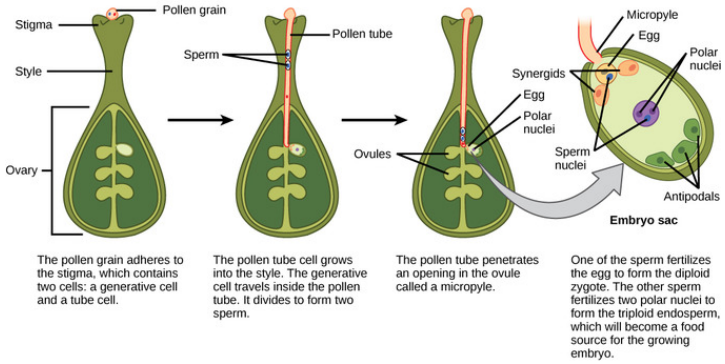


Figure **40.5.3.1**: Double fertilization: In angiosperms, one sperm fertilizes the egg to form the 2n zygote, while the other sperm fuses with two polar nuclei to form the 3n endosperm. This is called a double fertilization.

After fertilization, embryonic development begins. The zygote divides to form two cells: the upper cell (terminal cell) and the lower cell (basal cell). The division of the basal cell gives rise to the suspensor, which eventually makes connection with the maternal tissue. The suspensor provides a route for nutrition to be transported from the mother plant to the growing embryo. The terminal cell also divides, giving rise to a globular-shaped proembryo. In dicots (eudicots), the developing embryo has a heart shape due to the presence of the two rudimentary cotyledons. In non-endospermic dicots, such as *Capsella bursa*, the endosperm develops initially, but is then digested. In this case, the food reserves are moved into the two cotyledons. As the embryo and cotyledons enlarge, they become crowded inside the developing seed and are forced to bend. Ultimately, the embryo and cotyledons fill the seed, at which point, the seed is ready for dispersal. Embryonic development is suspended after some time; growth resumes only when the seed germinates. The developing seedling will rely on the food reserves stored in the cotyledons until the first set of leaves begin photosynthesis.

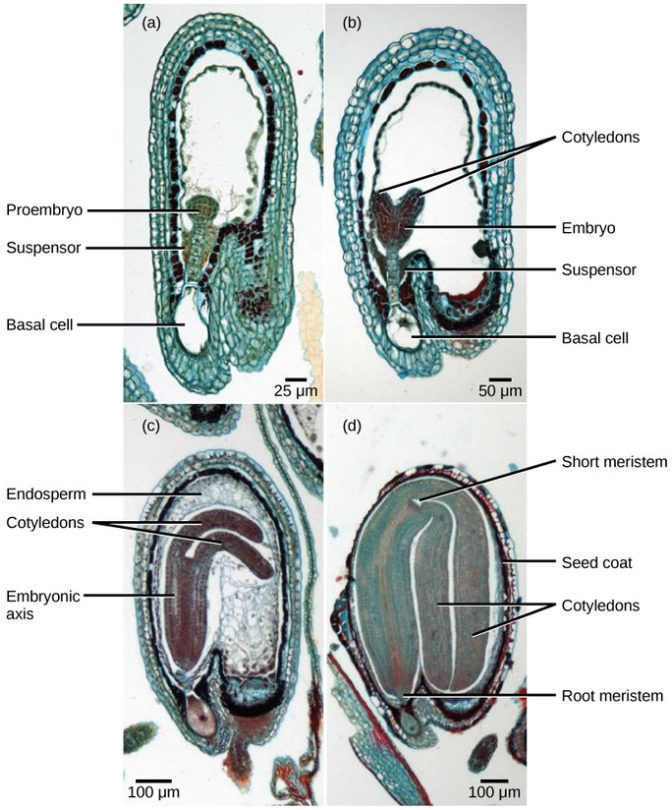


Figure 40.5.3.1: Embryo development: Shown are the stages of embryo development in the ovule of a shepherd's purse (*Capsella bursa*). After fertilization, the zygote divides to form an upper terminal cell and a lower basal cell. (a) In the first stage of development, the terminal cell divides, forming a globular pro-embryo. The basal cell also divides, giving rise to the suspensor. (b) In the second stage, the developing embryo has a heart shape due to the presence of cotyledons. (c) In the third stage, the growing embryo is crowded and begins to bend. (d) Eventually, it completely fills the seed.

Key Points

- Double fertilization involves two sperm cells; one fertilizes the egg cell to form the zygote, while the other fuses with the two polar nuclei that form the endosperm.
- After fertilization, the fertilized ovule forms the seed while the tissues of the ovary become the fruit.
- In the first stage of embryonic development, the zygote divides to form two cells; one will develop into a suspensor, while the other gives rise to a proembryo.
- In the second stage of embryonic development (in eudicots), the developing embryo has a heart shape due to the presence of cotyledons.
- As the embryo grows, it begins to bend as it fills the seed; at this point, the seed is ready for dispersal.

Key Terms

- **double fertilization**: a complex fertilization mechanism that has evolved in flowering plants; involves the joining of a female gametophyte with two male gametes (sperm)
- **suspensor**: found in plant zygotes in angiosperms; connects the endosperm to the embryo and provides a route for nutrition from the mother plant to the growing embryo
- **proembryo**: a cluster of cells in the ovule of a fertilized flowering plant that has not yet formed into an embryo

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40.6: Germination (NEW)

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40.6.1: Germination

Learning Objectives

- Identify the environmental factors that stimulate germination.
- Distinguish between epigeous and hypogeous germination.
- Compare germination in eudicots versus monocots.

Many mature seeds enter a period of inactivity, or extremely low metabolic activity: a process known as dormancy, which may last for months, years or even centuries. Dormancy helps keep seeds viable during unfavorable conditions. **Germination** occurs when the embryo, which is dormant within a mature seed, resumes growth upon a return to favorable conditions. The embryo becomes a young seedling that is no longer confined within the seed coat.

In many seeds, the presence of a thick seed coat can inhibit germination through several mechanisms: (1) the embryo may not be able to break through the thick seed coat; (2) the seed coat may contain chemicals inhibitors; and (3) the seed coat prevents the embryo from accessing water and oxygen. Dormancy is also maintained by the relative hormone concentrations in the embryo itself.

Environmental Requirements for Germination

The requirements for germination depend on the species. Common environmental requirements include light, the proper temperature, presence of oxygen, and presence of water. Seeds of small-seeded species usually require light as a germination cue. This ensures the seeds only germinate at or near the soil surface (where the light is greatest). If they were to germinate too far underneath the surface, the developing seedling would not have enough food reserves to reach the sunlight. (Recall from 14.5 Dormancy that red light induces germination by converting the inactive form of phytochrome (Pr) to the active form (Pfr), which leads to the production of amylase. This enzyme breaks down the limited food reserves in the seed, facilitating germination.)

Not only do some species require a specific temperature to germinate, but they may also require a prolonged cold period prior to germination. In this case, cold conditions gradually break down a chemical germination inhibitor. This mechanism prevents seeds from germinating during an unseasonably warm spell in the autumn or winter in temperate climates. Similarly, plants growing in hot climates may have seeds that need a hot period in order to germinate, an adaptation to avoid germination in the hot, dry summers.

Water is always needed to allow vigorous metabolism to begin. Additionally, water can leach away inhibitors in the seed coat. This is especially common among desert annuals. Seeds that are dispersed by animals may need to pass through an animal digestive tract to remove inhibitors prior to germination. Similarly, some species require mechanical abrasion of the seed coat, which could be achieved by water dispersal. Other species are fire adapted, requiring fire to break dormancy (Figure **40.6.1.1**).



Figure **40.6.1.1**: Coffeeberry (*Frangula californica*) at the Regional Park Botanic Garden in Berkeley Hills, California. This species naturally occurs in the chaparral where wildfires trigger germination of its seeds. Image by Daderot (public domain).

The Mechanism of Germination

The first step in germination and starts with the uptake of water, also known as **imbibition**. After imbibition, enzymes are activated that start to break down starch into sugars consumed by embryo. The first indication that germination has begun is a swelling in the radicle.

Depending on seed size, the time taken for a seedling to emerge may vary. Species with large seeds have enough food reserves to germinate deep below ground, and still extend their epicotyl all the way to the soil surface while the seedlings of small-seeded species emerge more quickly (and can only germinate close to the surface of the soil).

During **epigeous germination**, the hypocotyl elongates, and the cotyledons extend above ground. During **hypogeous germination**, the epicotyl elongates, and the cotyledon(s) remain belowground (Figure **40.6.1.2**). Some species (like beans and onions) have epigeous germination while others (like peas and corn) have hypogeous germination. In many epigeous species, the cotyledons not only transfer their food stores to the developing plant but also turn green and make more food by photosynthesis until they drop off.

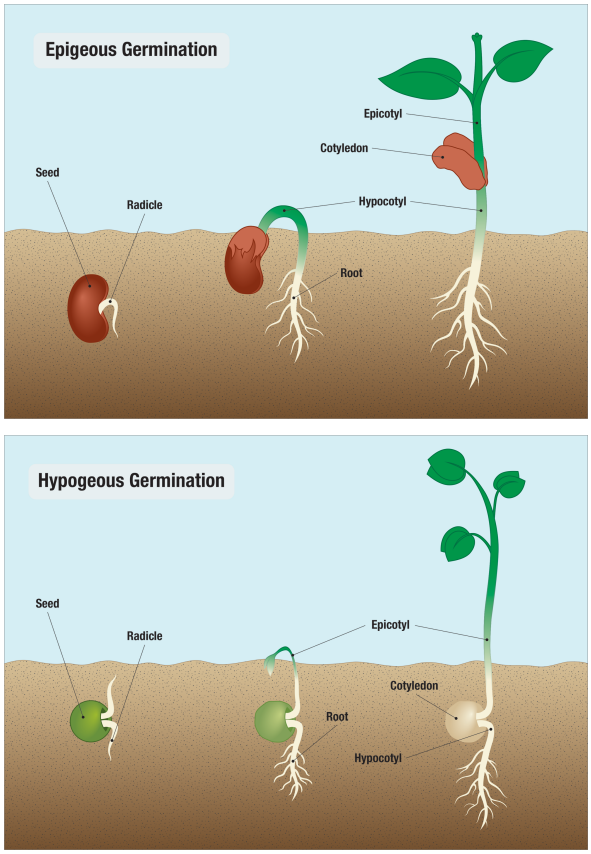


Figure **40.6.1.2**: Epigeous germination in bean (top) and hypogeous germination in pea (bottom). For the bean, the radicle emerges from the seed. Next, the hypocotyl elongates, and the cotyledons are pushed aboveground. The epicotyl is just above the cotyledon. For the pea, the radicle also emerges from the seed. The epicotyl elongates, and the cotyledons remain below the ground. The hypocotyl remains short and lies between the root and cotyledon. Image by Jen Valenzuela (CC-BY).

Germination in Eudicots

Upon germination in eudicot seeds, the radicle emerges from the seed coat while the seed is still buried in the soil.

For epigeous eudicots (like beans), the hypocotyl is shaped like a hook with the plumule pointing downwards. This shape is called the plumule hook, and it persists as long as germination proceeds in the dark. Therefore, as the hypocotyl pushes through the tough and abrasive soil, the plumule is protected from damage. Additionally, the two cotyledons additionally protect the from mechanical damage. Upon exposure to light, the hypocotyl hook straightens out, the young foliage leaves face the sun and expand, and the epicotyl elongates (Figure **40.6.1.3**).

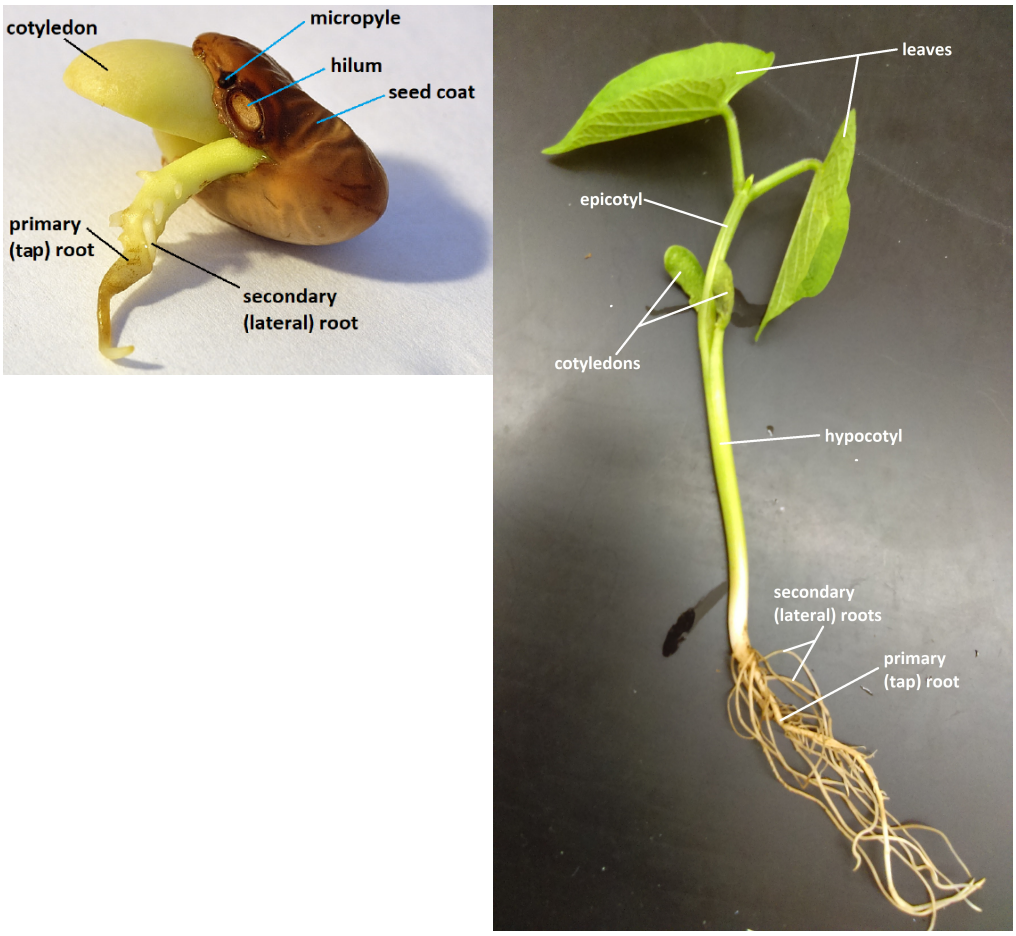


Figure **40.6.1.3**: A bean seed begins to germinate (left) and a germinated bean seedling (right). Beans are epigeous eudicots, meaning that the hypocotyl elongates, pushing the cotyledons above the ground. On the right, the large cotyledons have just emerged from the seed coat. The oval hilum is next to a tiny, round micropyle on the seed coat. The primary (tap) root has emerged, and secondary (lateral) roots begin to branch from the primary root. On the left, the green hypocotyl has elongated, pushing the cotyledons aboveground. The cotyledons are green and still have the shape of the bean seed. The epicotyl is the part of the stem above the cotyledons. Broad, heart-shaped leaves branch from it. Unlike the cotyledons, these are true leaves. At the tip of the stem, between the leaves is the shoot apical meristem. There is a central, thick root called the primary (tap) root. The roots that branch form it are secondary (lateral) roots. Left image by Doronenko (CC-BY-SA). Right image by Melissa Ha (CC-BY).

In hypogeous eudicots (like peas), the epicotyl rather than the hypocotyl forms a hook, and the cotyledons and hypocotyl thus remain underground. When the epicotyl emerges from the soil, the young foliage leaves expand. The epicotyl continues to elongate (Figure **40.6.1.4**).

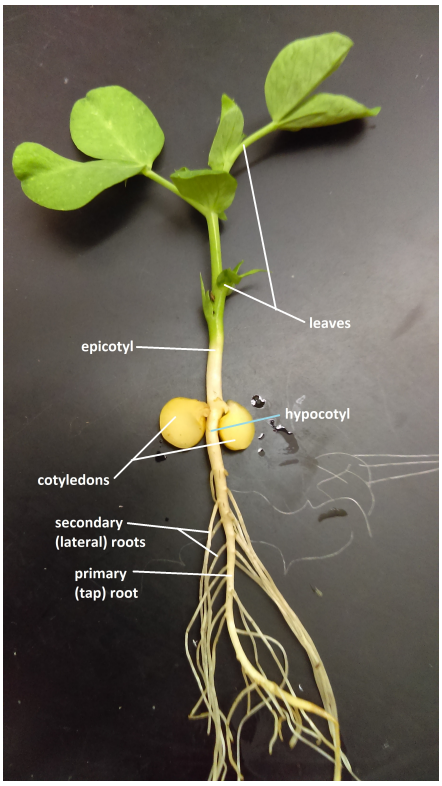


Figure **40.6.1.4**: A germinated pea seedling. Peas a hypogeous eudicots. The hypocotyl never elongates, and the cotyledons remain below ground. The green and white epicotyl has elongated, giving rise to true leaves, and the cotyledons remain belowground. These true leaves are compound (are composed of smaller leaflets). This seedling has been uprooted and washed, but everything below the epicotyl was belowground. The hypocotyl is the short segment of stem between the cotyledons and roots. It never elongated enough to push the cotyledons above the ground. There is a central, thick root called the primary (tap) root. The roots that branch form it are secondary (lateral) roots. Image by Melissa Ha (CC-BY).

The radicle continues to grown downwards and ultimately produces the tap root. Lateral roots then branch off to all sides, producing the typical eudicot tap root system.

Germination in Monocots

As the seed germinates, the radicle emerges and forms the first root. In epigeous monocots (such as onion), the single cotyledon will bend, forming a hook and emerge before the coleoptile (Figure **40.6.1.5**). In hypogeous monocots (such as corn), the cotyledon remains belowground, and the coleoptile emerges first. In either case, once the coleoptile has exited the soil and is exposed to light, it stops growing. The first leaf of the plumule then pieces the coleoptile (Figure **40.6.1.6**), and additional leaves expand and unfold. At the other end of the embryonic axis, the first root soon dies while adventitious roots (roots that arise directly from the shoot system) emerge from the base of the stem (Figure **40.6.1.7**). This gives the monocot a fibrous root system.



Figure **40.6.1.5**: The scallion (spring onion) is an epigeous monocot. The curved structure emerging from the ground is the single cotyledon. Later in the process, the coleoptile will emerge, and be pierced by the first leaf of the plumule. Image by Dennis Brown (CC-BY-SA)

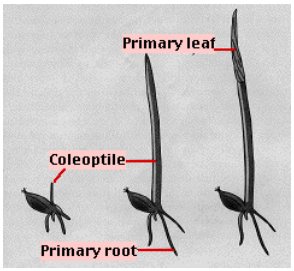


Figure **40.6.1.6**: Germination of an oat seed, a hypogeous monocot. Here the first root formed by the radicle is labeled "primary root", but note that this differs from the primary (main) root of a eudicot tap root system. Note that several adventitious roots have also formed and will ultimately produce a fibrous root system. The coleoptile is the first component of the shoot system to emerge in hypogeous monocots, but it is ultimately pieced by the first (primary) leaf of the plumule.

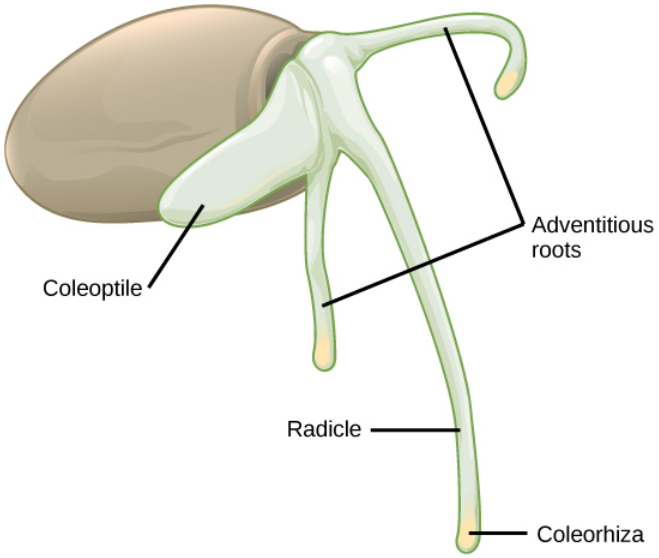


Figure **40.6.1.7**: As this monocot grass seed germinates, the radicle, emerges first, followed by the coleoptile, and the adventitious roots. The coleorhiza, a protective sheath that surrounded the radicle in the dormant seed, is now at the tip of the radicle.

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40.7: Asexual Reproduction

Skills to Develop

- Compare the mechanisms and methods of natural and artificial asexual reproduction
- Describe the advantages and disadvantages of natural and artificial asexual reproduction
- Discuss plant life spans

Many plants are able to propagate themselves using asexual reproduction. This method does not require the investment required to produce a flower, attract pollinators, or find a means of seed dispersal. Asexual reproduction produces plants that are genetically identical to the parent plant because no mixing of male and female gametes takes place. Traditionally, these plants survive well under stable environmental conditions when compared with plants produced from sexual reproduction because they carry genes identical to those of their parents.

Many different types of roots exhibit asexual reproduction Figure **40.7.1**. The corm is used by gladiolus and garlic. Bulbs, such as a scaly bulb in lilies and a tunicate bulb in daffodils, are other common examples. A potato is a stem tuber, while parsnip propagates from a taproot. Ginger and iris produce rhizomes, while ivy uses an adventitious root (a root arising from a plant part other than the main or primary root), and the strawberry plant has a stolon, which is also called a runner.

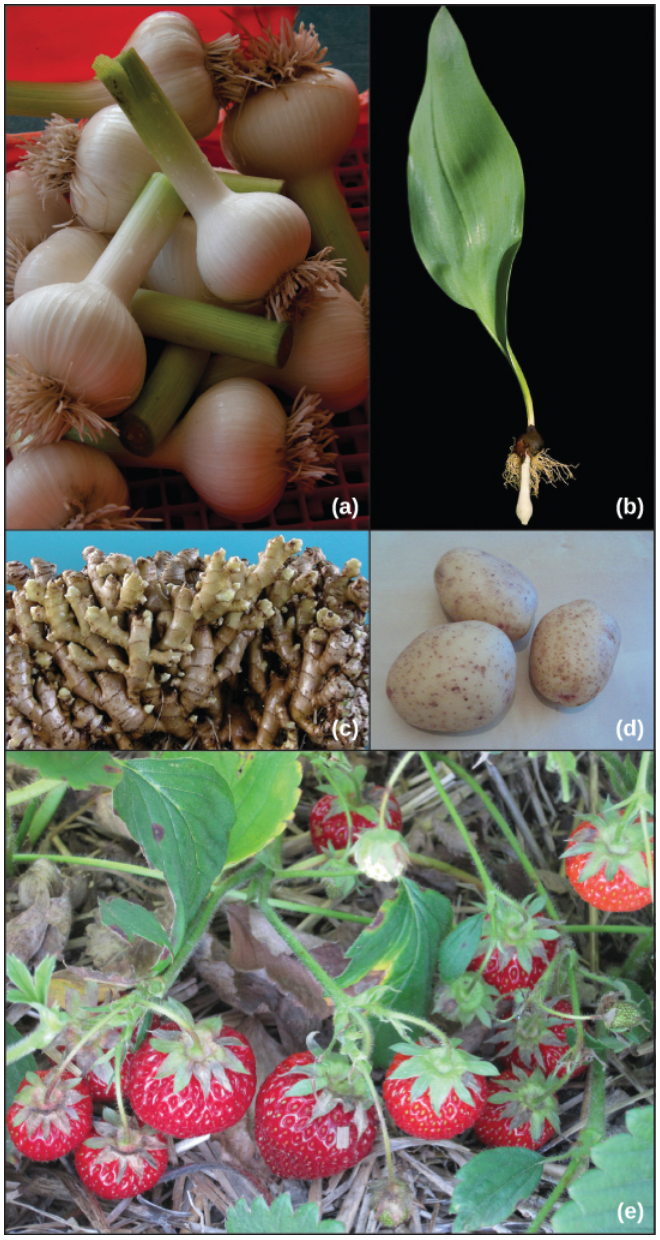


Figure 40.7.1: Different types of stems allow for asexual reproduction. (a) The corm of a garlic plant looks similar to (b) a tulip bulb, but the corm is solid tissue, while the bulb consists of layers of modified leaves that surround an underground stem. Both corms and bulbs can self-propagate, giving rise to new plants. (c) Ginger forms masses of stems called rhizomes that can give rise to multiple plants. (d) Potato plants form fleshy stem tubers. Each eye in the stem tuber can give rise to a new plant. (e) Strawberry plants form stolons: stems that grow at the soil surface or just below ground and can give rise to new plants. (credit a: modification of work by Dwight Sipler; credit c: modification of work by Albert Cahalan, USDA ARS; credit d: modification of work by Richard North; credit e: modification of work by Julie Magro)

Some plants can produce seeds without fertilization. Either the ovule or part of the ovary, which is diploid in nature, gives rise to a new seed. This method of reproduction is known as apomixis.

An advantage of asexual reproduction is that the resulting plant will reach maturity faster. Since the new plant is arising from an adult plant or plant parts, it will also be sturdier than a seedling. Asexual reproduction can take place by natural or artificial (assisted by humans) means.

Natural Methods of Asexual Reproduction

Natural methods of asexual reproduction include strategies that plants have developed to self-propagate. Many plants—like ginger, onion, gladioli, and dahlia—continue to grow from buds that are present on the surface of the stem. In some plants, such as the

sweet potato, adventitious roots or runners can give rise to new plants Figure **40.7.2**. In *Bryophyllum* and kalanchoe, the leaves have small buds on their margins. When these are detached from the plant, they grow into independent plants; or, they may start growing into independent plants if the leaf touches the soil. Some plants can be propagated through cuttings alone.

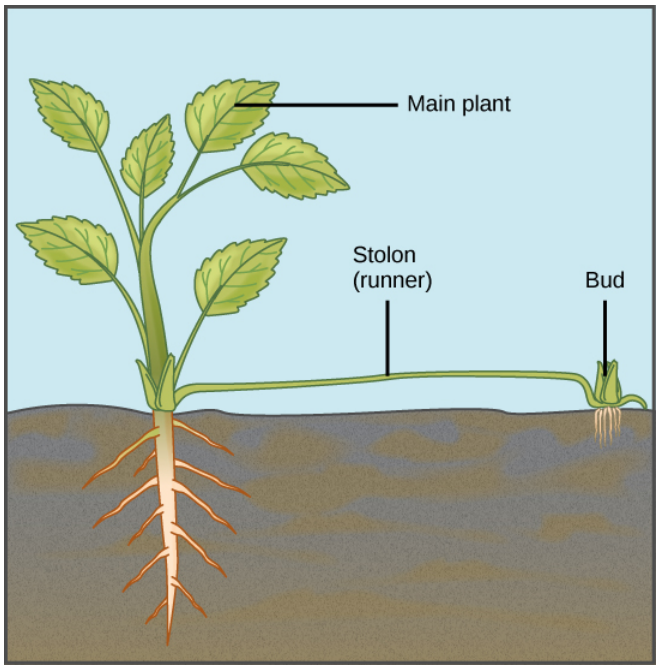


Figure **40.7.2**: A stolon, or runner, is a stem that runs along the ground. At the nodes, it forms adventitious roots and buds that grow into a new plant.

Artificial Methods of Asexual Reproduction

These methods are frequently employed to give rise to new, and sometimes novel, plants. They include grafting, cutting, layering, and micropropagation.

Grafting

Grafting has long been used to produce novel varieties of roses, citrus species, and other plants. In grafting, two plant species are used; part of the stem of the desirable plant is grafted onto a rooted plant called the stock. The part that is grafted or attached is called the scion. Both are cut at an oblique angle (any angle other than a right angle), placed in close contact with each other, and are then held together Figure **40.7.3**. Matching up these two surfaces as closely as possible is extremely important because these will be holding the plant together. The vascular systems of the two plants grow and fuse, forming a graft. After a period of time, the scion starts producing shoots, and eventually starts bearing flowers and fruits. Grafting is widely used in viticulture (grape growing) and the citrus industry. Scions capable of producing a particular fruit variety are grated onto root stock with specific resistance to disease.

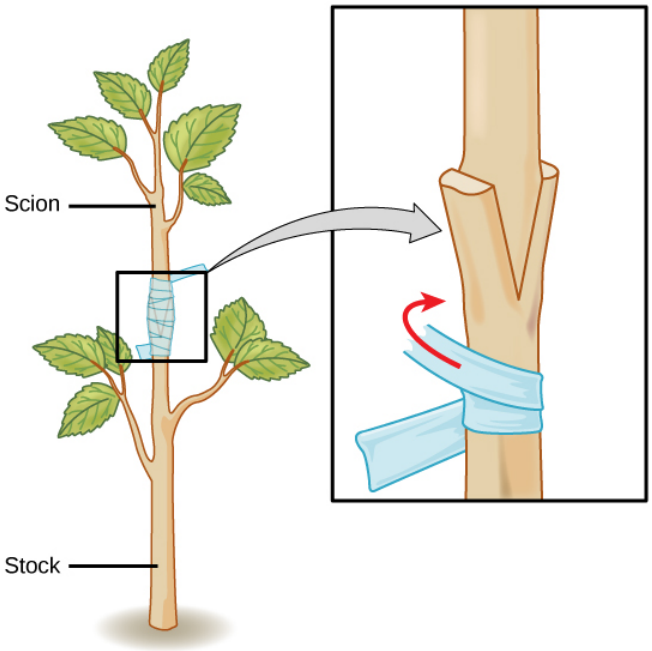


Figure **40.7.3**: Grafting is an artificial method of asexual reproduction used to produce plants combining favorable stem characteristics with favorable root characteristics. The stem of the plant to be grafted is known as the scion, and the root is called the stock.

Cutting

Plants such as coleus and money plant are propagated through stem cuttings, where a portion of the stem containing nodes and internodes is placed in moist soil and allowed to root. In some species, stems can start producing a root even when placed only in water. For example, leaves of the African violet will root if kept in water undisturbed for several weeks.

Layering

Layering is a method in which a stem attached to the plant is bent and covered with soil. Young stems that can be bent easily without any injury are preferred. Jasmine and bougainvillea (paper flower) can be propagated this way Figure **40.7.4**. In some plants, a modified form of layering known as air layering is employed. A portion of the bark or outermost covering of the stem is removed and covered with moss, which is then taped. Some gardeners also apply rooting hormone. After some time, roots will appear, and this portion of the plant can be removed and transplanted into a separate pot.

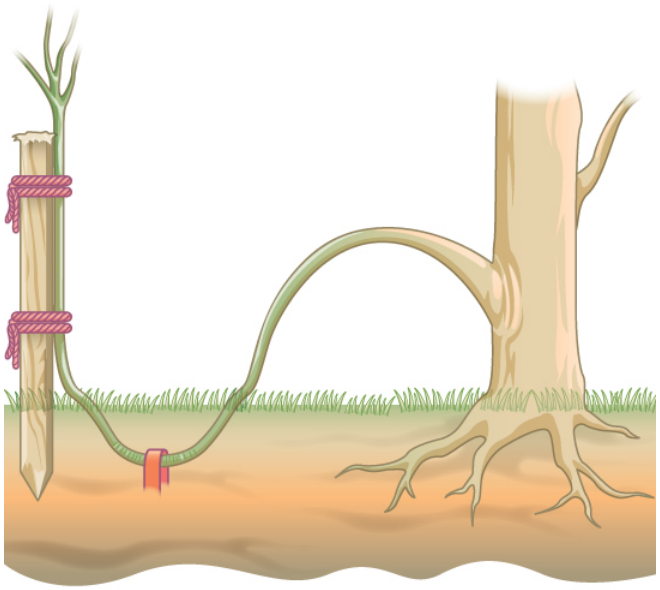


Figure **40.7.4**: In layering, a part of the stem is buried so that it forms a new plant. (credit: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

Micropropagation

Micropropagation (also called plant tissue culture) is a method of propagating a large number of plants from a single plant in a short time under laboratory conditions Figure **40.7.5**. This method allows propagation of rare, endangered species that may be difficult to grow under natural conditions, are economically important, or are in demand as disease-free plants.



Figure **40.7.5**: Micropropagation is used to propagate plants in sterile conditions. (credit: Nikhilesh Sanyal)

To start plant tissue culture, a part of the plant such as a stem, leaf, embryo, anther, or seed can be used. The plant material is thoroughly sterilized using a combination of chemical treatments standardized for that species. Under sterile conditions, the plant material is placed on a plant tissue culture medium that contains all the minerals, vitamins, and hormones required by the plant. The plant part often gives rise to an undifferentiated mass known as callus, from which individual plantlets begin to grow after a period of time. These can be separated and are first grown under greenhouse conditions before they are moved to field conditions.

Plant Life Spans

The length of time from the beginning of development to the death of a plant is called its life span. The life cycle, on the other hand, is the sequence of stages a plant goes through from seed germination to seed production of the mature plant. Some plants, such as annuals, only need a few weeks to grow, produce seeds and die. Other plants, such as the bristlecone pine, live for thousands of years. Some bristlecone pines have a documented age of 4,500 years Figure **40.7.6**. Even as some parts of a plant, such as regions containing meristematic tissue—the area of active plant growth consisting of undifferentiated cells capable of cell division—continue to grow, some parts undergo programmed cell death (apoptosis). The cork found on stems, and the water-conducting tissue of the xylem, for example, are composed of dead cells.



Figure **40.7.6**: The bristlecone pine, shown here in the Ancient Bristlecone Pine Forest in the White Mountains of eastern California, has been known to live for 4,500 years. (credit: Rick Goldwaser)

Plant species that complete their lifecycle in one season are known as annuals, an example of which is *Arabidopsis*, or mouse-ear cress. Biennials such as carrots complete their lifecycle in two seasons. In a biennial's first season, the plant has a vegetative phase, whereas in the next season, it completes its reproductive phase. Commercial growers harvest the carrot roots after the first year of growth, and do not allow the plants to flower. Perennials, such as the magnolia, complete their lifecycle in two years or more.

In another classification based on flowering frequency, monocarpic plants flower only once in their lifetime; examples include bamboo and yucca. During the vegetative period of their life cycle (which may be as long as 120 years in some bamboo species), these plants may reproduce asexually and accumulate a great deal of food material that will be required during their once-in-a-lifetime flowering and setting of seed after fertilization. Soon after flowering, these plants die. Polycarpic plants form flowers many times during their lifetime. Fruit trees, such as apple and orange trees, are polycarpic; they flower every year. Other polycarpic species, such as perennials, flower several times during their life span, but not each year. By this means, the plant does not require all its nutrients to be channelled towards flowering each year.

As is the case with all living organisms, genetics and environmental conditions have a role to play in determining how long a plant will live. Susceptibility to disease, changing environmental conditions, drought, cold, and competition for nutrients are some of the factors that determine the survival of a plant. Plants continue to grow, despite the presence of dead tissue such as cork. Individual parts of plants, such as flowers and leaves, have different rates of survival. In many trees, the older leaves turn yellow and eventually fall from the tree. Leaf fall is triggered by factors such as a decrease in photosynthetic efficiency, due to shading by upper leaves, or oxidative damage incurred as a result of photosynthetic reactions. The components of the part to be shed are recycled by the plant for use in other processes, such as development of seed and storage. This process is known as nutrient recycling.

The aging of a plant and all the associated processes is known as senescence, which is marked by several complex biochemical changes. One of the characteristics of senescence is the breakdown of chloroplasts, which is characterized by the yellowing of leaves. The chloroplasts contain components of photosynthetic machinery such as membranes and proteins. Chloroplasts also contain DNA. The proteins, lipids, and nucleic acids are broken down by specific enzymes into smaller molecules and salvaged by the plant to support the growth of other plant tissues.

The complex pathways of nutrient recycling within a plant are not well understood. Hormones are known to play a role in senescence. Applications of cytokinins and ethylene delay or prevent senescence; in contrast, abscissic acid causes premature onset of senescence.

Summary

Many plants reproduce asexually as well as sexually. In asexual reproduction, part of the parent plant is used to generate a new plant. Grafting, layering, and micropropagation are some methods used for artificial asexual reproduction. The new plant is genetically identical to the parent plant from which the stock has been taken. Asexually reproducing plants thrive well in stable environments.

Plants have different life spans, dependent on species, genotype, and environmental conditions. Parts of the plant, such as regions containing meristematic tissue, continue to grow, while other parts experience programmed cell death. Leaves that are no longer photosynthetically active are shed from the plant as part of senescence, and the nutrients from these leaves are recycled by the plant. Other factors, including the presence of hormones, are known to play a role in delaying senescence.

Glossary

apomixis
process by which seeds are produced without fertilization of sperm and egg

cutting
method of asexual reproduction where a portion of the stem contains notes and internodes is placed in moist soil and allowed to root

grafting
method of asexual reproduction where the stem from one plant species is spliced to a different plant

layering
method of propagating plants by bending a stem under the soil

micropropagation
propagation of desirable plants from a plant part; carried out in a laboratory

monocarpic
plants that flower once in their lifetime

polycarpic
plants that flower several times in their lifetime

scion
the part of a plant that is grafted onto the root stock of another plant

senescence
process that describes aging in plant tissues

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40.8: Plant Life Spans

Learning Objectives

- Explain the process of aging in plants

Plant Life Spans

The length of time from the beginning of development to the death of a plant is called its life span. The life cycle, on the other hand, is the sequence of stages a plant goes through from seed germination to seed production of the mature plant. Some plants, such as annuals, only need a few weeks to grow, produce seeds, and die. Other plants, such as the bristlecone pine, live for thousands of years. Some bristlecone pines have a documented age of 4,500 years. Even as some parts of a plant, such as regions containing meristematic tissue (the area of active plant growth consisting of undifferentiated cells capable of cell division) continue to grow, some parts undergo programmed cell death (apoptosis). The cork found on stems and the water-conducting tissue of the xylem, for example, are composed of dead cells.



Figure 40.8.1: Plant life spans: The bristlecone pine, shown here in the Ancient Bristlecone Pine Forest in the White Mountains of eastern California, has been known to live for 4,500 years.

Annuals, Biennial, and Perennials

Plant species that complete their life cycle in one season are known as annuals, an example of which is *Arabidopsis*, or mouse-ear cress. Biennials, such as carrots, complete their life cycle in two seasons. In a biennial's first season, the plant has a vegetative phase, whereas in the next season, it completes its reproductive phase. Commercial growers harvest the carrot roots after the first year of growth and do not allow the plants to flower. Perennials, such as the magnolia, complete their life cycle in two years or more.

Monocarpic and Polycarpic Plants

In another classification based on flowering frequency, monocarpic plants flower only once in their lifetime; examples of monocarpic plants include bamboo and yucca. During the vegetative period of their life cycle (which may be as long as 120 years in some bamboo species), these plants may reproduce asexually, accumulating a great deal of food material that will be required during their once-in-a-lifetime flowering and setting of seed after fertilization. Soon after flowering, these plants die. Polycarpic plants form flowers many times during their lifetime. Fruit trees, such as apple and orange trees, are polycarpic; they flower every year. Other polycarpic species, such as perennials, flower several times during their life span, but not each year. By this method, the plant does not require all its nutrients to be channeled towards flowering each year.

Genetics and Environmental Conditions

As is the case with all living organisms, genetics and environmental conditions have a role to play in determining how long a plant will live. Susceptibility to disease, changing environmental conditions, drought, cold, and competition for nutrients are some of the factors that determine the survival of a plant. Plants continue to grow, despite the presence of dead tissue, such as cork. Individual parts of plants, such as flowers and leaves, have different rates of survival. In many trees, the older leaves turn yellow and eventually fall from the tree. Leaf fall is triggered by factors such as a decrease in photosynthetic efficiency due to shading by upper leaves or oxidative damage incurred as a result of photosynthetic reactions. The components of the part to be shed are

recycled by the plant for use in other processes, such as development of seed and storage. This process is known as nutrient recycling. However, the complex pathways of nutrient recycling within a plant are not well understood

The aging of a plant and all the associated processes is known as senescence, which is marked by several complex biochemical changes. One of the characteristics of senescence is the breakdown of chloroplasts, which is characterized by the yellowing of leaves. The chloroplasts contain components of photosynthetic machinery, such as membranes and proteins. Chloroplasts also contain DNA. The proteins, lipids, and nucleic acids are broken down by specific enzymes into smaller molecules and salvaged by the plant to support the growth of other plant tissues. Hormones are known to play a role in senescence. Applications of cytokinins and ethylene delay or prevent senescence; in contrast, abscissic acid causes premature onset of senescence.



Figure 40.8.1: Plant senescence: The autumn color of these Oregon Grape leaves is an example of programmed plant senescence.

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Key Points

- The life span of a plant is the length of time it takes from the beginning of development until death, while the life cycle is the series of stages between the germination of the seed until the plant produces its own seeds.
- Annuals complete their life cycle in one season; biennials complete their life cycle in two seasons; and perennials complete their life cycle in more than two seasons.
- Monocarpic plants flower only once in their lifetime, while polycarpic plants flower more than once.
- Plant survival depends on changing environmental conditions, drought, cold, and competition.
- Senescence refers to aging of the plant, during which components of the plant cells are broken down and used to support the growth of other plant tissues.

Key Terms

- **annual**: a plant which naturally germinates, flowers, and dies in one year
- **biennial**: a plant that requires two years to complete its life cycle
- **perennial**: a plant that is active throughout the year or survives for more than two growing seasons
- **monocarpic**: a plant that flowers and bears fruit only once before dying
- **polycarpic**: bearing fruit repeatedly, or year after year
- **senescence**: aging of a plant; accumulated damage to macromolecules, cells, tissues, and organs with the passage of time

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CHAPTER OVERVIEW

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41.1: Organization of Animal Bodies

Skills to Develop

- Describe epithelial tissues
- Discuss the different types of connective tissues in animals
- Describe three types of muscle tissues
- Describe nervous tissue

The tissues of multicellular, complex animals are four primary types: epithelial, connective, muscle, and nervous. Recall that tissues are groups of similar cells group of similar cells carrying out related functions. These tissues combine to form organs—like the skin or kidney—that have specific, specialized functions within the body. Organs are organized into organ systems to perform functions; examples include the circulatory system, which consists of the heart and blood vessels, and the digestive system, consisting of several organs, including the stomach, intestines, liver, and pancreas. Organ systems come together to create an entire organism.

Epithelial Tissues

Epithelial tissues cover the outside of organs and structures in the body and line the lumens of organs in a single layer or multiple layers of cells. The types of epithelia are classified by the shapes of cells present and the number of layers of cells. Epithelia composed of a single layer of cells is called simple epithelia; epithelial tissue composed of multiple layers is called stratified epithelia. The table summarizes the different types of epithelial tissues.

Table 41.1.1: Different Types of Epithelial Tissues

Cell shape	Description	Location
squamous	flat, irregular round shape	simple: lung alveoli, capillaries stratified: skin, mouth, vagina
cuboidal	cube shaped, central nucleus	glands, renal tubules
columnar	tall, narrow, nucleus toward base tall, narrow, nucleus along cell	simple: digestive tract pseudostratified: respiratory tract
transitional	round, simple but appear stratified	urinary bladder

Squamous Epithelia

Squamous epithelial cells are generally round, flat, and have a small, centrally located nucleus. The cell outline is slightly irregular, and cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs and the exchange of nutrients and waste at blood capillaries.

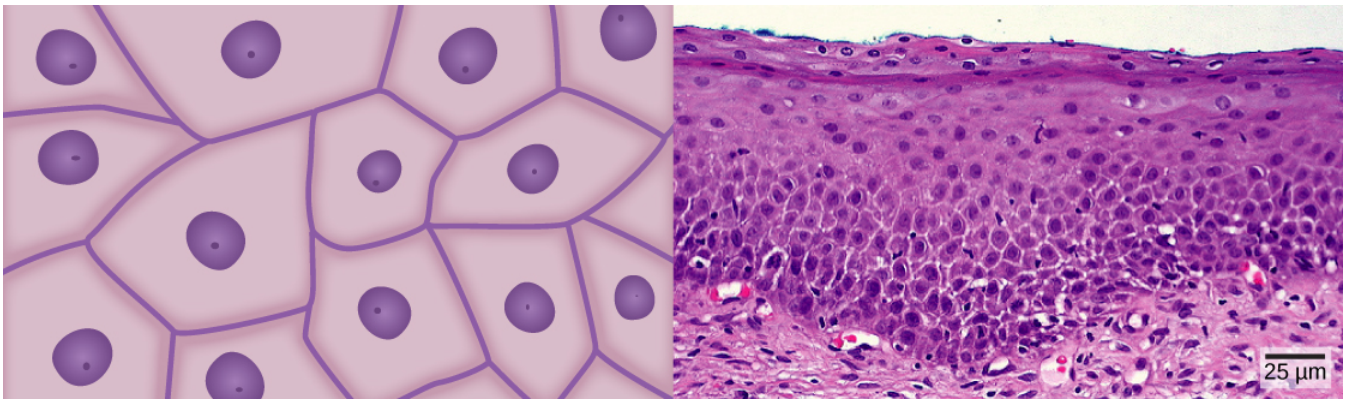


Figure **41.1.1**: Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Figure **41.1.1** illustrates a layer of squamous cells with their membranes joined together to form an epithelium. Image Figure **41.1.1** illustrates squamous epithelial cells arranged in stratified layers, where protection is needed on the body from outside abrasion and damage. This is called a stratified squamous epithelium and occurs in the skin and in tissues lining the mouth and vagina.

Cuboidal Epithelia

Cuboidal epithelial cells, shown in Figure **41.1.2**, are cube-shaped with a single, central nucleus. They are most commonly found in a single layer representing a simple epithelia in glandular tissues throughout the body where they prepare and secrete glandular material. They are also found in the walls of tubules and in the ducts of the kidney and liver.

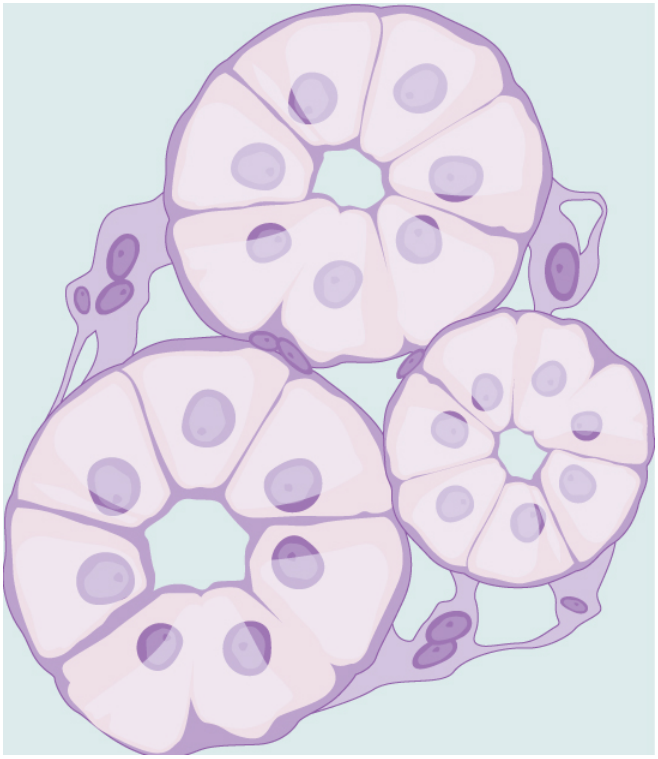


Figure **41.1.2**: Simple cuboidal epithelial cells line tubules in the mammalian kidney, where they are involved in filtering the blood.

Columnar Epithelia

Columnar epithelial cells are taller than they are wide: they resemble a stack of columns in an epithelial layer, and are most commonly found in a single-layer arrangement. The nuclei of columnar epithelial cells in the digestive tract appear to be lined up at the base of the cells, as illustrated in Figure **41.1.3**. These cells absorb material from the lumen of the digestive tract and prepare it for entry into the body through the circulatory and lymphatic systems.

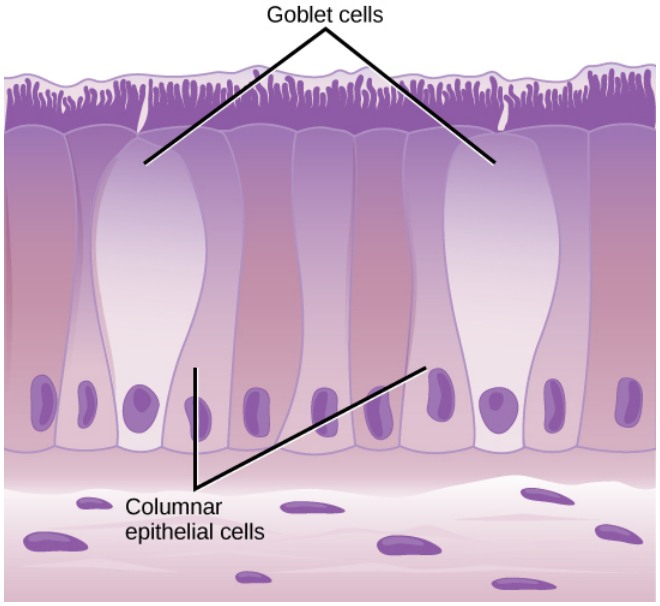


Figure **41.1.3**: Simple columnar epithelial cells absorb material from the digestive tract. Goblet cells secret mucous into the digestive tract lumen.

Columnar epithelial cells lining the respiratory tract appear to be stratified. However, each cell is attached to the base membrane of the tissue and, therefore, they are simple tissues. The nuclei are arranged at different levels in the layer of cells, making it appear as though there is more than one layer, as seen in Figure **41.1.4**. This is called pseudostratified, columnar epithelia. This cellular covering has cilia at the apical, or free, surface of the cells. The cilia enhance the movement of mucous and trapped particles out of the respiratory tract, helping to protect the system from invasive microorganisms and harmful material that has been breathed into the body. Goblet cells are interspersed in some tissues (such as the lining of the trachea). The goblet cells contain mucous that traps irritants, which in the case of the trachea keep these irritants from getting into the lungs.

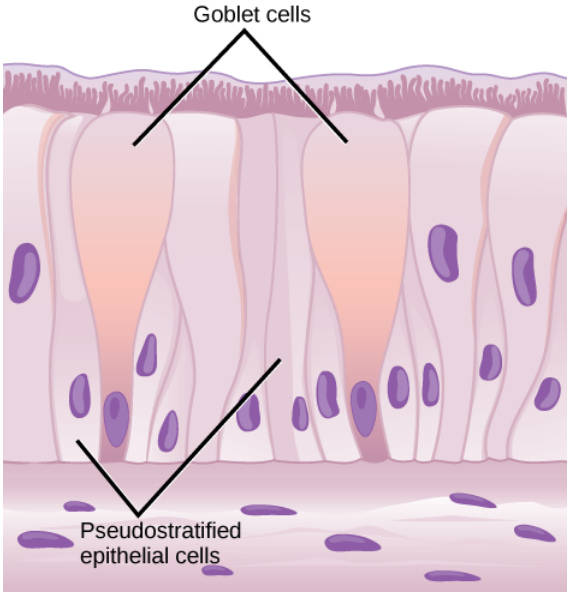


Figure **41.1.4**: Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucous into the respiratory tract.

Transitional Epithelia

Transitional or uroepithelial cells appear only in the urinary system, primarily in the bladder and ureter. These cells are arranged in a stratified layer, but they have the capability of appearing to pile up on top of each other in a relaxed, empty bladder, as illustrated in Figure **41.1.5**. As the urinary bladder fills, the epithelial layer unfolds and expands to hold the volume of urine introduced into it. As the bladder fills, it expands and the lining becomes thinner. In other words, the tissue transitions from thick to thin.

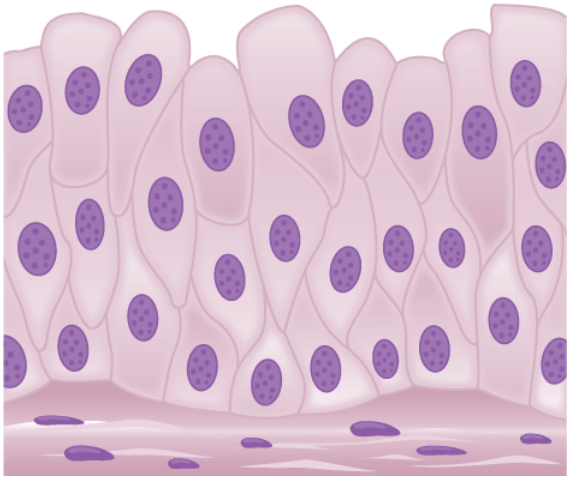


Figure **41.1.5**: Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is.

Exercise

Which of the following statements about types of epithelial cells is false?

A. Simple columnar epithelial cells line the tissue of the lung.
B. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
C. Pseudostratisfied columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
D. Transitional epithelia change in thickness depending on how full the bladder is.

Answer

A

Connective Tissues

Connective tissues are made up of a matrix consisting of living cells and a non-living substance, called the ground substance. The ground substance is made of an organic substance (usually a protein) and an inorganic substance (usually a mineral or water). The principal cell of connective tissues is the fibroblast. This cell makes the fibers found in nearly all of the connective tissues. Fibroblasts are motile, able to carry out mitosis, and can synthesize whichever connective tissue is needed. Macrophages, lymphocytes, and, occasionally, leukocytes can be found in some of the tissues. Some tissues have specialized cells that are not found in the others. The matrix in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has proportionally a less dense matrix.

The organic portion or protein fibers found in connective tissues are either collagen, elastic, or reticular fibers. Collagen fibers provide strength to the tissue, preventing it from being torn or separated from the surrounding tissues. Elastic fibers are made of the protein elastin; this fiber can stretch to one and one half of its length and return to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers are the third type of protein fiber found in connective tissues. This fiber consists of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected. The various types of connective tissues, the types of cells and fibers they are made of, and sample locations of the tissues is summarized in the table.

Table 41.1.2: Connective Tissues

Tissue	Cells	Fibers	Location
loose/areolar	fibroblasts, macrophages, some lymphocytes, some neutrophils	few: collagen, elastic, reticular	around blood vessels; anchors epithelia
dense, fibrous connective tissue	fibroblasts, macrophages,	mostly collagen	irregular: skin regular: tendons, ligaments
cartilage	chondrocytes, chondroblasts	hyaline: few collagen fibrocartilage: large amount of collagen	shark skeleton, fetal bones, human ears, intervertebral discs
bone	osteoblasts, osteocytes, osteoclasts	some: collagen, elastic	vertebrate skeletons
adipose	adipocytes	few	adipose (fat)
blood	red blood cells, white blood cells	none	blood

Loose/Areolar Connective Tissue

Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. As illustrated in Figure **41.1.6**, loose connective tissue has some fibroblasts; macrophages are present as well. Collagen fibers are relatively wide and stain a light pink, while elastic fibers are thin and stain dark blue to black. The space between the formed elements of the tissue is filled with the matrix. The material in the connective tissue gives it a loose consistency similar to a cotton ball that has been pulled apart. Loose connective tissue is found around every blood vessel and helps to keep the vessel in place. The tissue is also found around and between most body organs. In summary, areolar tissue is tough, yet flexible, and comprises membranes.

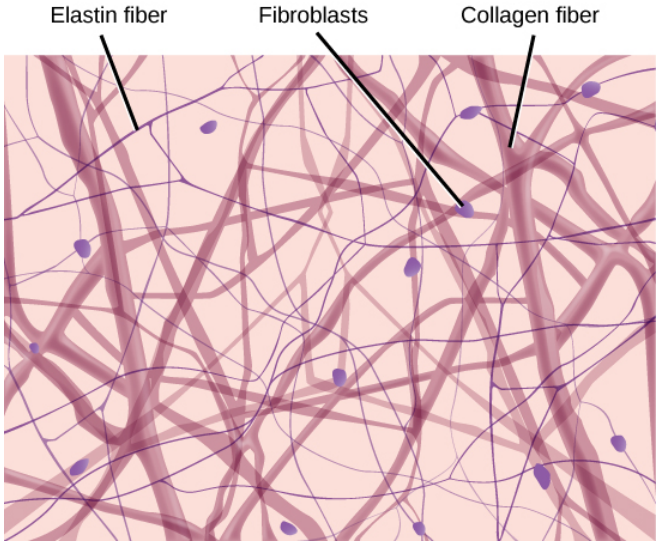


Figure **41.1.6**: Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts.

Fibrous Connective Tissue

Fibrous connective tissues contain large amounts of collagen fibers and few cells or matrix material. The fibers can be arranged irregularly or regularly with the strands lined up in parallel. Irregularly arranged fibrous connective tissues are found in areas of the body where stress occurs from all directions, such as the dermis of the skin. Regular fibrous connective tissue, shown in Figure **41.1.7**, is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).

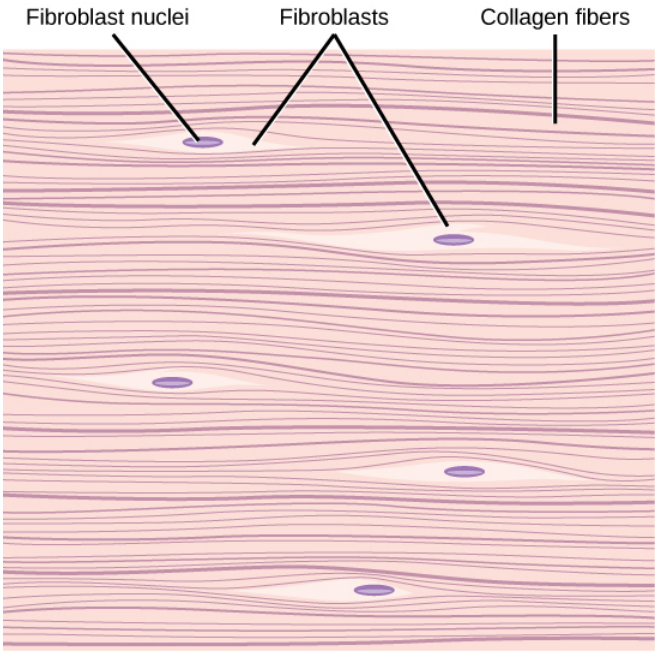


Figure **41.1.7**: Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel.

Cartilage

Cartilage is a connective tissue with a large amount of the matrix and variable amounts of fibers. The cells, called chondrocytes, make the matrix and fibers of the tissue. Chondrocytes are found in spaces within the tissue called lacunae.

A cartilage with few collagen and elastic fibers is hyaline cartilage, illustrated in Figure **41.1.8**. The lacunae are randomly scattered throughout the tissue and the matrix takes on a milky or scrubbed appearance with routine histological stains. Sharks have cartilaginous skeletons, as does nearly the entire human skeleton during a specific pre-birth developmental stage. A remnant of this cartilage persists in the outer portion of the human nose. Hyaline cartilage is also found at the ends of long bones, reducing friction and cushioning the articulations of these bones.

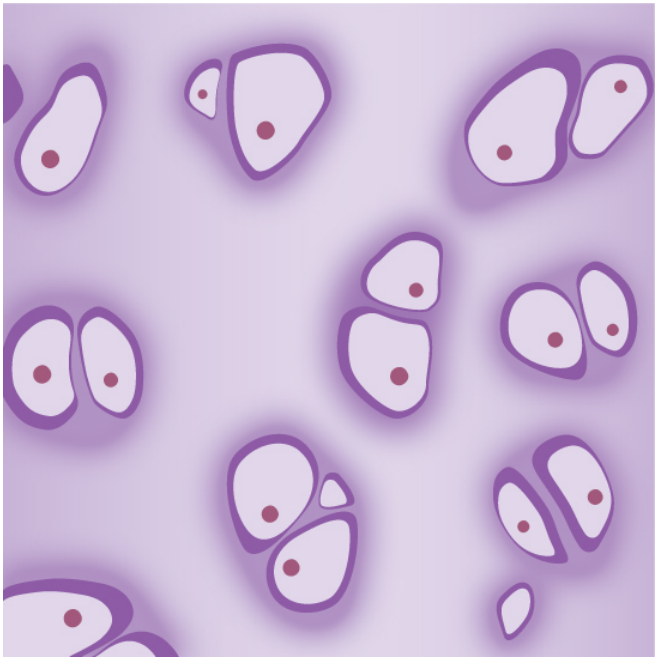


Figure **41.1.8**: Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae.

Elastic cartilage has a large amount of elastic fibers, giving it tremendous flexibility. The ears of most vertebrate animals contain this cartilage as do portions of the larynx, or voice box. Fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage comprises the intervertebral discs in vertebrate animals. Hyaline cartilage found in movable joints such as the knee and shoulder becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage and results in the joints becoming "stiff."

Bone

Bone, or osseous tissue, is a connective tissue that has a large amount of two different types of matrix material. The organic matrix is similar to the matrix material found in other connective tissues, including some amount of collagen and elastic fibers. This gives strength and flexibility to the tissue. The inorganic matrix consists of mineral salts—mostly calcium salts—that give the tissue hardness. Without adequate organic material in the matrix, the tissue breaks; without adequate inorganic material in the matrix, the tissue bends.

There are three types of cells in bone: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are active in making bone for growth and remodeling. Osteoblasts deposit bone material into the matrix and, after the matrix surrounds them, they continue to live, but in a reduced metabolic state as osteocytes. Osteocytes are found in lacunae of the bone. Osteoclasts are active in breaking down bone for bone remodeling, and they provide access to calcium stored in tissues. Osteoclasts are usually found on the surface of the tissue.

Bone can be divided into two types: compact and spongy. Compact bone is found in the shaft (or diaphysis) of a long bone and the surface of the flat bones, while spongy bone is found in the end (or epiphysis) of a long bone. Compact bone is organized into subunits called osteons, as illustrated in Figure **41.1.9**. A blood vessel and a nerve are found in the center of the structure within the Haversian canal, with radiating circles of lacunae around it known as lamellae. The wavy lines seen between the lacunae are microchannels called *canaliculi*; they connect the lacunae to aid diffusion between the cells. Spongy bone is made of tiny plates called trabeculae these plates serve as struts to give the spongy bone strength. Over time, these plates can break causing the bone to become less resilient. Bone tissue forms the internal skeleton of vertebrate animals, providing structure to the animal and points of attachment for tendons.

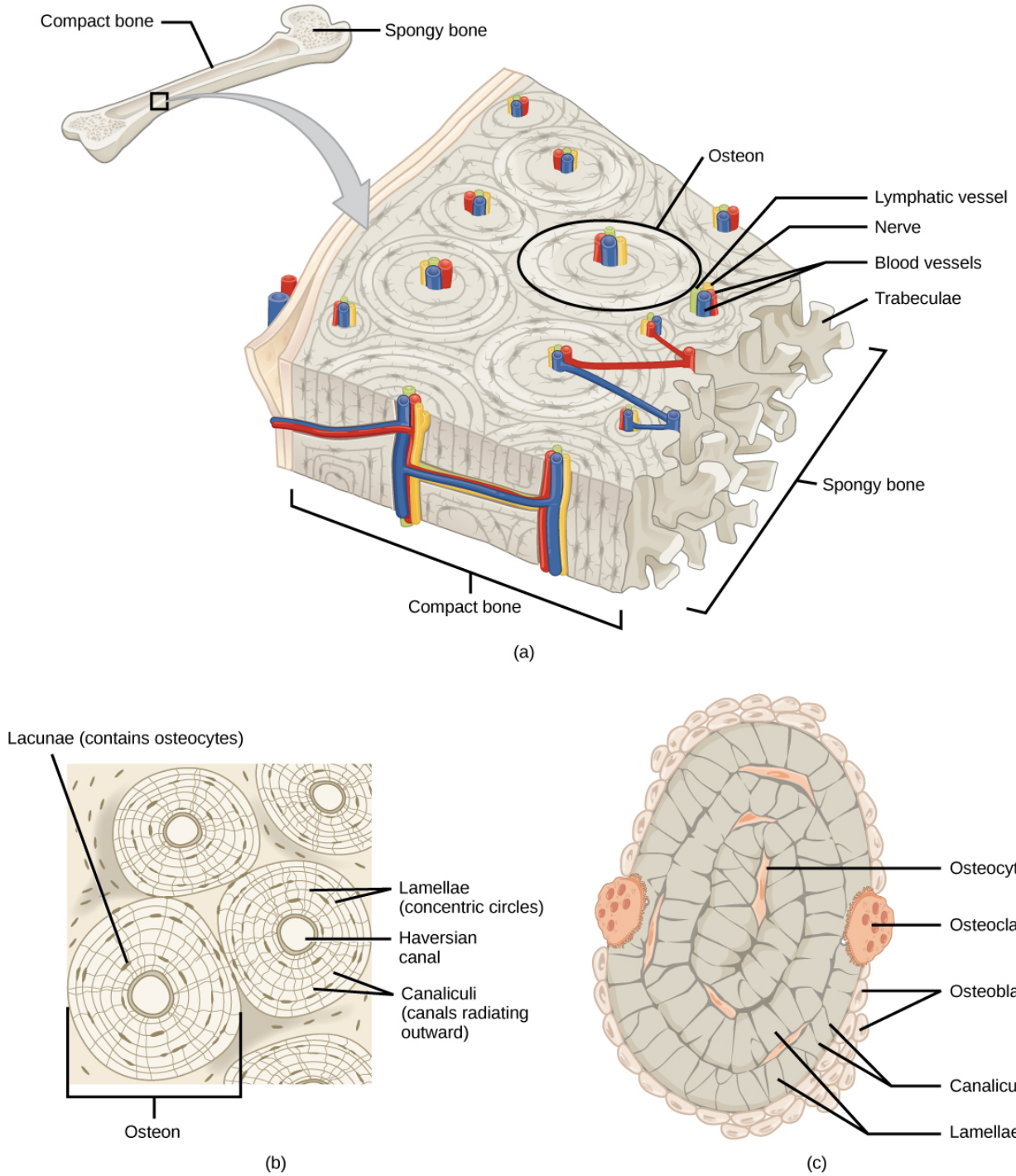


Figure **41.1.9**: (a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are microchannels connecting the lacunae together. (c) Osteoblasts surround the exterior of the bone. Osteoclasts bore tunnels into the bone and osteocytes are found in the lacunae.

Adipose Tissue

Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix and only has a few fibers. Adipose tissue is made up of cells called adipocytes that collect and store fat in the form of triglycerides, for energy metabolism. Adipose tissues additionally serve as insulation to help maintain body temperatures, allowing animals to be endothermic, and they function as cushioning against damage to body organs. Under a microscope, adipose tissue cells appear

empty due to the extraction of fat during the processing of the material for viewing, as seen in Figure **41.1.10**. The thin lines in the image are the cell membranes, and the nuclei are the small, black dots at the edges of the cells.

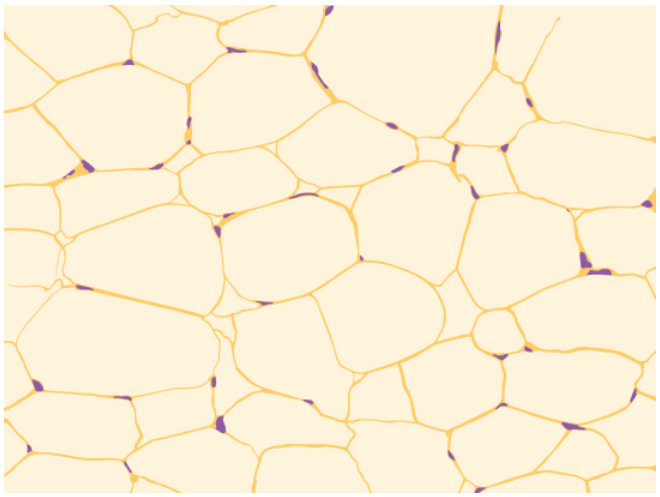


Figure **41.1.10**: Adipose is a connective tissue is made up of cells called adipocytes. Adipocytes have small nuclei localized at the cell edge.

Blood

Blood is considered a connective tissue because it has a matrix, as shown in Figure **41.1.11**. The living cell types are red blood cells (RBC), also called erythrocytes, and white blood cells (WBC), also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.

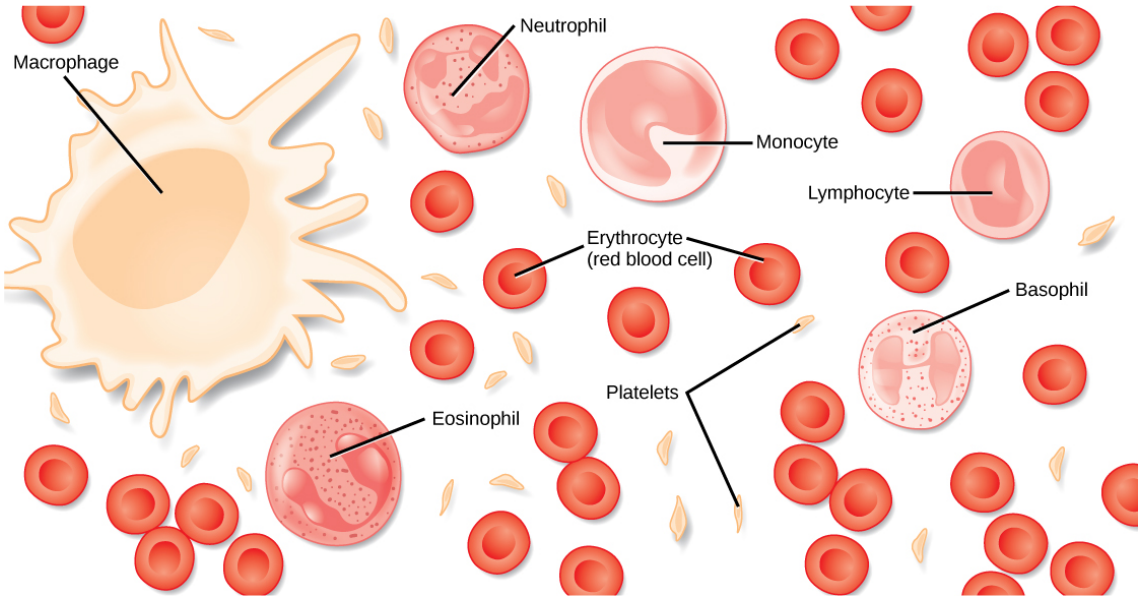


Figure **41.1.11**: Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

The cell found in greatest abundance in blood is the erythrocyte. Erythrocytes are counted in millions in a blood sample: the average number of red blood cells in primates is 4.7 to 5.5 million cells per microliter. Erythrocytes are consistently the same size in a species, but vary in size between species. For example, the average diameter of a primate red blood cell is 7.5 µl, a dog is close at 7.0 µl, but a cat's RBC diameter is 5.9 µl. Sheep erythrocytes are even smaller at 4.6 µl. Mammalian erythrocytes lose their nuclei and mitochondria when they are released from the bone marrow where they are made. Fish, amphibian, and avian red blood cells maintain their nuclei and mitochondria throughout the cell's life. The principal job of an erythrocyte is to carry and deliver oxygen to the tissues.

Leukocytes are the predominant white blood cells found in the peripheral blood. Leukocytes are counted in the thousands in the blood with measurements expressed as ranges: primate counts range from 4,800 to 10,800 cells per µl, dogs from 5,600 to 19,200 cells per µl, cats from 8,000 to 25,000 cells per µl, cattle from 4,000 to 12,000 cells per µl, and pigs from 11,000 to 22,000 cells per µl.

Lymphocytes function primarily in the immune response to foreign antigens or material. Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells and they participate in one of the early lines of defense against microbial invaders, aiding in the removal of bacteria that has entered the body. Another leukocyte that is found in the peripheral blood is the monocyte. Monocytes give rise to phagocytic macrophages that clean up dead and damaged cells in the body, whether they are foreign or from the host animal. Two additional leukocytes in the blood are eosinophils and basophils—both help to facilitate the inflammatory response.

The slightly granular material among the cells is a cytoplasmic fragment of a cell in the bone marrow. This is called a platelet or thrombocyte. Platelets participate in the stages leading up to coagulation of the blood to stop bleeding through damaged blood vessels. Blood has a number of functions, but primarily it transports material through the body to bring nutrients to cells and remove waste material from them.

Muscle Tissues

There are three types of muscle in animal bodies: smooth, skeletal, and cardiac. They differ by the presence or absence of striations or bands, the number and location of nuclei, whether they are voluntarily or involuntarily controlled, and their location within the body. The table summarizes these differences.

Table 41.1.3: Types of Muscles

Type of Muscle	Striations	Nuclei	Control	Location
smooth	no	single, in center	involuntary	visceral organs
skeletal	yes	many, at periphery	voluntary	skeletal muscles
cardiac	yes	single, in center	involuntary	heart

Smooth Muscle

Smooth muscle does not have striations in its cells. It has a single, centrally located nucleus, as shown in Figure **41.1.12**. Constriction of smooth muscle occurs under involuntary, autonomic nervous control and in response to local conditions in the tissues. Smooth muscle tissue is also called non-striated as it lacks the banded appearance of skeletal and cardiac muscle. The walls of blood vessels, the tubes of the digestive system, and the tubes of the reproductive systems are composed of mostly smooth muscle.

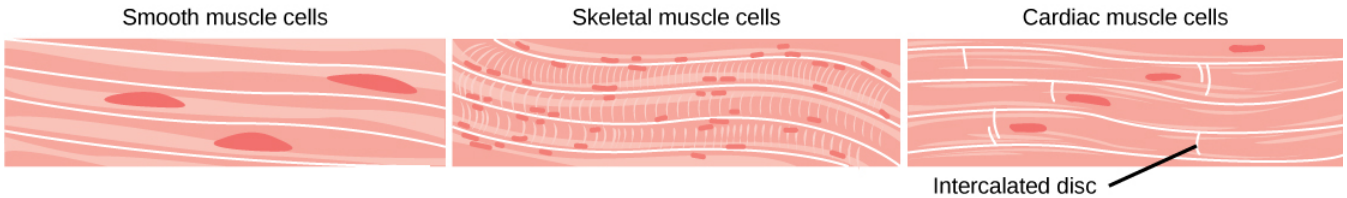


Figure **41.1.12**: Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

Skeletal Muscle

Skeletal muscle has striations across its cells caused by the arrangement of the contractile proteins actin and myosin. These muscle cells are relatively long and have multiple nuclei along the edge of the cell. Skeletal muscle is under voluntary, somatic nervous system control and is found in the muscles that move bones. Figure **41.1.12**illustrates the histology of skeletal muscle.

Cardiac Muscle

Cardiac muscle, shown in Figure **41.1.12**, is found only in the heart. Like skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally located nucleus. Cardiac muscle is not under voluntary control but can be influenced by the autonomic nervous system to speed up or slow down. An added feature to cardiac muscle cells is a line than extends along the end of the cell as it abuts the next cardiac cell in the row. This line is called an intercalated disc: it assists in passing electrical impulse efficiently from one cell to the next and maintains the strong connection between neighboring cardiac cells.

Nervous Tissues

Nervous tissues are made of cells specialized to receive and transmit electrical impulses from specific areas of the body and to send them to specific locations in the body. The main cell of the nervous system is the neuron, illustrated in Figure **41.1.13**. The large structure with a central nucleus is the cell body of the neuron. Projections from the cell body are either dendrites specialized in receiving input or a single axon specialized in transmitting impulses. Some glial cells are also shown. Astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells that are not shown support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic and remove debris or damaged cells from the tissue. A nerve consists of neurons and glial cells.

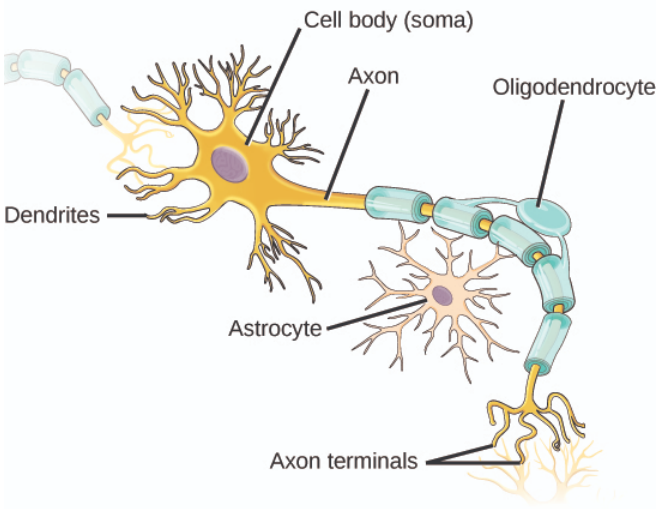


Figure **41.1.13**: The neuron has projections called dendrites that receive signals and projections called axons that send signals. Also shown are two types of glial cells: astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently.

Link to Learning

Click through the interactive review to learn more about epithelial tissues.

Career Connections: Pathologist

A pathologist is a medical doctor or veterinarian who has specialized in the laboratory detection of disease in animals, including humans. These professionals complete medical school education and follow it with an extensive post-graduate residency at a medical center. A pathologist may oversee clinical laboratories for the evaluation of body tissue and blood

samples for the detection of disease or infection. They examine tissue specimens through a microscope to identify cancers and other diseases. Some pathologists perform autopsies to determine the cause of death and the progression of disease.

Summary

The basic building blocks of complex animals are four primary tissues. These are combined to form organs, which have a specific, specialized function within the body, such as the skin or kidney. Organs are organized together to perform common functions in the form of systems. The four primary tissues are epithelia, connective tissues, muscle tissues, and nervous tissues.

Glossary

canaliculus
microchannel that connects the lacunae and aids diffusion between cells

cartilage
type of connective tissue with a large amount of ground substance matrix, cells called chondrocytes, and some amount of fibers

chondrocyte
cell found in cartilage

columnar epithelia
epithelia made of cells taller than they are wide, specialized in absorption

connective tissue
type of tissue made of cells, ground substance matrix, and fibers

cuboidal epithelia
epithelia made of cube-shaped cells, specialized in glandular functions

epithelial tissue
tissue that either lines or covers organs or other tissues

fibrous connective tissue
type of connective tissue with a high concentration of fibers

lacuna
space in cartilage and bone that contains living cells

loose (areolar) connective tissue
type of connective tissue with small amounts of cells, matrix, and fibers; found around blood vessels

matrix
component of connective tissue made of both living and non-living (ground substances) cells

osteon
subunit of compact bone

pseudostratified
layer of epithelia that appears multilayered, but is a simple covering

simple epithelia
single layer of epithelial cells

squamous epithelia

type of epithelia made of flat cells, specialized in aiding diffusion or preventing abrasion

stratified epithelia

multiple layers of epithelial cells

trabecula

tiny plate that makes up spongy bone and gives it strength

transitional epithelia

epithelia that can transition for appearing multilayered to simple; also called uroepithelial

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41.2: Epithelial Tissue

Skills to Develop

- Describe epithelial tissues
- Discuss the different types of connective tissues in animals
- Describe three types of muscle tissues
- Describe nervous tissue

The tissues of multicellular, complex animals are four primary types: epithelial, connective, muscle, and nervous. Recall that tissues are groups of similar cells group of similar cells carrying out related functions. These tissues combine to form organs—like the skin or kidney—that have specific, specialized functions within the body. Organs are organized into organ systems to perform functions; examples include the circulatory system, which consists of the heart and blood vessels, and the digestive system, consisting of several organs, including the stomach, intestines, liver, and pancreas. Organ systems come together to create an entire organism.

Epithelial Tissues

Epithelial tissues cover the outside of organs and structures in the body and line the lumens of organs in a single layer or multiple layers of cells. The types of epithelia are classified by the shapes of cells present and the number of layers of cells. Epithelia composed of a single layer of cells is called simple epithelia; epithelial tissue composed of multiple layers is called stratified epithelia. The table summarizes the different types of epithelial tissues.

Table 41.2.1: Different Types of Epithelial Tissues

Cell shape	Description	Location
squamous	flat, irregular round shape	simple: lung alveoli, capillaries stratified: skin, mouth, vagina
cuboidal	cube shaped, central nucleus	glands, renal tubules
columnar	tall, narrow, nucleus toward base tall, narrow, nucleus along cell	simple: digestive tract pseudostratified: respiratory tract
transitional	round, simple but appear stratified	urinary bladder

Squamous Epithelia

Squamous epithelial cells are generally round, flat, and have a small, centrally located nucleus. The cell outline is slightly irregular, and cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs and the exchange of nutrients and waste at blood capillaries.

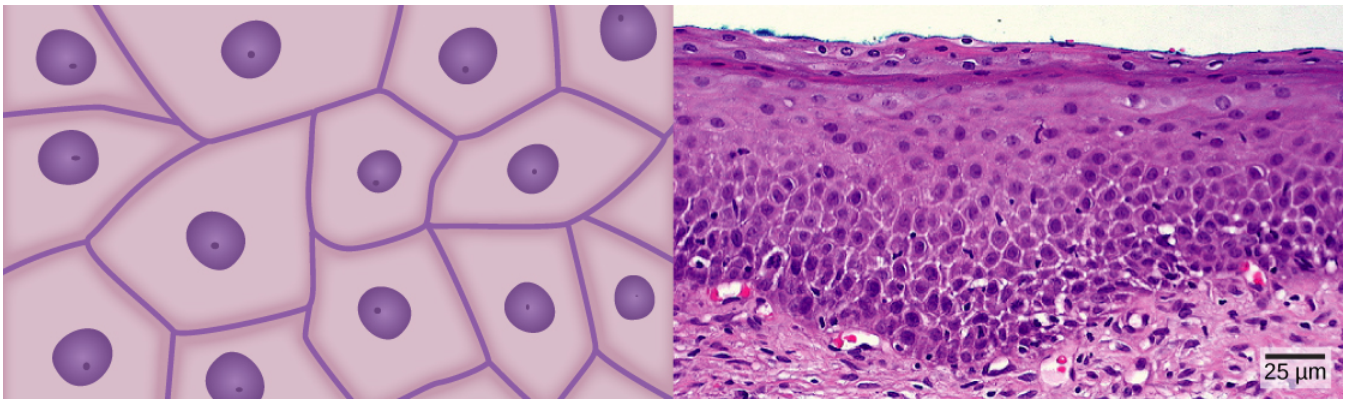


Figure 41.2.1: Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Figure 41.2.1 illustrates a layer of squamous cells with their membranes joined together to form an epithelium. Image Figure 41.2.1 illustrates squamous epithelial cells arranged in stratified layers, where protection is needed on the body from outside abrasion and damage. This is called a stratified squamous epithelium and occurs in the skin and in tissues lining the mouth and vagina.

Cuboidal Epithelia

Cuboidal epithelial cells, shown in Figure 41.2.2, are cube-shaped with a single, central nucleus. They are most commonly found in a single layer representing a simple epithelia in glandular tissues throughout the body where they prepare and secrete glandular material. They are also found in the walls of tubules and in the ducts of the kidney and liver.

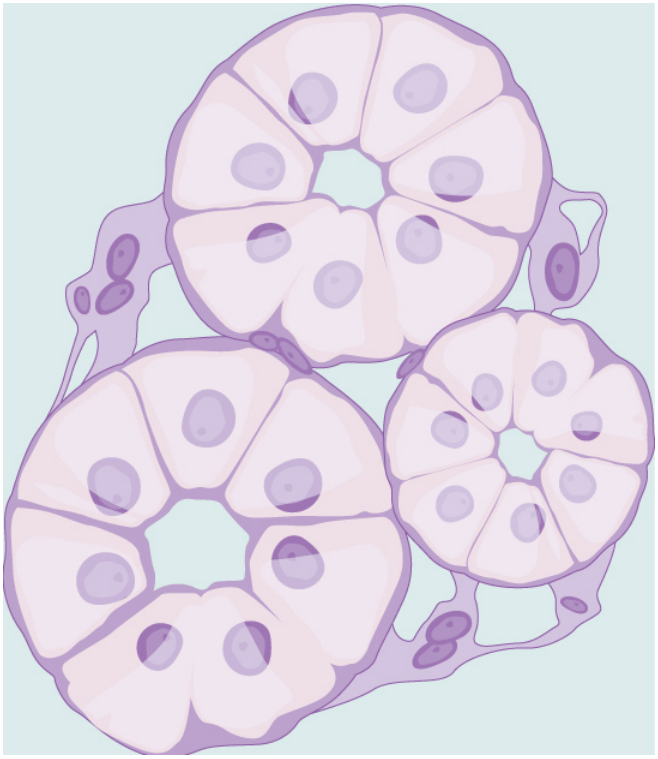


Figure 41.2.2: Simple cuboidal epithelial cells line tubules in the mammalian kidney, where they are involved in filtering the blood.

Columnar Epithelia

Columnar epithelial cells are taller than they are wide: they resemble a stack of columns in an epithelial layer, and are most commonly found in a single-layer arrangement. The nuclei of columnar epithelial cells in the digestive tract appear to be lined up at the base of the cells, as illustrated in Figure 41.2.3. These cells absorb material from the lumen of the digestive tract and prepare it for entry into the body through the circulatory and lymphatic systems.

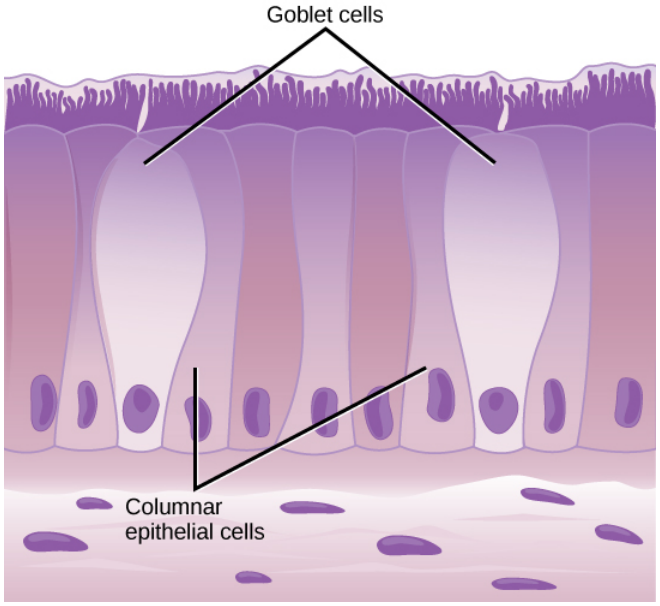


Figure **41.2.3**: Simple columnar epithelial cells absorb material from the digestive tract. Goblet cells secret mucous into the digestive tract lumen.

Columnar epithelial cells lining the respiratory tract appear to be stratified. However, each cell is attached to the base membrane of the tissue and, therefore, they are simple tissues. The nuclei are arranged at different levels in the layer of cells, making it appear as though there is more than one layer, as seen in Figure **41.2.4**. This is called pseudostratified, columnar epithelia. This cellular covering has cilia at the apical, or free, surface of the cells. The cilia enhance the movement of mucous and trapped particles out of the respiratory tract, helping to protect the system from invasive microorganisms and harmful material that has been breathed into the body. Goblet cells are interspersed in some tissues (such as the lining of the trachea). The goblet cells contain mucous that traps irritants, which in the case of the trachea keep these irritants from getting into the lungs.

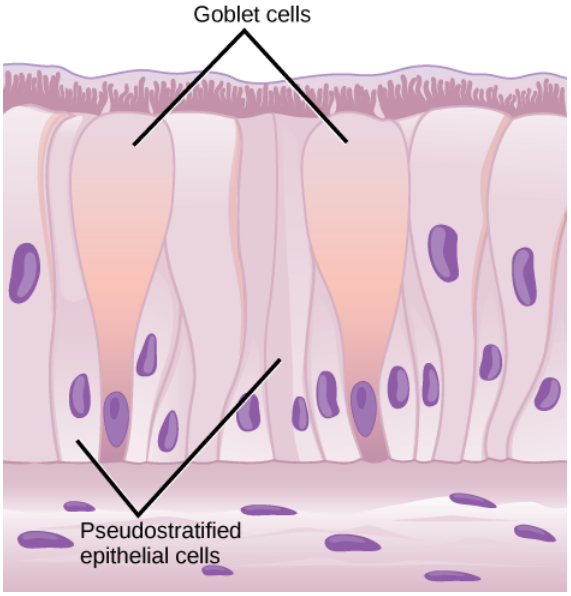


Figure **41.2.4**: Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucous into the respiratory tract.

Transitional Epithelia

Transitional or uroepithelial cells appear only in the urinary system, primarily in the bladder and ureter. These cells are arranged in a stratified layer, but they have the capability of appearing to pile up on top of each other in a relaxed, empty bladder, as illustrated in Figure **41.2.5**. As the urinary bladder fills, the epithelial layer unfolds and expands to hold the volume of urine introduced into it. As the bladder fills, it expands and the lining becomes thinner. In other words, the tissue transitions from thick to thin.

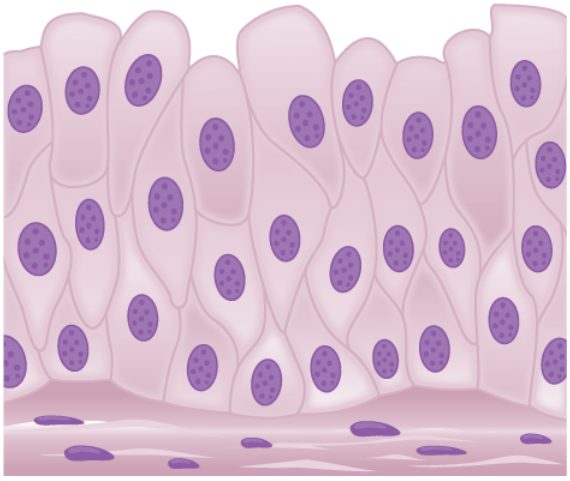


Figure **41.2.5**: Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is.

Exercise

Which of the following statements about types of epithelial cells is false?

A. Simple columnar epithelial cells line the tissue of the lung.
B. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
C. Pseudostratisfied columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
D. Transitional epithelia change in thickness depending on how full the bladder is.

Answer

A

Connective Tissues

Connective tissues are made up of a matrix consisting of living cells and a non-living substance, called the ground substance. The ground substance is made of an organic substance (usually a protein) and an inorganic substance (usually a mineral or water). The principal cell of connective tissues is the fibroblast. This cell makes the fibers found in nearly all of the connective tissues. Fibroblasts are motile, able to carry out mitosis, and can synthesize whichever connective tissue is needed. Macrophages, lymphocytes, and, occasionally, leukocytes can be found in some of the tissues. Some tissues have specialized cells that are not found in the others. The matrix in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has proportionally a less dense matrix.

The organic portion or protein fibers found in connective tissues are either collagen, elastic, or reticular fibers. Collagen fibers provide strength to the tissue, preventing it from being torn or separated from the surrounding tissues. Elastic fibers are made of the protein elastin; this fiber can stretch to one and one half of its length and return to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers are the third type of protein fiber found in connective tissues. This fiber consists of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected. The various types of connective tissues, the types of cells and fibers they are made of, and sample locations of the tissues is summarized in the table.

Table 41.2.2: Connective Tissues

Tissue	Cells	Fibers	Location
loose/areolar	fibroblasts, macrophages, some lymphocytes, some neutrophils	few: collagen, elastic, reticular	around blood vessels; anchors epithelia
dense, fibrous connective tissue	fibroblasts, macrophages,	mostly collagen	irregular: skin regular: tendons, ligaments
cartilage	chondrocytes, chondroblasts	hyaline: few collagen fibrocartilage: large amount of collagen	shark skeleton, fetal bones, human ears, intervertebral discs
bone	osteoblasts, osteocytes, osteoclasts	some: collagen, elastic	vertebrate skeletons
adipose	adipocytes	few	adipose (fat)
blood	red blood cells, white blood cells	none	blood

Loose/Areolar Connective Tissue

Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. As illustrated in Figure **41.2.6**, loose connective tissue has some fibroblasts; macrophages are present as well. Collagen fibers are relatively wide and stain a light pink, while elastic fibers are thin and stain dark blue to black. The space between the formed elements of the tissue is filled with the matrix. The material in the connective tissue gives it a loose consistency similar to a cotton ball that has been pulled apart. Loose connective tissue is found around every blood vessel and helps to keep the vessel in place. The tissue is also found around and between most body organs. In summary, areolar tissue is tough, yet flexible, and comprises membranes.

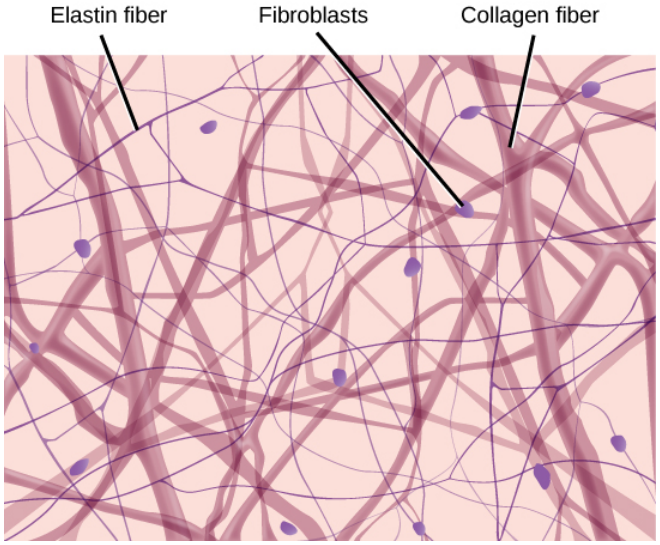


Figure **41.2.6**: Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts.

Fibrous Connective Tissue

Fibrous connective tissues contain large amounts of collagen fibers and few cells or matrix material. The fibers can be arranged irregularly or regularly with the strands lined up in parallel. Irregularly arranged fibrous connective tissues are found in areas of the body where stress occurs from all directions, such as the dermis of the skin. Regular fibrous connective tissue, shown in Figure **41.2.7**, is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).

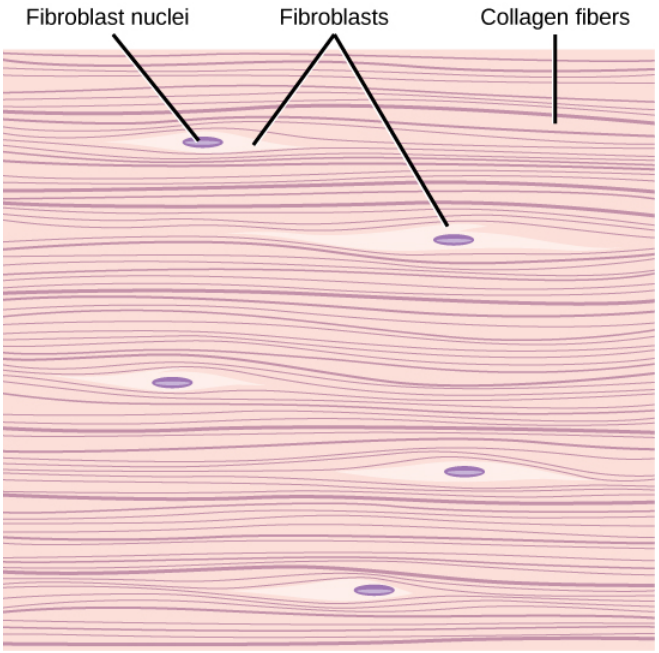


Figure **41.2.7**: Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel.

Cartilage

Cartilage is a connective tissue with a large amount of the matrix and variable amounts of fibers. The cells, called chondrocytes, make the matrix and fibers of the tissue. Chondrocytes are found in spaces within the tissue called lacunae.

A cartilage with few collagen and elastic fibers is hyaline cartilage, illustrated in Figure **41.2.8**. The lacunae are randomly scattered throughout the tissue and the matrix takes on a milky or scrubbed appearance with routine histological stains. Sharks have cartilaginous skeletons, as does nearly the entire human skeleton during a specific pre-birth developmental stage. A remnant of this cartilage persists in the outer portion of the human nose. Hyaline cartilage is also found at the ends of long bones, reducing friction and cushioning the articulations of these bones.

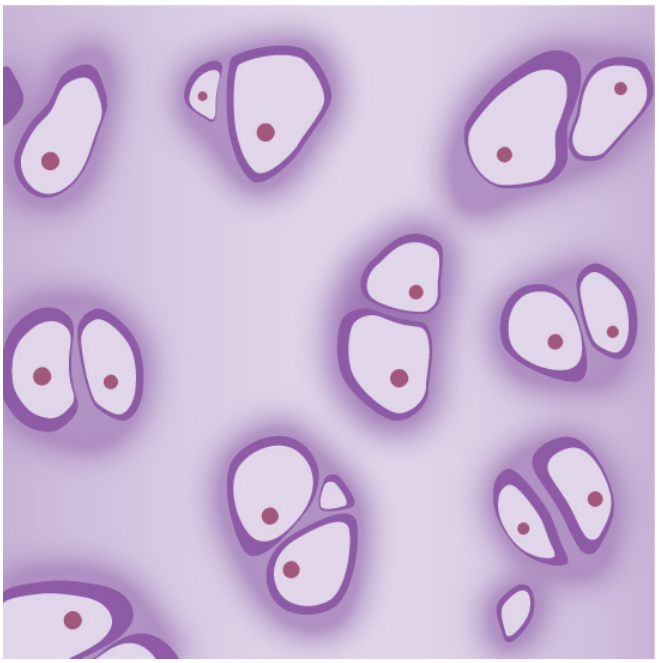


Figure **41.2.8**: Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae.

Elastic cartilage has a large amount of elastic fibers, giving it tremendous flexibility. The ears of most vertebrate animals contain this cartilage as do portions of the larynx, or voice box. Fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage comprises the intervertebral discs in vertebrate animals. Hyaline cartilage found in movable joints such as the knee and shoulder becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage and results in the joints becoming "stiff."

Bone

Bone, or osseous tissue, is a connective tissue that has a large amount of two different types of matrix material. The organic matrix is similar to the matrix material found in other connective tissues, including some amount of collagen and elastic fibers. This gives strength and flexibility to the tissue. The inorganic matrix consists of mineral salts—mostly calcium salts—that give the tissue hardness. Without adequate organic material in the matrix, the tissue breaks; without adequate inorganic material in the matrix, the tissue bends.

There are three types of cells in bone: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are active in making bone for growth and remodeling. Osteoblasts deposit bone material into the matrix and, after the matrix surrounds them, they continue to live, but in a reduced metabolic state as osteocytes. Osteocytes are found in lacunae of the bone. Osteoclasts are active in breaking down bone for bone remodeling, and they provide access to calcium stored in tissues. Osteoclasts are usually found on the surface of the tissue.

Bone can be divided into two types: compact and spongy. Compact bone is found in the shaft (or diaphysis) of a long bone and the surface of the flat bones, while spongy bone is found in the end (or epiphysis) of a long bone. Compact bone is organized into subunits called osteons, as illustrated in Figure **41.2.9**. A blood vessel and a nerve are found in the center of the structure within the Haversian canal, with radiating circles of lacunae around it known as lamellae. The wavy lines seen between the lacunae are microchannels called *canaliculi*; they connect the lacunae to aid diffusion between the cells. Spongy bone is made of tiny plates called trabeculae these plates serve as struts to give the spongy bone strength. Over time, these plates can break causing the bone to become less resilient. Bone tissue forms the internal skeleton of vertebrate animals, providing structure to the animal and points of attachment for tendons.

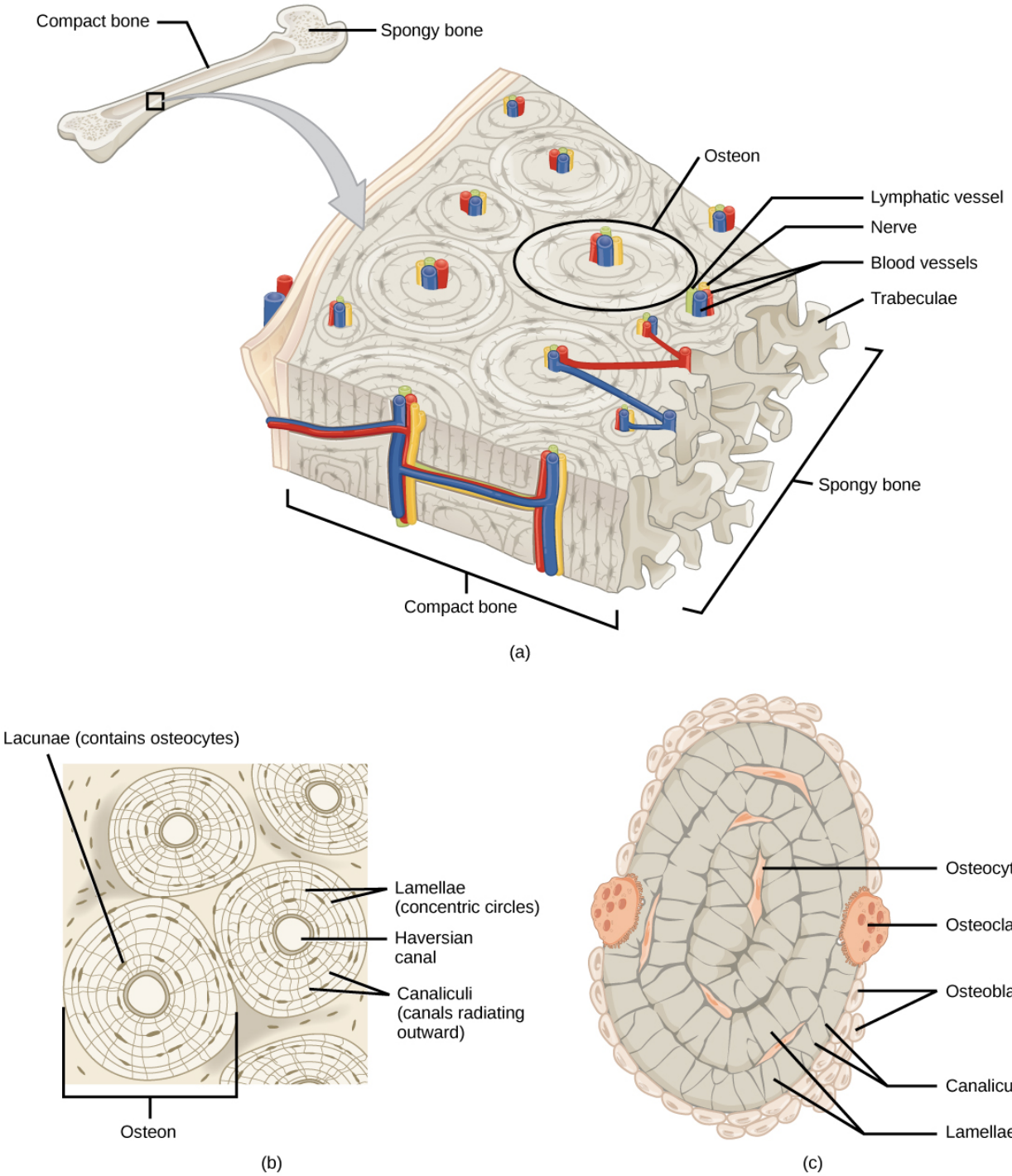


Figure **41.2.9**: (a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are microchannels connecting the lacunae together. (c) Osteoblasts surround the exterior of the bone. Osteoclasts bore tunnels into the bone and osteocytes are found in the lacunae.

Adipose Tissue

Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix and only has a few fibers. Adipose tissue is made up of cells called adipocytes that collect and store fat in the form of triglycerides, for energy metabolism. Adipose tissues additionally serve as insulation to help maintain body temperatures, allowing animals to be endothermic, and they function as cushioning against damage to body organs. Under a microscope, adipose tissue cells appear

empty due to the extraction of fat during the processing of the material for viewing, as seen in Figure 41.2.10. The thin lines in the image are the cell membranes, and the nuclei are the small, black dots at the edges of the cells.

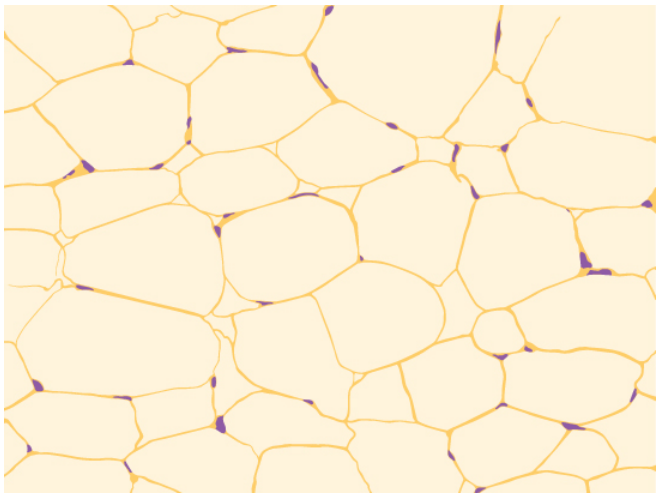


Figure 41.2.10: Adipose is a connective tissue is made up of cells called adipocytes. Adipocytes have small nuclei localized at the cell edge.

Blood

Blood is considered a connective tissue because it has a matrix, as shown in Figure 41.2.11. The living cell types are red blood cells (RBC), also called erythrocytes, and white blood cells (WBC), also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.

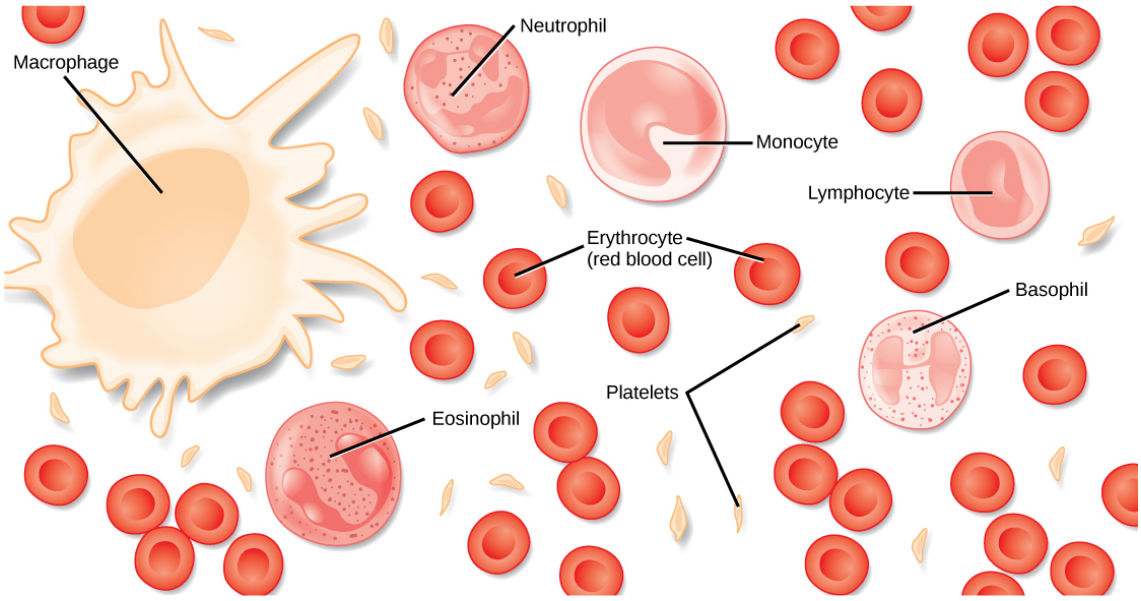


Figure 41.2.11: Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

The cell found in greatest abundance in blood is the erythrocyte. Erythrocytes are counted in millions in a blood sample: the average number of red blood cells in primates is 4.7 to 5.5 million cells per microliter. Erythrocytes are consistently the same size in a species, but vary in size between species. For example, the average diameter of a primate red blood cell is 7.5 µl, a dog is close at 7.0 µl, but a cat's RBC diameter is 5.9 µl. Sheep erythrocytes are even smaller at 4.6 µl. Mammalian erythrocytes lose their nuclei and mitochondria when they are released from the bone marrow where they are made. Fish, amphibian, and avian red blood cells maintain their nuclei and mitochondria throughout the cell's life. The principal job of an erythrocyte is to carry and deliver oxygen to the tissues.

Leukocytes are the predominant white blood cells found in the peripheral blood. Leukocytes are counted in the thousands in the blood with measurements expressed as ranges: primate counts range from 4,800 to 10,800 cells per µl, dogs from 5,600 to 19,200 cells per µl, cats from 8,000 to 25,000 cells per µl, cattle from 4,000 to 12,000 cells per µl, and pigs from 11,000 to 22,000 cells per µl.

Lymphocytes function primarily in the immune response to foreign antigens or material. Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells and they participate in one of the early lines of defense against microbial invaders, aiding in the removal of bacteria that has entered the body. Another leukocyte that is found in the peripheral blood is the monocyte. Monocytes give rise to phagocytic macrophages that clean up dead and damaged cells in the body, whether they are foreign or from the host animal. Two additional leukocytes in the blood are eosinophils and basophils—both help to facilitate the inflammatory response.

The slightly granular material among the cells is a cytoplasmic fragment of a cell in the bone marrow. This is called a platelet or thrombocyte. Platelets participate in the stages leading up to coagulation of the blood to stop bleeding through damaged blood vessels. Blood has a number of functions, but primarily it transports material through the body to bring nutrients to cells and remove waste material from them.

Muscle Tissues

There are three types of muscle in animal bodies: smooth, skeletal, and cardiac. They differ by the presence or absence of striations or bands, the number and location of nuclei, whether they are voluntarily or involuntarily controlled, and their location within the body. The table summarizes these differences.

Table 41.2.3: Types of Muscles

Type of Muscle	Striations	Nuclei	Control	Location
smooth	no	single, in center	involuntary	visceral organs
skeletal	yes	many, at periphery	voluntary	skeletal muscles
cardiac	yes	single, in center	involuntary	heart

Smooth Muscle

Smooth muscle does not have striations in its cells. It has a single, centrally located nucleus, as shown in Figure **41.2.12**. Constriction of smooth muscle occurs under involuntary, autonomic nervous control and in response to local conditions in the tissues. Smooth muscle tissue is also called non-striated as it lacks the banded appearance of skeletal and cardiac muscle. The walls of blood vessels, the tubes of the digestive system, and the tubes of the reproductive systems are composed of mostly smooth muscle.

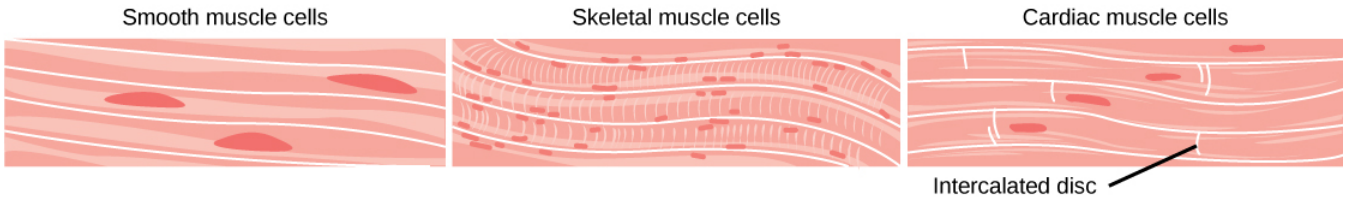


Figure **41.2.12**: Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

Skeletal Muscle

Skeletal muscle has striations across its cells caused by the arrangement of the contractile proteins actin and myosin. These muscle cells are relatively long and have multiple nuclei along the edge of the cell. Skeletal muscle is under voluntary, somatic nervous system control and is found in the muscles that move bones. Figure **41.2.12**illustrates the histology of skeletal muscle.

Cardiac Muscle

Cardiac muscle, shown in Figure **41.2.12**, is found only in the heart. Like skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally located nucleus. Cardiac muscle is not under voluntary control but can be influenced by the autonomic nervous system to speed up or slow down. An added feature to cardiac muscle cells is a line than extends along the end of the cell as it abuts the next cardiac cell in the row. This line is called an intercalated disc: it assists in passing electrical impulse efficiently from one cell to the next and maintains the strong connection between neighboring cardiac cells.

Nervous Tissues

Nervous tissues are made of cells specialized to receive and transmit electrical impulses from specific areas of the body and to send them to specific locations in the body. The main cell of the nervous system is the neuron, illustrated in Figure **41.2.13**. The large structure with a central nucleus is the cell body of the neuron. Projections from the cell body are either dendrites specialized in receiving input or a single axon specialized in transmitting impulses. Some glial cells are also shown. Astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells that are not shown support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic and remove debris or damaged cells from the tissue. A nerve consists of neurons and glial cells.

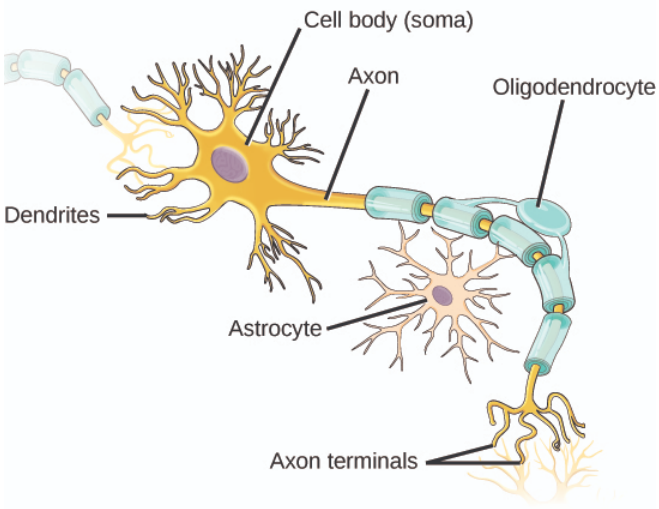


Figure **41.2.13**: The neuron has projections called dendrites that receive signals and projections called axons that send signals. Also shown are two types of glial cells: astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently.

Link to Learning

Click through the interactive review to learn more about epithelial tissues.

Career Connections: Pathologist

A pathologist is a medical doctor or veterinarian who has specialized in the laboratory detection of disease in animals, including humans. These professionals complete medical school education and follow it with an extensive post-graduate residency at a medical center. A pathologist may oversee clinical laboratories for the evaluation of body tissue and blood

samples for the detection of disease or infection. They examine tissue specimens through a microscope to identify cancers and other diseases. Some pathologists perform autopsies to determine the cause of death and the progression of disease.

Summary

The basic building blocks of complex animals are four primary tissues. These are combined to form organs, which have a specific, specialized function within the body, such as the skin or kidney. Organs are organized together to perform common functions in the form of systems. The four primary tissues are epithelia, connective tissues, muscle tissues, and nervous tissues.

Glossary

canaliculus
microchannel that connects the lacunae and aids diffusion between cells

cartilage
type of connective tissue with a large amount of ground substance matrix, cells called chondrocytes, and some amount of fibers

chondrocyte
cell found in cartilage

columnar epithelia
epithelia made of cells taller than they are wide, specialized in absorption

connective tissue
type of tissue made of cells, ground substance matrix, and fibers

cuboidal epithelia
epithelia made of cube-shaped cells, specialized in glandular functions

epithelial tissue
tissue that either lines or covers organs or other tissues

fibrous connective tissue
type of connective tissue with a high concentration of fibers

lacuna
space in cartilage and bone that contains living cells

loose (areolar) connective tissue
type of connective tissue with small amounts of cells, matrix, and fibers; found around blood vessels

matrix
component of connective tissue made of both living and non-living (ground substances) cells

osteon
subunit of compact bone

pseudostratified
layer of epithelia that appears multilayered, but is a simple covering

simple epithelia
single layer of epithelial cells

squamous epithelia

type of epithelia made of flat cells, specialized in aiding diffusion or preventing abrasion

stratified epithelia

multiple layers of epithelial cells

trabecula

tiny plate that makes up spongy bone and gives it strength

transitional epithelia

epithelia that can transition for appearing multilayered to simple; also called uroepithelial

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41.3: Connective Tissue

Skills to Develop

- Describe epithelial tissues
- Discuss the different types of connective tissues in animals
- Describe three types of muscle tissues
- Describe nervous tissue

The tissues of multicellular, complex animals are four primary types: epithelial, connective, muscle, and nervous. Recall that tissues are groups of similar cells group of similar cells carrying out related functions. These tissues combine to form organs—like the skin or kidney—that have specific, specialized functions within the body. Organs are organized into organ systems to perform functions; examples include the circulatory system, which consists of the heart and blood vessels, and the digestive system, consisting of several organs, including the stomach, intestines, liver, and pancreas. Organ systems come together to create an entire organism.

Epithelial Tissues

Epithelial tissues cover the outside of organs and structures in the body and line the lumens of organs in a single layer or multiple layers of cells. The types of epithelia are classified by the shapes of cells present and the number of layers of cells. Epithelia composed of a single layer of cells is called simple epithelia; epithelial tissue composed of multiple layers is called stratified epithelia. The table summarizes the different types of epithelial tissues.

Table 41.3.1: Different Types of Epithelial Tissues

Cell shape	Description	Location
squamous	flat, irregular round shape	simple: lung alveoli, capillaries stratified: skin, mouth, vagina
cuboidal	cube shaped, central nucleus	glands, renal tubules
columnar	tall, narrow, nucleus toward base tall, narrow, nucleus along cell	simple: digestive tract pseudostratified: respiratory tract
transitional	round, simple but appear stratified	urinary bladder

Squamous Epithelia

Squamous epithelial cells are generally round, flat, and have a small, centrally located nucleus. The cell outline is slightly irregular, and cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs and the exchange of nutrients and waste at blood capillaries.

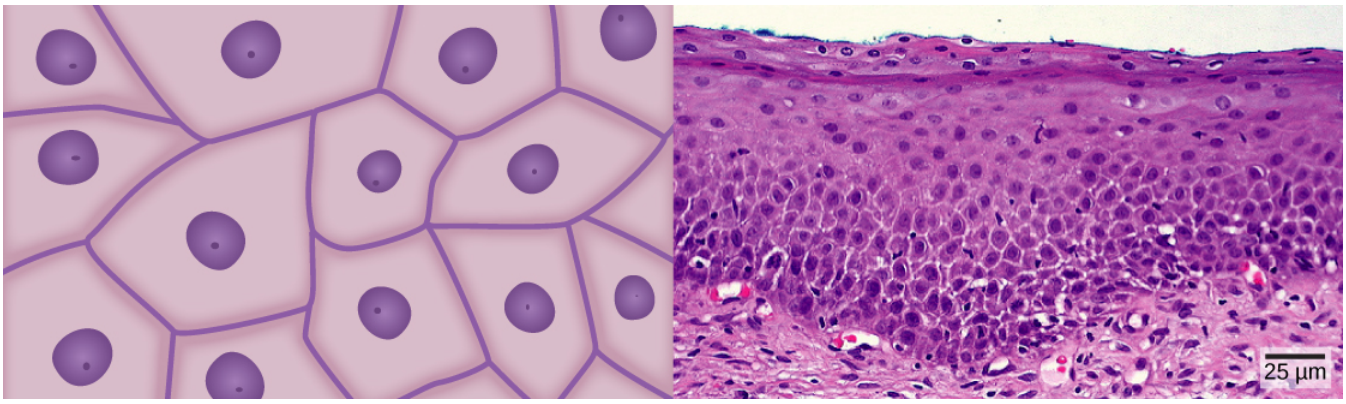


Figure 41.3.1: Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Figure 41.3.1 illustrates a layer of squamous cells with their membranes joined together to form an epithelium. Image Figure 41.3.1 illustrates squamous epithelial cells arranged in stratified layers, where protection is needed on the body from outside abrasion and damage. This is called a stratified squamous epithelium and occurs in the skin and in tissues lining the mouth and vagina.

Cuboidal Epithelia

Cuboidal epithelial cells, shown in Figure 41.3.2, are cube-shaped with a single, central nucleus. They are most commonly found in a single layer representing a simple epithelia in glandular tissues throughout the body where they prepare and secrete glandular material. They are also found in the walls of tubules and in the ducts of the kidney and liver.

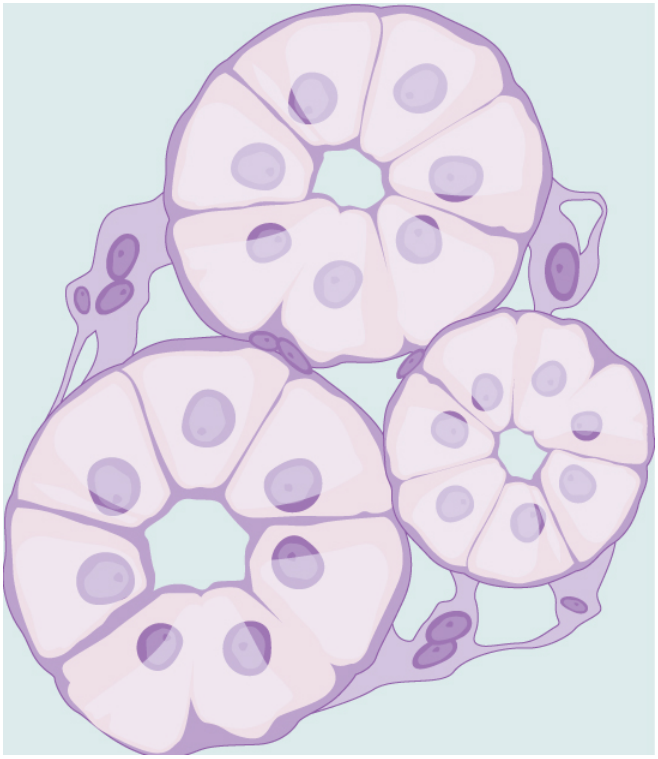


Figure 41.3.2: Simple cuboidal epithelial cells line tubules in the mammalian kidney, where they are involved in filtering the blood.

Columnar Epithelia

Columnar epithelial cells are taller than they are wide: they resemble a stack of columns in an epithelial layer, and are most commonly found in a single-layer arrangement. The nuclei of columnar epithelial cells in the digestive tract appear to be lined up at the base of the cells, as illustrated in Figure 41.3.3. These cells absorb material from the lumen of the digestive tract and prepare it for entry into the body through the circulatory and lymphatic systems.

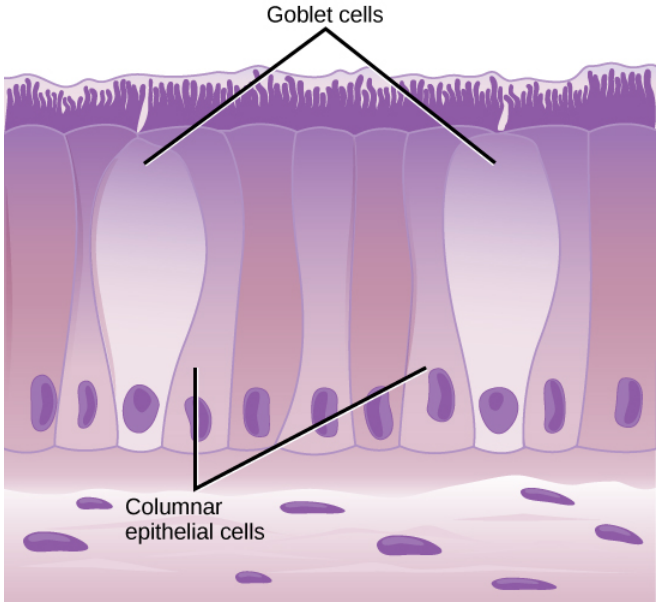


Figure **41.3.3**: Simple columnar epithelial cells absorb material from the digestive tract. Goblet cells secret mucous into the digestive tract lumen.

Columnar epithelial cells lining the respiratory tract appear to be stratified. However, each cell is attached to the base membrane of the tissue and, therefore, they are simple tissues. The nuclei are arranged at different levels in the layer of cells, making it appear as though there is more than one layer, as seen in Figure **41.3.4**. This is called pseudostratified, columnar epithelia. This cellular covering has cilia at the apical, or free, surface of the cells. The cilia enhance the movement of mucous and trapped particles out of the respiratory tract, helping to protect the system from invasive microorganisms and harmful material that has been breathed into the body. Goblet cells are interspersed in some tissues (such as the lining of the trachea). The goblet cells contain mucous that traps irritants, which in the case of the trachea keep these irritants from getting into the lungs.

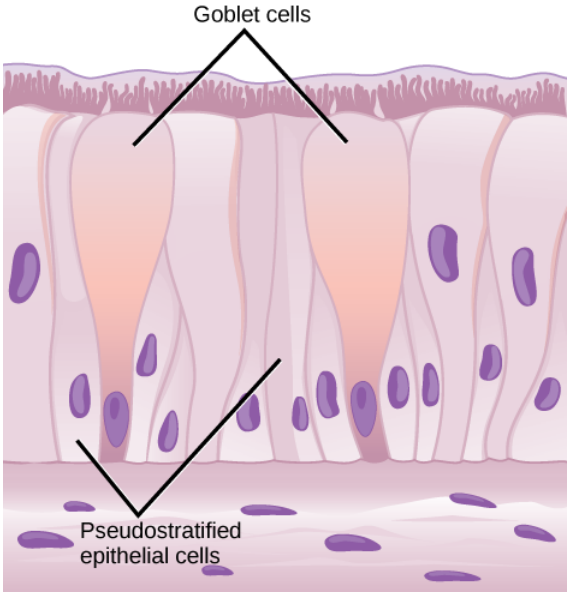


Figure **41.3.4**: Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucous into the respiratory tract.

Transitional Epithelia

Transitional or uroepithelial cells appear only in the urinary system, primarily in the bladder and ureter. These cells are arranged in a stratified layer, but they have the capability of appearing to pile up on top of each other in a relaxed, empty bladder, as illustrated in Figure **41.3.5**. As the urinary bladder fills, the epithelial layer unfolds and expands to hold the volume of urine introduced into it. As the bladder fills, it expands and the lining becomes thinner. In other words, the tissue transitions from thick to thin.

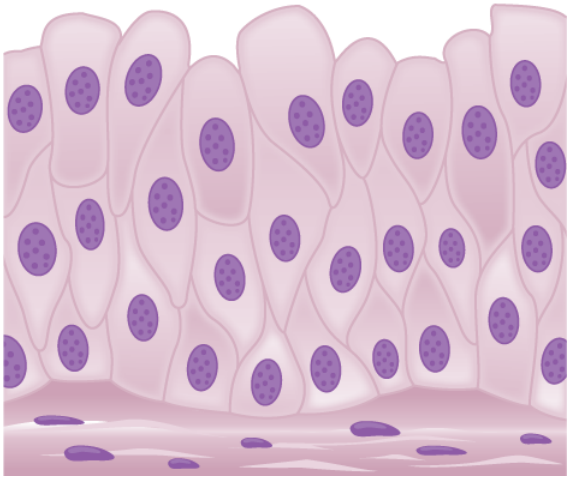


Figure **41.3.5**: Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is.

Exercise

Which of the following statements about types of epithelial cells is false?

A. Simple columnar epithelial cells line the tissue of the lung.
B. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
C. Pseudostratisfied columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
D. Transitional epithelia change in thickness depending on how full the bladder is.

Answer

A

Connective Tissues

Connective tissues are made up of a matrix consisting of living cells and a non-living substance, called the ground substance. The ground substance is made of an organic substance (usually a protein) and an inorganic substance (usually a mineral or water). The principal cell of connective tissues is the fibroblast. This cell makes the fibers found in nearly all of the connective tissues. Fibroblasts are motile, able to carry out mitosis, and can synthesize whichever connective tissue is needed. Macrophages, lymphocytes, and, occasionally, leukocytes can be found in some of the tissues. Some tissues have specialized cells that are not found in the others. The matrix in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has proportionally a less dense matrix.

The organic portion or protein fibers found in connective tissues are either collagen, elastic, or reticular fibers. Collagen fibers provide strength to the tissue, preventing it from being torn or separated from the surrounding tissues. Elastic fibers are made of the protein elastin; this fiber can stretch to one and one half of its length and return to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers are the third type of protein fiber found in connective tissues. This fiber consists of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected. The various types of connective tissues, the types of cells and fibers they are made of, and sample locations of the tissues is summarized in the table.

Table 41.3.2: Connective Tissues

Tissue	Cells	Fibers	Location
loose/areolar	fibroblasts, macrophages, some lymphocytes, some neutrophils	few: collagen, elastic, reticular	around blood vessels; anchors epithelia
dense, fibrous connective tissue	fibroblasts, macrophages,	mostly collagen	irregular: skin regular: tendons, ligaments
cartilage	chondrocytes, chondroblasts	hyaline: few collagen fibrocartilage: large amount of collagen	shark skeleton, fetal bones, human ears, intervertebral discs
bone	osteoblasts, osteocytes, osteoclasts	some: collagen, elastic	vertebrate skeletons
adipose	adipocytes	few	adipose (fat)
blood	red blood cells, white blood cells	none	blood

Loose/Areolar Connective Tissue

Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. As illustrated in Figure **41.3.6**, loose connective tissue has some fibroblasts; macrophages are present as well. Collagen fibers are relatively wide and stain a light pink, while elastic fibers are thin and stain dark blue to black. The space between the formed elements of the tissue is filled with the matrix. The material in the connective tissue gives it a loose consistency similar to a cotton ball that has been pulled apart. Loose connective tissue is found around every blood vessel and helps to keep the vessel in place. The tissue is also found around and between most body organs. In summary, areolar tissue is tough, yet flexible, and comprises membranes.

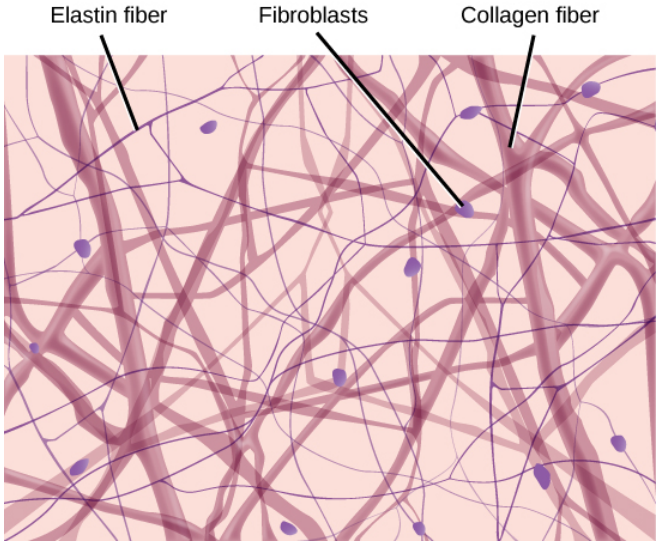


Figure **41.3.6**: Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts.

Fibrous Connective Tissue

Fibrous connective tissues contain large amounts of collagen fibers and few cells or matrix material. The fibers can be arranged irregularly or regularly with the strands lined up in parallel. Irregularly arranged fibrous connective tissues are found in areas of the body where stress occurs from all directions, such as the dermis of the skin. Regular fibrous connective tissue, shown in Figure **41.3.7**, is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).

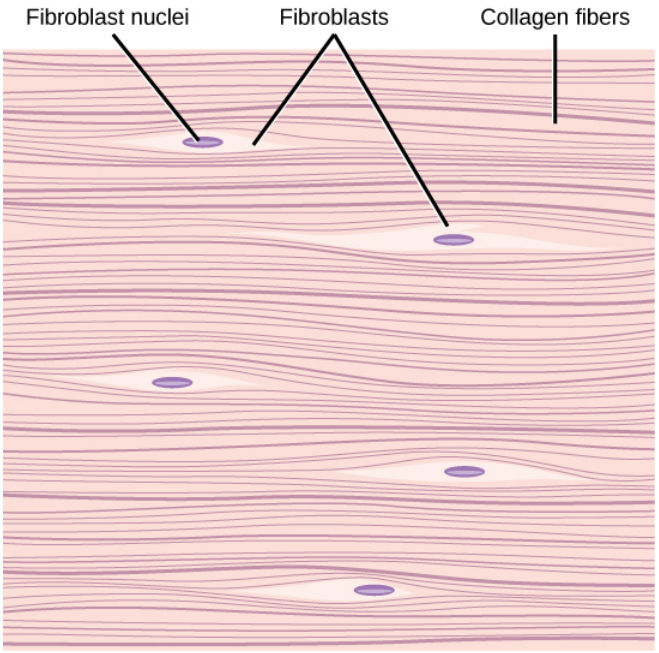


Figure **41.3.7**: Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel.

Cartilage

Cartilage is a connective tissue with a large amount of the matrix and variable amounts of fibers. The cells, called chondrocytes, make the matrix and fibers of the tissue. Chondrocytes are found in spaces within the tissue called lacunae.

A cartilage with few collagen and elastic fibers is hyaline cartilage, illustrated in Figure **41.3.8**. The lacunae are randomly scattered throughout the tissue and the matrix takes on a milky or scrubbed appearance with routine histological stains. Sharks have cartilaginous skeletons, as does nearly the entire human skeleton during a specific pre-birth developmental stage. A remnant of this cartilage persists in the outer portion of the human nose. Hyaline cartilage is also found at the ends of long bones, reducing friction and cushioning the articulations of these bones.

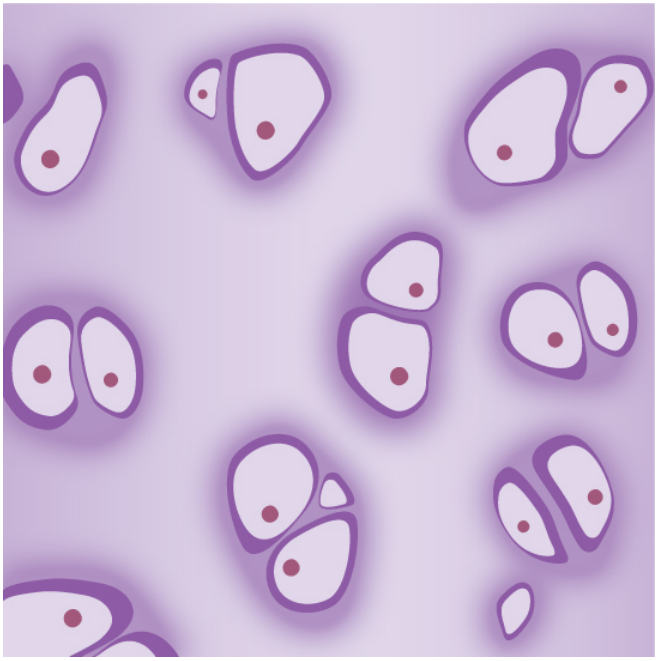


Figure **41.3.8**: Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae.

Elastic cartilage has a large amount of elastic fibers, giving it tremendous flexibility. The ears of most vertebrate animals contain this cartilage as do portions of the larynx, or voice box. Fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage comprises the intervertebral discs in vertebrate animals. Hyaline cartilage found in movable joints such as the knee and shoulder becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage and results in the joints becoming "stiff."

Bone

Bone, or osseous tissue, is a connective tissue that has a large amount of two different types of matrix material. The organic matrix is similar to the matrix material found in other connective tissues, including some amount of collagen and elastic fibers. This gives strength and flexibility to the tissue. The inorganic matrix consists of mineral salts—mostly calcium salts—that give the tissue hardness. Without adequate organic material in the matrix, the tissue breaks; without adequate inorganic material in the matrix, the tissue bends.

There are three types of cells in bone: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are active in making bone for growth and remodeling. Osteoblasts deposit bone material into the matrix and, after the matrix surrounds them, they continue to live, but in a reduced metabolic state as osteocytes. Osteocytes are found in lacunae of the bone. Osteoclasts are active in breaking down bone for bone remodeling, and they provide access to calcium stored in tissues. Osteoclasts are usually found on the surface of the tissue.

Bone can be divided into two types: compact and spongy. Compact bone is found in the shaft (or diaphysis) of a long bone and the surface of the flat bones, while spongy bone is found in the end (or epiphysis) of a long bone. Compact bone is organized into subunits called osteons, as illustrated in Figure **41.3.9**. A blood vessel and a nerve are found in the center of the structure within the Haversian canal, with radiating circles of lacunae around it known as lamellae. The wavy lines seen between the lacunae are microchannels called *canaliculi*; they connect the lacunae to aid diffusion between the cells. Spongy bone is made of tiny plates called trabeculae these plates serve as struts to give the spongy bone strength. Over time, these plates can break causing the bone to become less resilient. Bone tissue forms the internal skeleton of vertebrate animals, providing structure to the animal and points of attachment for tendons.

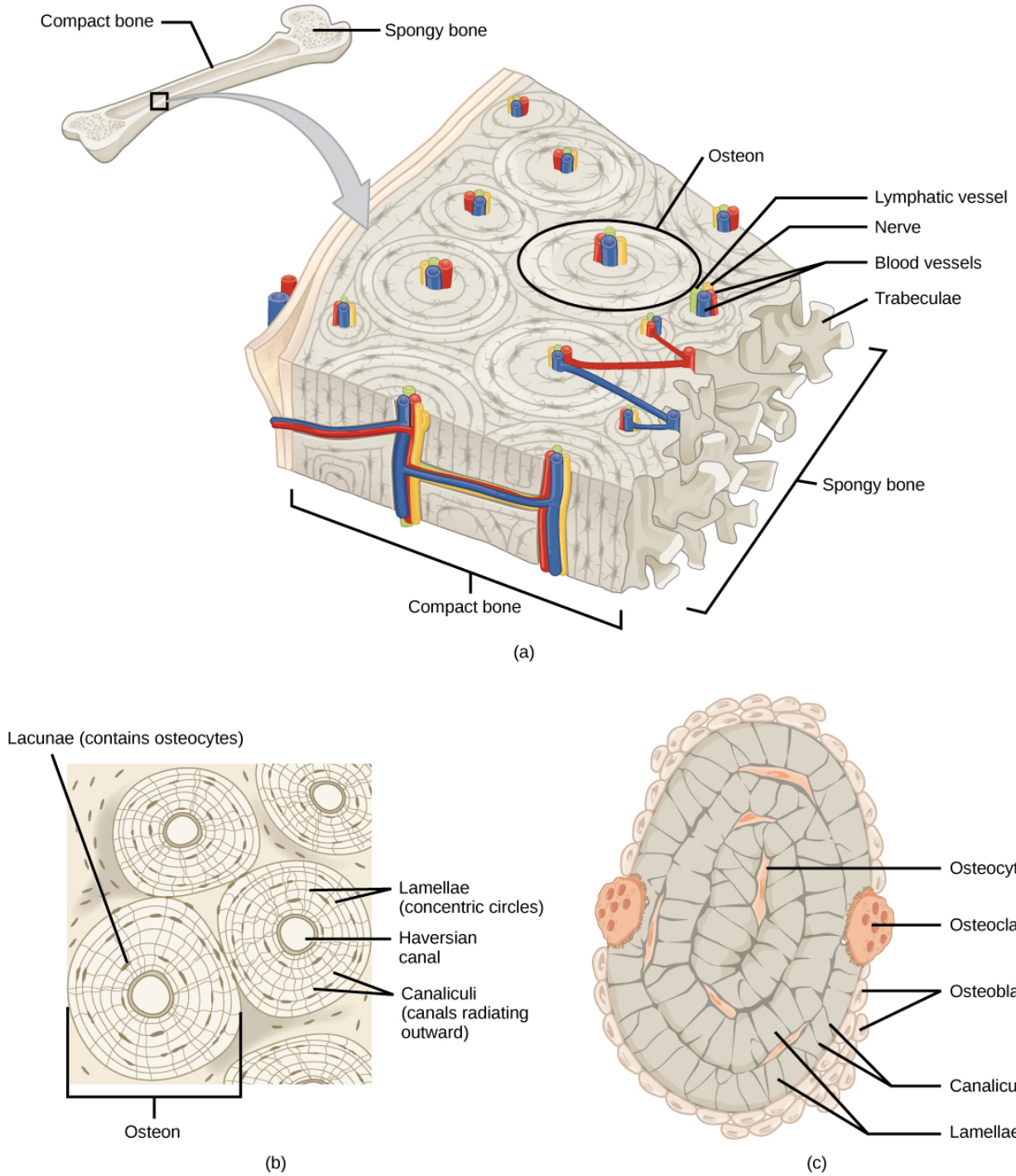


Figure **41.3.9**: (a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are microchannels connecting the lacunae together. (c) Osteoblasts surround the exterior of the bone. Osteoclasts bore tunnels into the bone and osteocytes are found in the lacunae.

Adipose Tissue

Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix and only has a few fibers. Adipose tissue is made up of cells called adipocytes that collect and store fat in the form of triglycerides, for energy metabolism. Adipose tissues additionally serve as insulation to help maintain body temperatures, allowing animals to be endothermic, and they function as cushioning against damage to body organs. Under a microscope, adipose tissue cells appear

empty due to the extraction of fat during the processing of the material for viewing, as seen in Figure **41.3.10**. The thin lines in the image are the cell membranes, and the nuclei are the small, black dots at the edges of the cells.

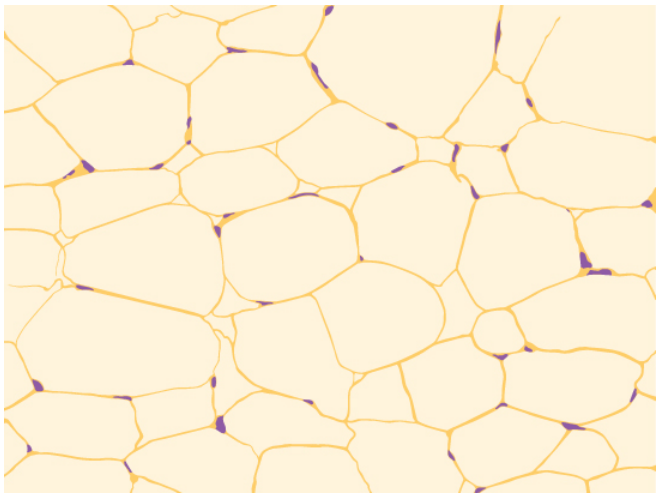


Figure **41.3.10**: Adipose is a connective tissue is made up of cells called adipocytes. Adipocytes have small nuclei localized at the cell edge.

Blood

Blood is considered a connective tissue because it has a matrix, as shown in Figure **41.3.11**. The living cell types are red blood cells (RBC), also called erythrocytes, and white blood cells (WBC), also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.

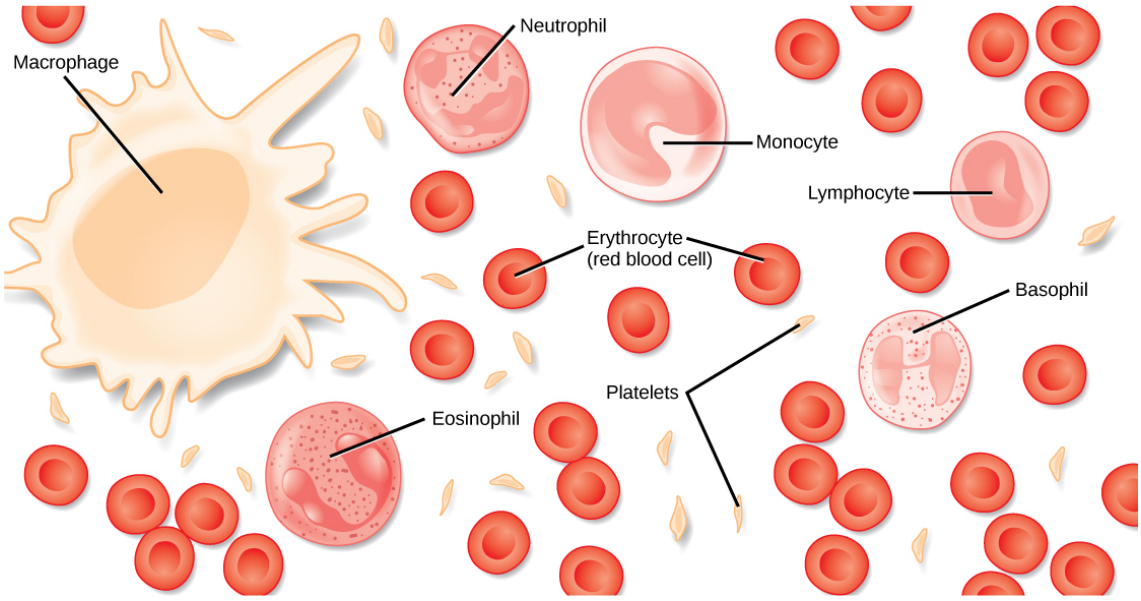


Figure **41.3.11**: Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

The cell found in greatest abundance in blood is the erythrocyte. Erythrocytes are counted in millions in a blood sample: the average number of red blood cells in primates is 4.7 to 5.5 million cells per microliter. Erythrocytes are consistently the same size in a species, but vary in size between species. For example, the average diameter of a primate red blood cell is 7.5 µl, a dog is close at 7.0 µl, but a cat's RBC diameter is 5.9 µl. Sheep erythrocytes are even smaller at 4.6 µl. Mammalian erythrocytes lose their nuclei and mitochondria when they are released from the bone marrow where they are made. Fish, amphibian, and avian red blood cells maintain their nuclei and mitochondria throughout the cell's life. The principal job of an erythrocyte is to carry and deliver oxygen to the tissues.

Leukocytes are the predominant white blood cells found in the peripheral blood. Leukocytes are counted in the thousands in the blood with measurements expressed as ranges: primate counts range from 4,800 to 10,800 cells per µl, dogs from 5,600 to 19,200 cells per µl, cats from 8,000 to 25,000 cells per µl, cattle from 4,000 to 12,000 cells per µl, and pigs from 11,000 to 22,000 cells per µl.

Lymphocytes function primarily in the immune response to foreign antigens or material. Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells and they participate in one of the early lines of defense against microbial invaders, aiding in the removal of bacteria that has entered the body. Another leukocyte that is found in the peripheral blood is the monocyte. Monocytes give rise to phagocytic macrophages that clean up dead and damaged cells in the body, whether they are foreign or from the host animal. Two additional leukocytes in the blood are eosinophils and basophils—both help to facilitate the inflammatory response.

The slightly granular material among the cells is a cytoplasmic fragment of a cell in the bone marrow. This is called a platelet or thrombocyte. Platelets participate in the stages leading up to coagulation of the blood to stop bleeding through damaged blood vessels. Blood has a number of functions, but primarily it transports material through the body to bring nutrients to cells and remove waste material from them.

Muscle Tissues

There are three types of muscle in animal bodies: smooth, skeletal, and cardiac. They differ by the presence or absence of striations or bands, the number and location of nuclei, whether they are voluntarily or involuntarily controlled, and their location within the body. The table summarizes these differences.

Table 41.3.3: Types of Muscles

Type of Muscle	Striations	Nuclei	Control	Location
smooth	no	single, in center	involuntary	visceral organs
skeletal	yes	many, at periphery	voluntary	skeletal muscles
cardiac	yes	single, in center	involuntary	heart

Smooth Muscle

Smooth muscle does not have striations in its cells. It has a single, centrally located nucleus, as shown in Figure **41.3.12**. Constriction of smooth muscle occurs under involuntary, autonomic nervous control and in response to local conditions in the tissues. Smooth muscle tissue is also called non-striated as it lacks the banded appearance of skeletal and cardiac muscle. The walls of blood vessels, the tubes of the digestive system, and the tubes of the reproductive systems are composed of mostly smooth muscle.

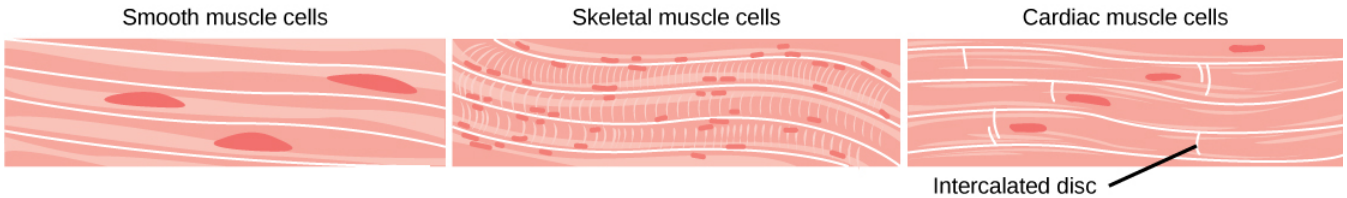


Figure **41.3.12**: Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

Skeletal Muscle

Skeletal muscle has striations across its cells caused by the arrangement of the contractile proteins actin and myosin. These muscle cells are relatively long and have multiple nuclei along the edge of the cell. Skeletal muscle is under voluntary, somatic nervous system control and is found in the muscles that move bones. Figure **41.3.12**illustrates the histology of skeletal muscle.

Cardiac Muscle

Cardiac muscle, shown in Figure **41.3.12**, is found only in the heart. Like skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally located nucleus. Cardiac muscle is not under voluntary control but can be influenced by the autonomic nervous system to speed up or slow down. An added feature to cardiac muscle cells is a line than extends along the end of the cell as it abuts the next cardiac cell in the row. This line is called an intercalated disc: it assists in passing electrical impulse efficiently from one cell to the next and maintains the strong connection between neighboring cardiac cells.

Nervous Tissues

Nervous tissues are made of cells specialized to receive and transmit electrical impulses from specific areas of the body and to send them to specific locations in the body. The main cell of the nervous system is the neuron, illustrated in Figure **41.3.13**. The large structure with a central nucleus is the cell body of the neuron. Projections from the cell body are either dendrites specialized in receiving input or a single axon specialized in transmitting impulses. Some glial cells are also shown. Astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells that are not shown support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic and remove debris or damaged cells from the tissue. A nerve consists of neurons and glial cells.

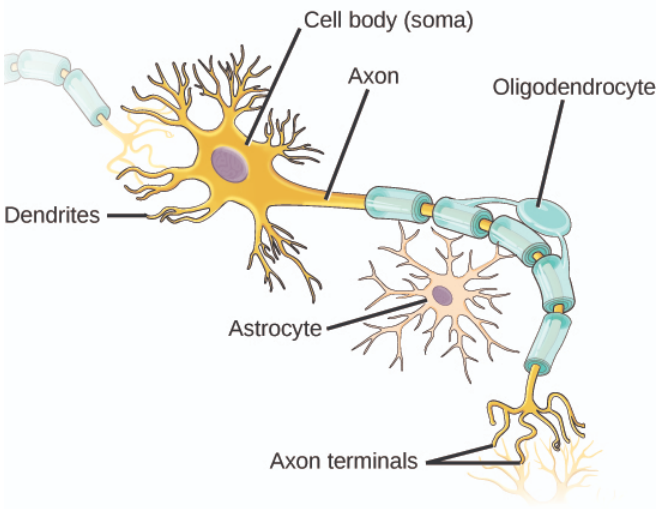


Figure **41.3.13**: The neuron has projections called dendrites that receive signals and projections called axons that send signals. Also shown are two types of glial cells: astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently.

Link to Learning

Click through the interactive review to learn more about epithelial tissues.

Career Connections: Pathologist

A pathologist is a medical doctor or veterinarian who has specialized in the laboratory detection of disease in animals, including humans. These professionals complete medical school education and follow it with an extensive post-graduate residency at a medical center. A pathologist may oversee clinical laboratories for the evaluation of body tissue and blood

samples for the detection of disease or infection. They examine tissue specimens through a microscope to identify cancers and other diseases. Some pathologists perform autopsies to determine the cause of death and the progression of disease.

Summary

The basic building blocks of complex animals are four primary tissues. These are combined to form organs, which have a specific, specialized function within the body, such as the skin or kidney. Organs are organized together to perform common functions in the form of systems. The four primary tissues are epithelia, connective tissues, muscle tissues, and nervous tissues.

Glossary

canaliculus
microchannel that connects the lacunae and aids diffusion between cells

cartilage
type of connective tissue with a large amount of ground substance matrix, cells called chondrocytes, and some amount of fibers

chondrocyte
cell found in cartilage

columnar epithelia
epithelia made of cells taller than they are wide, specialized in absorption

connective tissue
type of tissue made of cells, ground substance matrix, and fibers

cuboidal epithelia
epithelia made of cube-shaped cells, specialized in glandular functions

epithelial tissue
tissue that either lines or covers organs or other tissues

fibrous connective tissue
type of connective tissue with a high concentration of fibers

lacuna
space in cartilage and bone that contains living cells

loose (areolar) connective tissue
type of connective tissue with small amounts of cells, matrix, and fibers; found around blood vessels

matrix
component of connective tissue made of both living and non-living (ground substances) cells

osteon
subunit of compact bone

pseudostratified
layer of epithelia that appears multilayered, but is a simple covering

simple epithelia
single layer of epithelial cells

squamous epithelia

type of epithelia made of flat cells, specialized in aiding diffusion or preventing abrasion

stratified epithelia

multiple layers of epithelial cells

trabecula

tiny plate that makes up spongy bone and gives it strength

transitional epithelia

epithelia that can transition for appearing multilayered to simple; also called uroepithelial

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41.3.1: Animal Tissues

The development of a fertilized egg into a newborn child requires an average of 41 rounds of mitosis ($2^{41} = 2.2 \times 10^{12}$). During this period, the cells produced by mitosis enter different pathways of differentiation; some becoming blood cells, some muscle cells, and so on. There are more than 100 visibly-distinguishable kinds of differentiated cells in the vertebrate animal. These are organized into tissues; the tissues into organs. Groups of organs make up the various systems — digestive, excretory, etc. — of the body (Figure **41.3.1.1** and Table **41.3.1.1**).

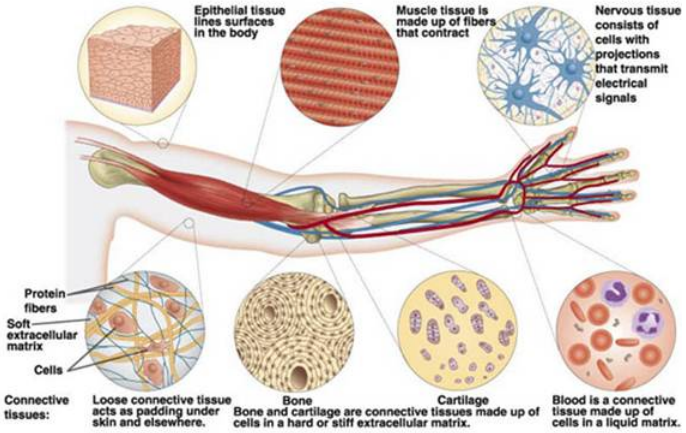


Figure **41.3.1.1**: Animal Tissues

The actual number of differentiated cell types is surely much larger than 100. All lymphocytes, for example, look alike but actually represent a variety of different functional types, e.g., B cells, T cells of various subsets. The neurons of the central nervous system must exist in a thousand or more different functional types, each representing the result of a particular pathway of differentiation. This page will give a brief introduction to the major types of animal tissues.

Table **41.3.1.1**: Classification of Animal Tissues

Epithelial Tissues	Linings and Coverings	Simple Epithelia
	Classifying or Naming Epithelia	Stratified Epithelia
	Glands	Exocrine Glands
		Endocrine Glands
Connective Tissues	Fluid Connective Tissues	Lymph
		Blood
	Connective Tissues Proper	Loose Connective Tissues
		Loose Connective Tissues and Inflammation
		Dense Connective Tissues
	Supportive Connective Tissues	Osseous Tissue
		Cartilage
Muscle Tissues	Non-striated	Smooth muscle
	Striated	Skeletal Muscle
		Cardiac Muscle
Nervous Tissues	Neurons	Multipolar Neurons in CNS
	Nerves	Nerves of the PNS
	Receptors	Miessner's and Pacinian Corpuscles

Epithelial

Epithelial tissue is made of closely-packed cells arranged in flat sheets. Epithelia form the surface of the skin, line the various cavities and tubes of the body, and cover the internal organs. Epithelia that form the interface between the internal and external environments. Skin as well as the lining of the mouth and nasal cavity. These are derived from **ectoderm**. Inner lining of the GI tract, lungs, urinary bladder, exocrine glands, vagina and more. These are derived from **endoderm**.

The **apical surface** of these epithelial cells is exposed to the "external environment", the lumen of the organ or the air.

- **Mesothelia**. These are derived from mesoderm.
  - pleura — the outer covering of the lungs and the inner lining of the thoracic (chest) cavity.
  - peritoneum — the outer covering of all the abdominal organs and the inner lining of the abdominal cavity.
  - pericardium — the outer lining of the heart.
- **Endothelia**. These are derived from mesoderm. The inner lining of the heart, all blood and lymphatic vessels.

The **basolateral surface** of all epithelia is exposed to the internal environment - extracellular fluid (ECF). The entire sheet of epithelial cells is attached to a layer of extracellular matrix that is called the basement membrane or, better (because it is not a membrane in the biological sense), the **basal lamina**.

The function of epithelia always reflects the fact that they are boundaries between masses of cells and a cavity or space. Some examples include:

- The epithelium of the skin protects the underlying tissues from mechanical damage, ultraviolet light, dehydration and invasion by bacteria
- The columnar epithelium of the intestine secretes digestive enzymes into the intestine and absorbs the products of digestion from it.

- An epithelium also lines our air passages and the alveoli of the lungs. It secretes mucus which keeps it from drying out and traps inhaled dust particles. Most of its cells have cilia on their apical surface that propel the mucus with its load of foreign matter back up to the throat.

Muscle

Three kinds of muscle are found in vertebrates. **Skeletal muscle** is made of long fibers whose contraction provides the force of locomotion and other **voluntary** body movements. **Smooth muscle** lines the walls of the hollow structures of the body, such as the intestine, urinary bladder, uterus, and blood vessels. Its contraction, which is **involuntary**, reduces the size of these hollow organs. The heart is made of **cardiac muscle**.

Connective

The cells of connective tissue are embedded in a great amount of extracellular material. This **matrix** is secreted by the cells. It consists of protein fibers embedded in an amorphous mixture of protein-polysaccharide ("proteoglycan") molecules. Supporting connective tissue gives strength, support, and protection to the soft parts of the body.

- **cartilage**. Example: the outer ear
- **bone**. The matrix of bone contains collagen fibers and mineral deposits. The most abundant mineral is calcium phosphate, although magnesium, carbonate, and fluoride ions are also present.

Dense connective tissue is often called fibrous connective tissue and include **Tendons** and **Ligaments**. Tendons connect muscle to bone with a The matrix is principally Type I collagen, and the fibers are all oriented parallel to each other. Tendons are strong but not elastic. **Ligaments** attach one bone to another and contain both collagen and also the protein **elastin**. Elastin permits ligaments to be stretched.

Loose connective tissue is distributed throughout the body. It serves as a packing and binding material for most of our organs. Sheets of loose connective tissue that bind muscles and other structures together are called **fascia**. Collagen, elastin, and other proteins are found in the matrix of loose connective tissue. Both dense and loose connective tissue are derived from cells called **fibroblasts**, which secrete the extracellular matrix.

Adipose Tissue

Adipose tissue is "fat". There are two kinds found in mammals: **white adipose tissue** (WAT) and **brown adipose tissue** (BAT). The WAT in which the cells, called **adipocytes**, have become almost filled with oil, which is confined within a single membrane-enclosed droplet. Virtually all of the "fat" in adult humans is white adipose tissue. BAT in which the adipocytes contain many small droplets of oil as well as many mitochondria. White adipose tissue and brown adipose tissue differ in function as well as cellular structure. These differences are described elsehwhere.

New adipocytes in white adipose tissue are formed throughout life from a pool of precursor cells. These are needed to replace those that die (after an average life span of 10 years). Whether the total **number** of these adipocytes increases in humans becoming fatter as adults is still uncertain. If not, why do so many of us get fatter as we age? Because of the increased **size** of individual adipocytes as they become filled with oil. The adipocytes of white adipose tissue secrete several hormones, including leptin and adiponectin.

Nerve

Nerve tissue is composed of nerve cells called neurons and glial cells. Neurons are specialized for the conduction of nerve impulses; a typical neuron consists of a **cell body** which contains the nucleus; a number of short fibers — **dendrites** — extending from the cell body and a single long fiber, the **axon**. The nerve impulse is conducted along the axon. The tips of axons meet other neurons at junctions called **synapses, muscles (called neuromuscular junctions) and** glands.

Glia

Glial cells surround neurons. Once thought to be simply support for neurons (*glia* = glue), they turn out to serve several important functions. There are three types:

- **Schwann cells**. These produce the myelin sheath that surrounds many axons in the peripheral nervous system.

- **Oligodendrocytes**. These produce the myelin sheath that surrounds many axons in the central nervous system (brain and spinal cord).
- **Astrocytes**. These, often star-shaped cells are clustered around synapses and the nodes of Ranvier where they perform a variety of functions such as:
  - modulating the activity of neurons
  - supplying neurons with materials (e.g. glucose and lactate) as well as some signaling molecules
  - regulating the flow of blood to their region of the brain. It is primarily the metabolic activity of astrocytes that is being measured in brain imaging by positron-emission tomography (PET) and functional magnetic resonance imaging (fMRI).
  - pruning away (by phagocytosis) weak synapses

In addition, the central nervous system contains many **microglia** — mobile cells (macrophages) that respond to damage (e.g., from an infection) by engulfing cell debris and secreting inflammatory cytokines like tumor necrosis factor (TNF-α) and interleukin-1 (IL-1). Microglia are also active in the healthy brain, at least in young mice where, like astrocytes, they engulf synapses thus reducing the number of synapses in the developing brain.

Blood

The **bone marrow** is the source of all the cells of the blood. These include **red blood cells** (RBCs or **erythrocytes**), five kinds of **white blood cells** (WBCs or **leukocytes**), and **platelets** (or **thrombocytes**).

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41.4: Muscle Tissue

Skills to Develop

- Describe epithelial tissues
- Discuss the different types of connective tissues in animals
- Describe three types of muscle tissues
- Describe nervous tissue

The tissues of multicellular, complex animals are four primary types: epithelial, connective, muscle, and nervous. Recall that tissues are groups of similar cells group of similar cells carrying out related functions. These tissues combine to form organs—like the skin or kidney—that have specific, specialized functions within the body. Organs are organized into organ systems to perform functions; examples include the circulatory system, which consists of the heart and blood vessels, and the digestive system, consisting of several organs, including the stomach, intestines, liver, and pancreas. Organ systems come together to create an entire organism.

Epithelial Tissues

Epithelial tissues cover the outside of organs and structures in the body and line the lumens of organs in a single layer or multiple layers of cells. The types of epithelia are classified by the shapes of cells present and the number of layers of cells. Epithelia composed of a single layer of cells is called simple epithelia; epithelial tissue composed of multiple layers is called stratified epithelia. The table summarizes the different types of epithelial tissues.

Table 41.4.1: Different Types of Epithelial Tissues

Cell shape	Description	Location
squamous	flat, irregular round shape	simple: lung alveoli, capillaries stratified: skin, mouth, vagina
cuboidal	cube shaped, central nucleus	glands, renal tubules
columnar	tall, narrow, nucleus toward base tall, narrow, nucleus along cell	simple: digestive tract pseudostratified: respiratory tract
transitional	round, simple but appear stratified	urinary bladder

Squamous Epithelia

Squamous epithelial cells are generally round, flat, and have a small, centrally located nucleus. The cell outline is slightly irregular, and cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs and the exchange of nutrients and waste at blood capillaries.

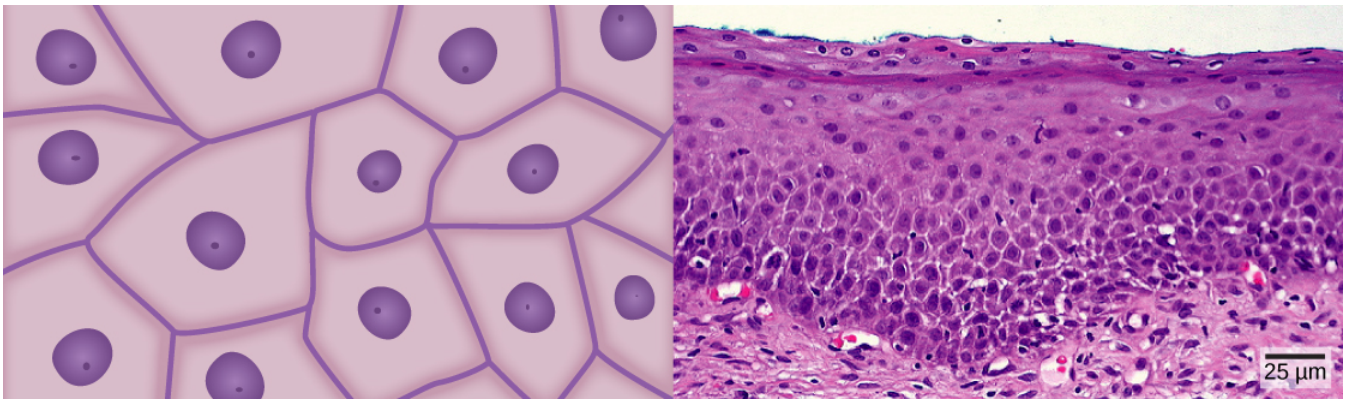


Figure **41.4.1**: Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Figure **41.4.1** illustrates a layer of squamous cells with their membranes joined together to form an epithelium. Image Figure **41.4.1** illustrates squamous epithelial cells arranged in stratified layers, where protection is needed on the body from outside abrasion and damage. This is called a stratified squamous epithelium and occurs in the skin and in tissues lining the mouth and vagina.

Cuboidal Epithelia

Cuboidal epithelial cells, shown in Figure **41.4.2**, are cube-shaped with a single, central nucleus. They are most commonly found in a single layer representing a simple epithelia in glandular tissues throughout the body where they prepare and secrete glandular material. They are also found in the walls of tubules and in the ducts of the kidney and liver.

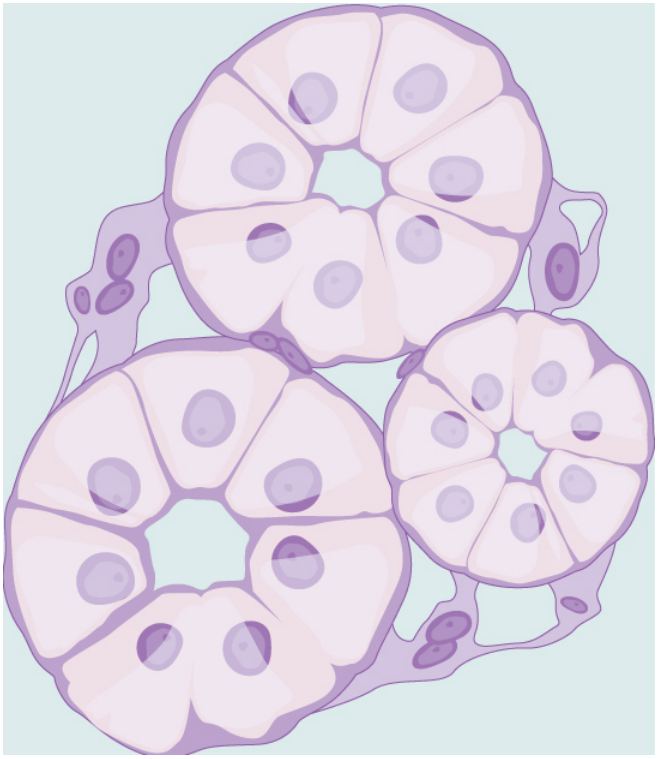


Figure **41.4.2**: Simple cuboidal epithelial cells line tubules in the mammalian kidney, where they are involved in filtering the blood.

Columnar Epithelia

Columnar epithelial cells are taller than they are wide: they resemble a stack of columns in an epithelial layer, and are most commonly found in a single-layer arrangement. The nuclei of columnar epithelial cells in the digestive tract appear to be lined up at the base of the cells, as illustrated in Figure **41.4.3**. These cells absorb material from the lumen of the digestive tract and prepare it for entry into the body through the circulatory and lymphatic systems.

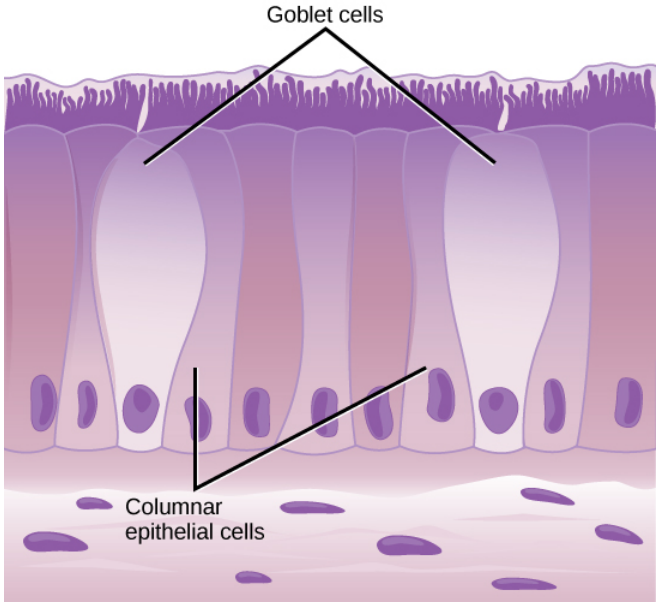


Figure **41.4.3**: Simple columnar epithelial cells absorb material from the digestive tract. Goblet cells secret mucous into the digestive tract lumen.

Columnar epithelial cells lining the respiratory tract appear to be stratified. However, each cell is attached to the base membrane of the tissue and, therefore, they are simple tissues. The nuclei are arranged at different levels in the layer of cells, making it appear as though there is more than one layer, as seen in Figure **41.4.4**. This is called pseudostratified, columnar epithelia. This cellular covering has cilia at the apical, or free, surface of the cells. The cilia enhance the movement of mucous and trapped particles out of the respiratory tract, helping to protect the system from invasive microorganisms and harmful material that has been breathed into the body. Goblet cells are interspersed in some tissues (such as the lining of the trachea). The goblet cells contain mucous that traps irritants, which in the case of the trachea keep these irritants from getting into the lungs.

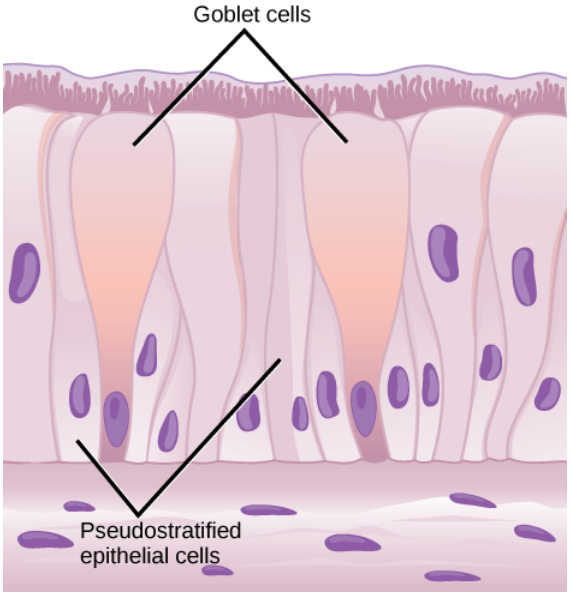


Figure **41.4.4**: Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucous into the respiratory tract.

Transitional Epithelia

Transitional or uroepithelial cells appear only in the urinary system, primarily in the bladder and ureter. These cells are arranged in a stratified layer, but they have the capability of appearing to pile up on top of each other in a relaxed, empty bladder, as illustrated in Figure **41.4.5**. As the urinary bladder fills, the epithelial layer unfolds and expands to hold the volume of urine introduced into it. As the bladder fills, it expands and the lining becomes thinner. In other words, the tissue transitions from thick to thin.

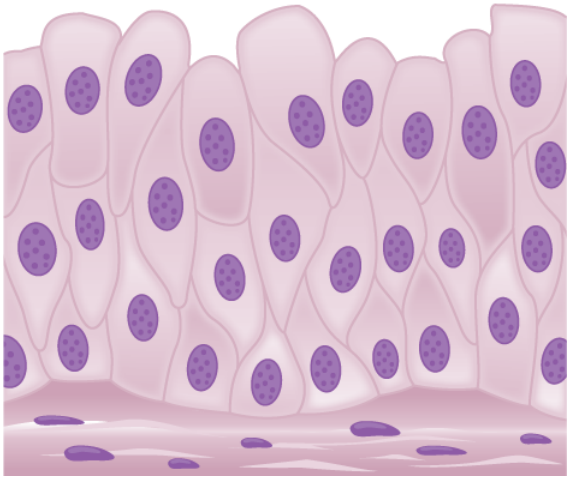


Figure **41.4.5**: Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is.

Exercise

Which of the following statements about types of epithelial cells is false?

A. Simple columnar epithelial cells line the tissue of the lung.
B. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
C. Pseudostratisfied columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
D. Transitional epithelia change in thickness depending on how full the bladder is.

Answer

A

Connective Tissues

Connective tissues are made up of a matrix consisting of living cells and a non-living substance, called the ground substance. The ground substance is made of an organic substance (usually a protein) and an inorganic substance (usually a mineral or water). The principal cell of connective tissues is the fibroblast. This cell makes the fibers found in nearly all of the connective tissues. Fibroblasts are motile, able to carry out mitosis, and can synthesize whichever connective tissue is needed. Macrophages, lymphocytes, and, occasionally, leukocytes can be found in some of the tissues. Some tissues have specialized cells that are not found in the others. The matrix in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has proportionally a less dense matrix.

The organic portion or protein fibers found in connective tissues are either collagen, elastic, or reticular fibers. Collagen fibers provide strength to the tissue, preventing it from being torn or separated from the surrounding tissues. Elastic fibers are made of the protein elastin; this fiber can stretch to one and one half of its length and return to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers are the third type of protein fiber found in connective tissues. This fiber consists of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected. The various types of connective tissues, the types of cells and fibers they are made of, and sample locations of the tissues is summarized in the table.

Table 41.4.2: Connective Tissues

Tissue	Cells	Fibers	Location
loose/areolar	fibroblasts, macrophages, some lymphocytes, some neutrophils	few: collagen, elastic, reticular	around blood vessels; anchors epithelia
dense, fibrous connective tissue	fibroblasts, macrophages,	mostly collagen	irregular: skin regular: tendons, ligaments
cartilage	chondrocytes, chondroblasts	hyaline: few collagen fibrocartilage: large amount of collagen	shark skeleton, fetal bones, human ears, intervertebral discs
bone	osteoblasts, osteocytes, osteoclasts	some: collagen, elastic	vertebrate skeletons
adipose	adipocytes	few	adipose (fat)
blood	red blood cells, white blood cells	none	blood

Loose/Areolar Connective Tissue

Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. As illustrated in Figure **41.4.6**, loose connective tissue has some fibroblasts; macrophages are present as well. Collagen fibers are relatively wide and stain a light pink, while elastic fibers are thin and stain dark blue to black. The space between the formed elements of the tissue is filled with the matrix. The material in the connective tissue gives it a loose consistency similar to a cotton ball that has been pulled apart. Loose connective tissue is found around every blood vessel and helps to keep the vessel in place. The tissue is also found around and between most body organs. In summary, areolar tissue is tough, yet flexible, and comprises membranes.

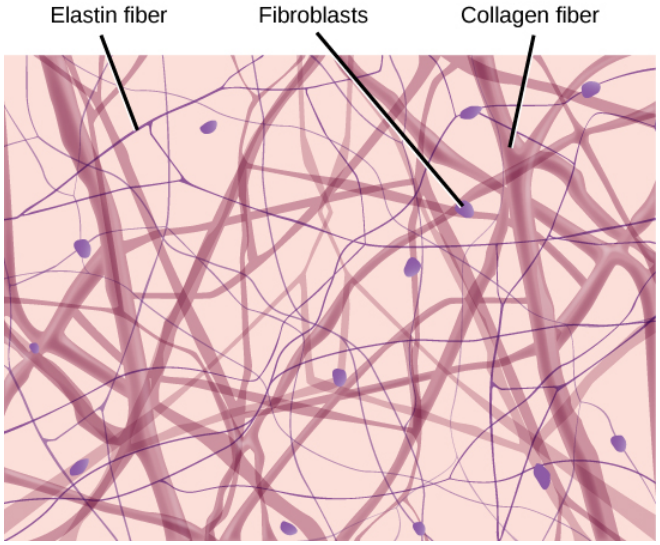


Figure **41.4.6**: Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts.

Fibrous Connective Tissue

Fibrous connective tissues contain large amounts of collagen fibers and few cells or matrix material. The fibers can be arranged irregularly or regularly with the strands lined up in parallel. Irregularly arranged fibrous connective tissues are found in areas of the body where stress occurs from all directions, such as the dermis of the skin. Regular fibrous connective tissue, shown in Figure **41.4.7**, is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).

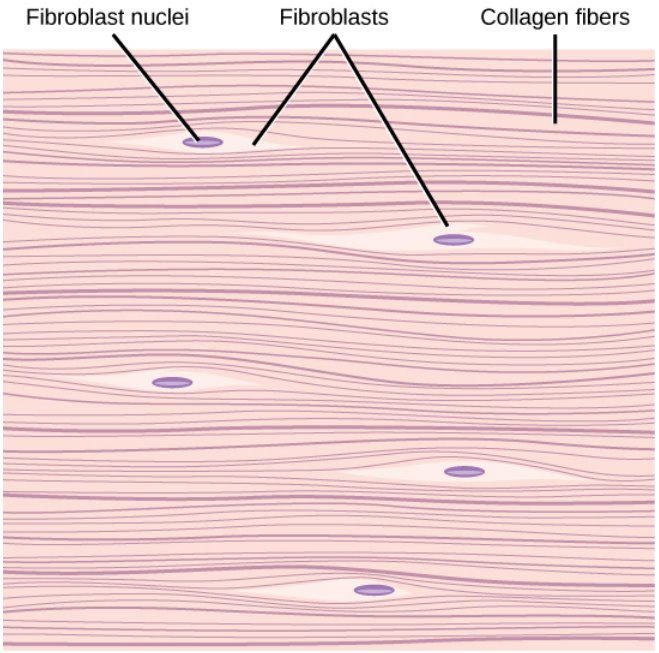


Figure **41.4.7**: Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel.

Cartilage

Cartilage is a connective tissue with a large amount of the matrix and variable amounts of fibers. The cells, called chondrocytes, make the matrix and fibers of the tissue. Chondrocytes are found in spaces within the tissue called lacunae.

A cartilage with few collagen and elastic fibers is hyaline cartilage, illustrated in Figure **41.4.8**. The lacunae are randomly scattered throughout the tissue and the matrix takes on a milky or scrubbed appearance with routine histological stains. Sharks have cartilaginous skeletons, as does nearly the entire human skeleton during a specific pre-birth developmental stage. A remnant of this cartilage persists in the outer portion of the human nose. Hyaline cartilage is also found at the ends of long bones, reducing friction and cushioning the articulations of these bones.

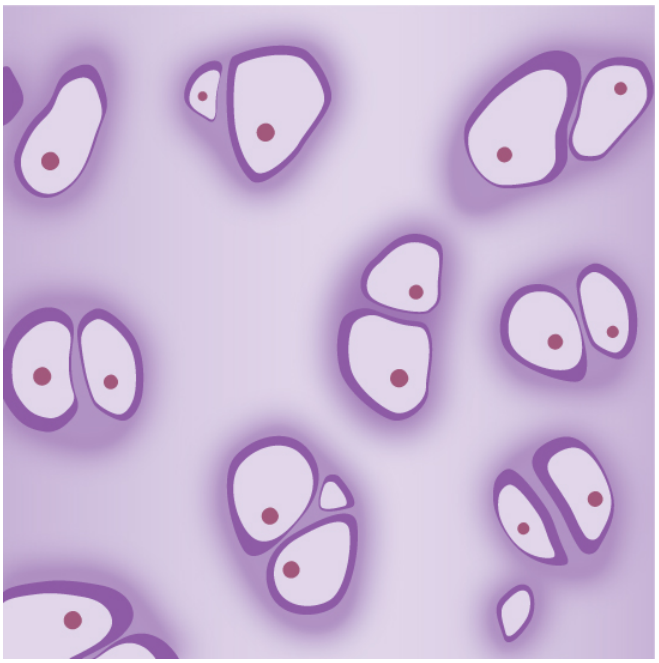


Figure **41.4.8**: Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae.

Elastic cartilage has a large amount of elastic fibers, giving it tremendous flexibility. The ears of most vertebrate animals contain this cartilage as do portions of the larynx, or voice box. Fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage comprises the intervertebral discs in vertebrate animals. Hyaline cartilage found in movable joints such as the knee and shoulder becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage and results in the joints becoming "stiff."

Bone

Bone, or osseous tissue, is a connective tissue that has a large amount of two different types of matrix material. The organic matrix is similar to the matrix material found in other connective tissues, including some amount of collagen and elastic fibers. This gives strength and flexibility to the tissue. The inorganic matrix consists of mineral salts—mostly calcium salts—that give the tissue hardness. Without adequate organic material in the matrix, the tissue breaks; without adequate inorganic material in the matrix, the tissue bends.

There are three types of cells in bone: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are active in making bone for growth and remodeling. Osteoblasts deposit bone material into the matrix and, after the matrix surrounds them, they continue to live, but in a reduced metabolic state as osteocytes. Osteocytes are found in lacunae of the bone. Osteoclasts are active in breaking down bone for bone remodeling, and they provide access to calcium stored in tissues. Osteoclasts are usually found on the surface of the tissue.

Bone can be divided into two types: compact and spongy. Compact bone is found in the shaft (or diaphysis) of a long bone and the surface of the flat bones, while spongy bone is found in the end (or epiphysis) of a long bone. Compact bone is organized into subunits called osteons, as illustrated in Figure **41.4.9**. A blood vessel and a nerve are found in the center of the structure within the Haversian canal, with radiating circles of lacunae around it known as lamellae. The wavy lines seen between the lacunae are microchannels called *canaliculi*; they connect the lacunae to aid diffusion between the cells. Spongy bone is made of tiny plates called trabeculae these plates serve as struts to give the spongy bone strength. Over time, these plates can break causing the bone to become less resilient. Bone tissue forms the internal skeleton of vertebrate animals, providing structure to the animal and points of attachment for tendons.

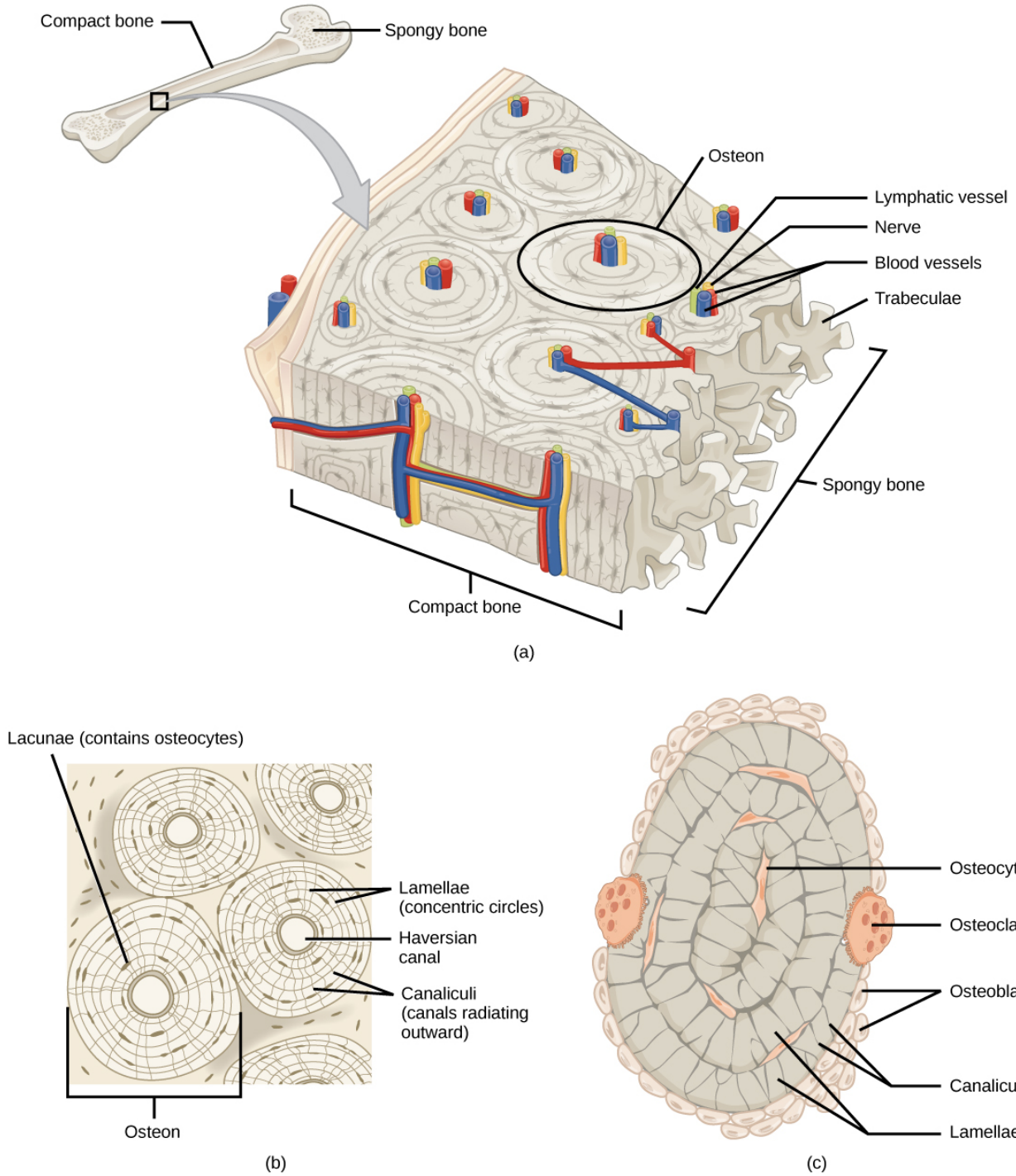


Figure **41.4.9**: (a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are microchannels connecting the lacunae together. (c) Osteoblasts surround the exterior of the bone. Osteoclasts bore tunnels into the bone and osteocytes are found in the lacunae.

Adipose Tissue

Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix and only has a few fibers. Adipose tissue is made up of cells called adipocytes that collect and store fat in the form of triglycerides, for energy metabolism. Adipose tissues additionally serve as insulation to help maintain body temperatures, allowing animals to be endothermic, and they function as cushioning against damage to body organs. Under a microscope, adipose tissue cells appear

empty due to the extraction of fat during the processing of the material for viewing, as seen in Figure **41.4.10**. The thin lines in the image are the cell membranes, and the nuclei are the small, black dots at the edges of the cells.

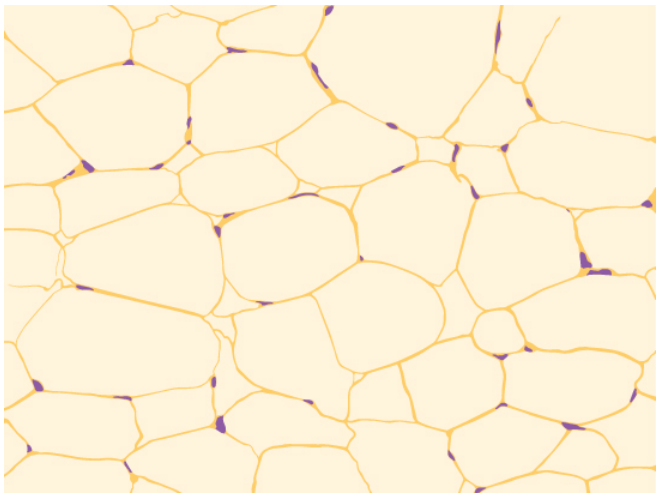


Figure **41.4.10**: Adipose is a connective tissue is made up of cells called adipocytes. Adipocytes have small nuclei localized at the cell edge.

Blood

Blood is considered a connective tissue because it has a matrix, as shown in Figure **41.4.11**. The living cell types are red blood cells (RBC), also called erythrocytes, and white blood cells (WBC), also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.

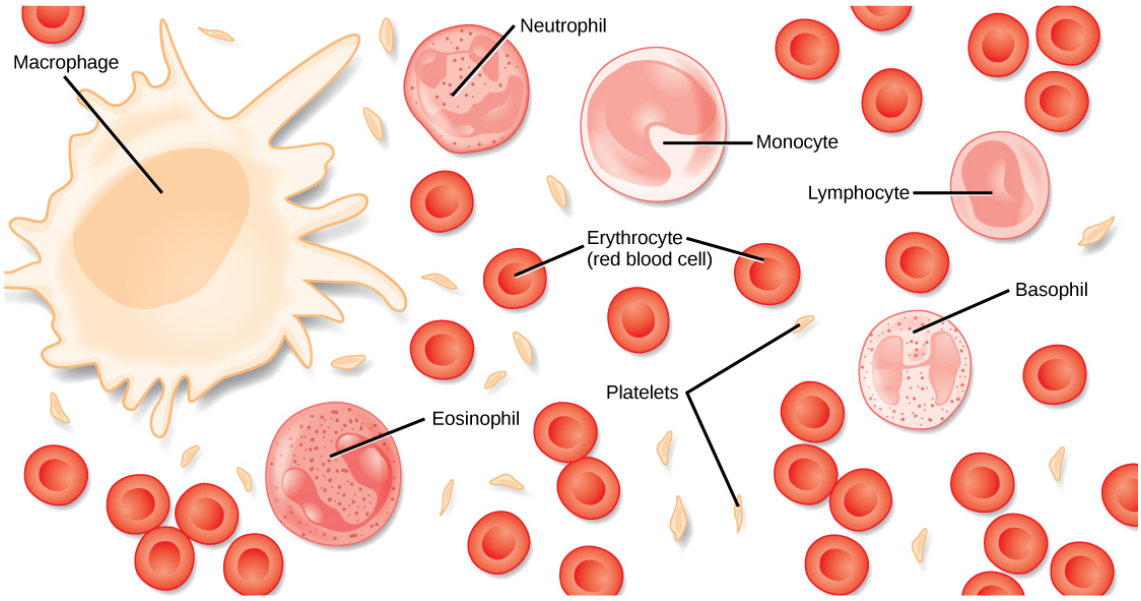


Figure **41.4.11**: Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

The cell found in greatest abundance in blood is the erythrocyte. Erythrocytes are counted in millions in a blood sample: the average number of red blood cells in primates is 4.7 to 5.5 million cells per microliter. Erythrocytes are consistently the same size in a species, but vary in size between species. For example, the average diameter of a primate red blood cell is 7.5 µl, a dog is close at 7.0 µl, but a cat's RBC diameter is 5.9 µl. Sheep erythrocytes are even smaller at 4.6 µl. Mammalian erythrocytes lose their nuclei and mitochondria when they are released from the bone marrow where they are made. Fish, amphibian, and avian red blood cells maintain their nuclei and mitochondria throughout the cell's life. The principal job of an erythrocyte is to carry and deliver oxygen to the tissues.

Leukocytes are the predominant white blood cells found in the peripheral blood. Leukocytes are counted in the thousands in the blood with measurements expressed as ranges: primate counts range from 4,800 to 10,800 cells per µl, dogs from 5,600 to 19,200 cells per µl, cats from 8,000 to 25,000 cells per µl, cattle from 4,000 to 12,000 cells per µl, and pigs from 11,000 to 22,000 cells per µl.

Lymphocytes function primarily in the immune response to foreign antigens or material. Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells and they participate in one of the early lines of defense against microbial invaders, aiding in the removal of bacteria that has entered the body. Another leukocyte that is found in the peripheral blood is the monocyte. Monocytes give rise to phagocytic macrophages that clean up dead and damaged cells in the body, whether they are foreign or from the host animal. Two additional leukocytes in the blood are eosinophils and basophils—both help to facilitate the inflammatory response.

The slightly granular material among the cells is a cytoplasmic fragment of a cell in the bone marrow. This is called a platelet or thrombocyte. Platelets participate in the stages leading up to coagulation of the blood to stop bleeding through damaged blood vessels. Blood has a number of functions, but primarily it transports material through the body to bring nutrients to cells and remove waste material from them.

Muscle Tissues

There are three types of muscle in animal bodies: smooth, skeletal, and cardiac. They differ by the presence or absence of striations or bands, the number and location of nuclei, whether they are voluntarily or involuntarily controlled, and their location within the body. The table summarizes these differences.

Table 41.4.3: Types of Muscles

Type of Muscle	Striations	Nuclei	Control	Location
smooth	no	single, in center	involuntary	visceral organs
skeletal	yes	many, at periphery	voluntary	skeletal muscles
cardiac	yes	single, in center	involuntary	heart

Smooth Muscle

Smooth muscle does not have striations in its cells. It has a single, centrally located nucleus, as shown in Figure **41.4.12**. Constriction of smooth muscle occurs under involuntary, autonomic nervous control and in response to local conditions in the tissues. Smooth muscle tissue is also called non-striated as it lacks the banded appearance of skeletal and cardiac muscle. The walls of blood vessels, the tubes of the digestive system, and the tubes of the reproductive systems are composed of mostly smooth muscle.

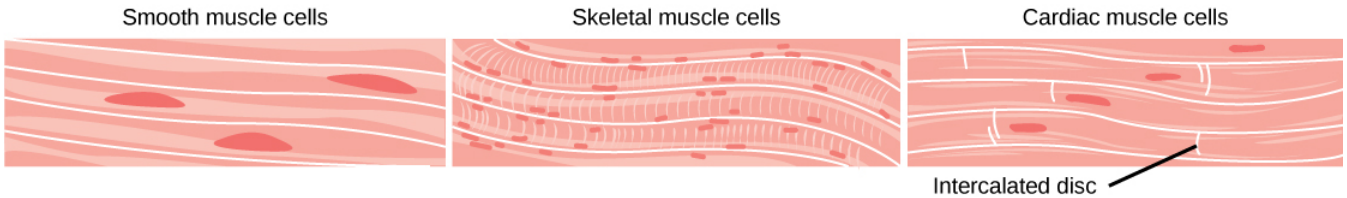


Figure **41.4.12**: Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

Skeletal Muscle

Skeletal muscle has striations across its cells caused by the arrangement of the contractile proteins actin and myosin. These muscle cells are relatively long and have multiple nuclei along the edge of the cell. Skeletal muscle is under voluntary, somatic nervous system control and is found in the muscles that move bones. Figure **41.4.12**illustrates the histology of skeletal muscle.

Cardiac Muscle

Cardiac muscle, shown in Figure **41.4.12**, is found only in the heart. Like skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally located nucleus. Cardiac muscle is not under voluntary control but can be influenced by the autonomic nervous system to speed up or slow down. An added feature to cardiac muscle cells is a line than extends along the end of the cell as it abuts the next cardiac cell in the row. This line is called an intercalated disc: it assists in passing electrical impulse efficiently from one cell to the next and maintains the strong connection between neighboring cardiac cells.

Nervous Tissues

Nervous tissues are made of cells specialized to receive and transmit electrical impulses from specific areas of the body and to send them to specific locations in the body. The main cell of the nervous system is the neuron, illustrated in Figure **41.4.13**. The large structure with a central nucleus is the cell body of the neuron. Projections from the cell body are either dendrites specialized in receiving input or a single axon specialized in transmitting impulses. Some glial cells are also shown. Astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells that are not shown support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic and remove debris or damaged cells from the tissue. A nerve consists of neurons and glial cells.

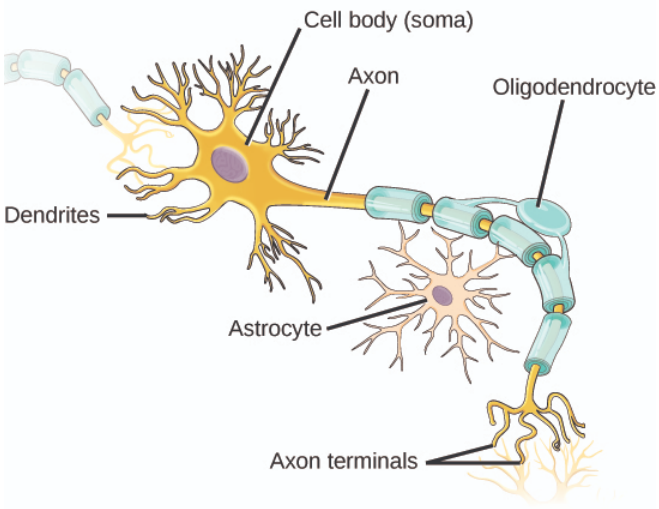


Figure **41.4.13**: The neuron has projections called dendrites that receive signals and projections called axons that send signals. Also shown are two types of glial cells: astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently.

Link to Learning

Click through the interactive review to learn more about epithelial tissues.

Career Connections: Pathologist

A pathologist is a medical doctor or veterinarian who has specialized in the laboratory detection of disease in animals, including humans. These professionals complete medical school education and follow it with an extensive post-graduate residency at a medical center. A pathologist may oversee clinical laboratories for the evaluation of body tissue and blood

samples for the detection of disease or infection. They examine tissue specimens through a microscope to identify cancers and other diseases. Some pathologists perform autopsies to determine the cause of death and the progression of disease.

Summary

The basic building blocks of complex animals are four primary tissues. These are combined to form organs, which have a specific, specialized function within the body, such as the skin or kidney. Organs are organized together to perform common functions in the form of systems. The four primary tissues are epithelia, connective tissues, muscle tissues, and nervous tissues.

Glossary

canaliculus
microchannel that connects the lacunae and aids diffusion between cells

cartilage
type of connective tissue with a large amount of ground substance matrix, cells called chondrocytes, and some amount of fibers

chondrocyte
cell found in cartilage

columnar epithelia
epithelia made of cells taller than they are wide, specialized in absorption

connective tissue
type of tissue made of cells, ground substance matrix, and fibers

cuboidal epithelia
epithelia made of cube-shaped cells, specialized in glandular functions

epithelial tissue
tissue that either lines or covers organs or other tissues

fibrous connective tissue
type of connective tissue with a high concentration of fibers

lacuna
space in cartilage and bone that contains living cells

loose (areolar) connective tissue
type of connective tissue with small amounts of cells, matrix, and fibers; found around blood vessels

matrix
component of connective tissue made of both living and non-living (ground substances) cells

osteon
subunit of compact bone

pseudostratified
layer of epithelia that appears multilayered, but is a simple covering

simple epithelia
single layer of epithelial cells

squamous epithelia

type of epithelia made of flat cells, specialized in aiding diffusion or preventing abrasion

stratified epithelia

multiple layers of epithelial cells

trabecula

tiny plate that makes up spongy bone and gives it strength

transitional epithelia

epithelia that can transition for appearing multilayered to simple; also called uroepithelial

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41.4B: Muscles

Animals use muscles to convert the chemical energy of ATP into mechanical work. Three different kinds of muscles are found in vertebrate animals.

- **Heart muscle** also called **cardiac muscle** makes up the wall of the heart. Throughout our life, it contracts some 70 times per minute pumping about 5 liters of blood each minute.
- **Smooth muscle** is found in the walls of all the hollow organs of the body (except the heart). Its contraction reduces the size of these structures. Thus it
  - regulates the flow of blood in the arteries
  - moves your breakfast along through your gastrointestinal tract
  - expels urine from your urinary bladder
  - sends babies out into the world from the uterus
  - regulates the flow of air through the lungs

  The contraction of smooth muscle is generally **not** under voluntary control.
- **Skeletal muscle**, as its name implies, is the muscle attached to the skeleton. It is also called **striated muscle**. The contraction of skeletal muscle is under voluntary control.

Anatomy of Skeletal Muscle

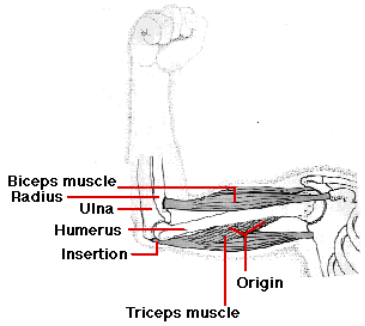


Figure 15.10.2.1 Forearm

A single skeletal muscle, such as the **triceps** muscle, is attached at its

- **origin** to a large area of bone; in this case, the **humerus**.
- at its other end, the **insertion**, it tapers into a glistening white **tendon** which, in this case, is attached to the **ulna**, one of the bones of the lower arm.

As the triceps contracts, the insertion is pulled toward the origin and the arm is straightened or extended at the elbow. Thus the triceps is an **extensor**. Because skeletal muscle exerts force only when it contracts, a second muscle - a **flexor** - is needed to flex or bend the joint. The **biceps** muscle is the flexor of the lower arm. Together, the biceps and triceps make up an **antagonistic pair** of muscles. Similar pairs, working antagonistically across other joints, provide for almost all the movement of the skeleton.

The Muscle Fiber

Skeletal muscle is made up of thousands of cylindrical muscle **fibers** often running all the way from origin to insertion. The fibers are bound together by connective tissue through which run blood vessels and nerves.Each muscle fibers contains:

- an array of **myofibrils** that are stacked lengthwise and run the entire length of the fiber;
- **mitochondria**;
- an extensive **smooth endoplasmic reticulum (SER)**;
- **many nuclei** (thus each skeletal muscle fiber is a syncytium).

The multiple nuclei arise from the fact that each muscle fiber develops from the fusion of many cells (called **myoblasts**). The number of fibers is probably fixed early in life. This is regulated by **myostatin**, a cytokine that is synthesized in muscle cells (and circulates as a hormone later in life). Myostatin **suppresses** skeletal muscle development. (Cytokines secreted by a cell type that

inhibit proliferation of that same type of cell are called **chalones**.) Cattle and mice with inactivating mutations in their myostatin genes develop much larger muscles. Some athletes and other remarkably strong people have been found to carry one mutant myostatin gene. These discoveries have already led to the growth of an illicit market in drugs supposedly able to suppress myostatin.

In adults, increased muscle mass comes about through an increase in the thickness of the individual fibers and increase in the amount of connective tissue. In the mouse, at least, fibers increase in size by attracting more myoblasts to fuse with them. The fibers attract more myoblasts by releasing the cytokine interleukin 4 (IL-4). Anything that lowers the level of myostatin also leads to an increase in fiber size.

Because a muscle fiber is not a single cell, its parts are often given special names such as

- **sarcolemma** for plasma membrane
- **sarcoplasmic reticulum** for endoplasmic reticulum
- **sarcosomes** for mitochondria
- **sarcoplasm** for cytoplasm

Although this tends to obscure the essential similarity in structure and function of these structures and those found in other cells.

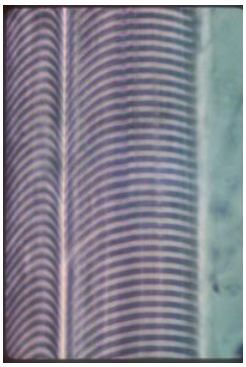


Figure 15.10.2.2 Striated muscle

The nuclei and mitochondria are located just beneath the plasma membrane. The endoplasmic reticulum extends between the myofibrils. Seen from the side under the microscope, skeletal muscle fibers show a pattern of cross banding, which gives rise to the other name: **striated muscle**. The striated appearance of the muscle fiber is created by a pattern of alternating dark **A bands** and light **I bands**.

- The A bands are bisected by the **H zone** running through the center of which is the **M line**.
- The I bands are bisected by the **Z disk**.

Each myofibril is made up of arrays of parallel **filaments**.

- The **thick filaments** have a diameter of about 15 nm. They are composed of the protein **myosin**.
- The **thin filaments** have a diameter of about 5 nm. They are composed chiefly of the protein **actin** along with smaller amounts of two other proteins - **troponin** and **tropomyosin**.

The anatomy of a sarcomere

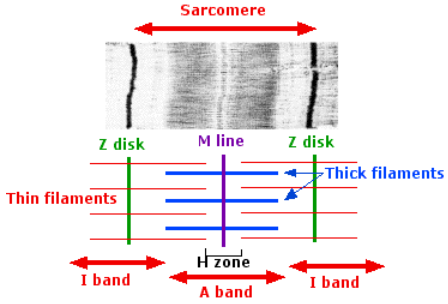


Figure 15.10.2.3 Sacromere

The entire array of thick and thin filaments between the Z disks is called a **sarcomere**.

- The **thick filaments** produce the dark **A band**.
- The **thin filaments** extend in each direction from the Z disk. Where they do not overlap the thick filaments, they create the light **I band**.
- The **H zone** is that portion of the A band where the thick and thin filaments do not overlap.
- The **M line** runs through the exact center of the sarcomere. Molecules of the giant protein, **titin**, extend from the M line to the Z disk. One of its functions is to provide elasticity to the muscle. It also provides a scaffold for the assembly of a precise number of myosin molecules in the thick filament (294 in one case). It may also dictate the number of actin molecules in the thin filaments.

Shortening of the sarcomeres in a myofibril produces the shortening of the myofibril and, in turn, of the muscle fiber of which it is a part. [This electron micrograph of a single sarcomere was kindly provided by Dr. H. E. Huxley.]

Activation of Skeletal Muscle

The contraction of skeletal muscle is controlled by the nervous system. The Dying Lioness (an Assyrian relief dating from about 650 B.C.) shows this vividly. Injury to the spinal cord has paralyzed the otherwise undamaged hind legs. In this respect, skeletal muscle differs from smooth and cardiac muscle. Both cardiac and smooth muscle can contract without being stimulated by the nervous system. Nerves of the autonomic branch of the nervous system lead to both smooth and cardiac muscle, but their effect is one of moderating the rate and/or strength of contraction.

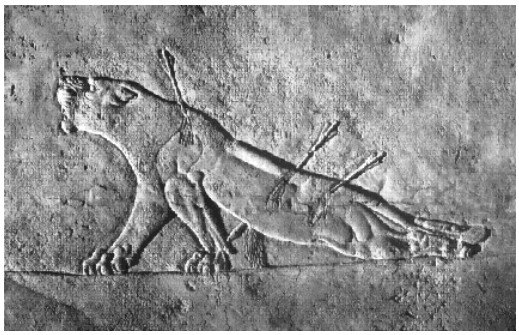


Figure 15.10.2.4: The Dying Lionesssupplied through the courtesy of The Trustees of the British Museum

The Neuromuscular Junction

Nerve impulses (action potentials) traveling down the motor neurons of the sensory-somatic branch of the nervous system cause the skeletal muscle fibers at which they terminate to contract. The junction between the terminal of a motor neuron and a muscle fiber is called the neuromuscular junction. It is simply one kind of synapse. (The neuromuscular junction is also called the myoneural junction.)

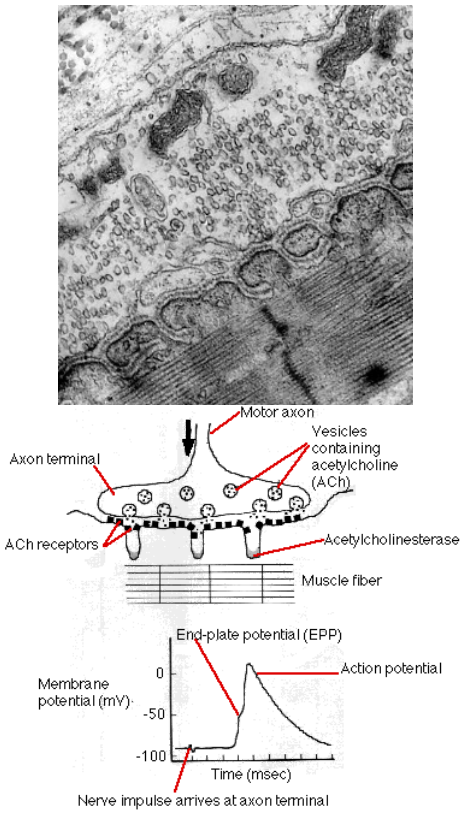


Figure 15.10.2.5 NM Junction

The terminals of motor axons contain thousands of vesicles filled with **acetylcholine** (**ACh**). Many of these can be seen in the electron micrograph on the left (courtesy of Prof. B. Katz).

When an action potential reaches the axon terminal, hundreds of these vesicles discharge their ACh onto a specialized area of postsynaptic membrane on the muscle fiber (the folded membrane running diagonally upward from the lower left). This area contains a cluster of transmembrane channels that are opened by ACh and let sodium ions (Na^+) diffuse in.

The interior of a resting muscle fiber has a **resting potential** of about −95 mV. The influx of sodium ions reduces the charge, creating an **end plate potential**. If the end plate potential reaches the **threshold** voltage (approximately −50 mV), sodium ions flow in with a rush and an **action potential** is created in the fiber. The action potential sweeps down the length of the fiber just as it does in an axon. No visible change occurs in the muscle fiber during (and immediately following) the action potential. This period, called the **latent period**, lasts from 3–10 msec.

Before the latent period is over,

- the enzyme **acetylcholinesterase**
  - breaks down the ACh in the neuromuscular junction (at a speed of 25,000 molecules per second)
  - the sodium channels close, and
  - the field is cleared for the arrival of another nerve impulse.
- the resting potential of the fiber is restored by an outflow of **potassium ions**.

The brief (1–2 msec) period needed to restore the resting potential is called the **refractory period**.

Tetanus

The process of contracting takes some 50 msec; relaxation of the fiber takes another 50–100 msec. Because the refractory period is so much shorter than the time needed for contraction and relaxation, the fiber can be maintained in the contracted state so long as it is stimulated frequently enough (e.g., 50 stimuli per second). Such sustained contraction is called **tetanus**.

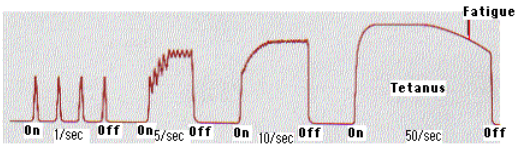


Figure 15.10.2.6 Tetanus

In the above figure:

- When shocks are given at 1/sec, the muscle responds with a single twitch.
- At 5/sec and 10/sec, the individual twitches begin to fuse together, a phenomenon called **clonus**.
- At 50 shocks per second, the muscle goes into the smooth, sustained contraction of tetanus.

Clonus and tetanus are possible because the refractory period is much briefer than the time needed to complete a cycle of contraction and relaxation. Note that the amount of contraction is greater in clonus and tetanus than in a single twitch.

As we normally use our muscles, the individual fibers go into tetanus for brief periods rather than simply undergoing single twitches.

The Sliding-Filament Model

Each molecule of myosin in the **thick filaments** contains a globular subunit called the **myosin head**. The myosin heads have binding sites for the **actin** molecules in the **thin filaments** and **ATP.** Activation of the muscle fiber causes the myosin heads to bind to actin. An allosteric change occurs which draws the thin filament a short distance (~10 nm) past the thick filament. Then the linkages break (for which ATP is needed) and reform farther along the thin filament to repeat the process. As a result, the filaments are pulled past each other in a ratchetlike action. There is no shortening, thickening, or folding of the individual filaments.

Electron microscopy supports this model.

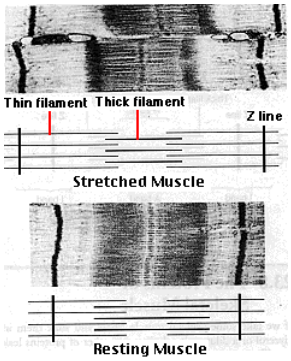


Figure 15.10.2.7 Sliding - Filament model courtesy of Dr. H. E. Huxley

As a muscle contracts,

- the Z disks come closer together
- the width of the I bands decreases
- the width of the H zones decreases
- there is no change in the width of the A band

Conversely, as a muscle is stretched,

- the width of the I bands and H zones increases
- but there is still no change in the width of the A band

Coupling Excitation to Contraction

Calcium ions (Ca^{2+}) link action potentials in a muscle fiber to contraction.

- In resting muscle fibers, Ca^{2+} is stored in the endoplasmic (sarcoplasmic) reticulum.
- Spaced along the plasma membrane (**sarcolemma**) of the muscle fiber are inpocketings of the membrane that form **"T-tubules"**. These tubules plunge repeatedly into the interior of the fiber.

- The T-tubules terminate near the calcium-filled sacs of the **sarcoplasmic reticulum**.
- Each action potential created at the neuromuscular junction sweeps quickly along the sarcolemma and is carried into the T-tubules.

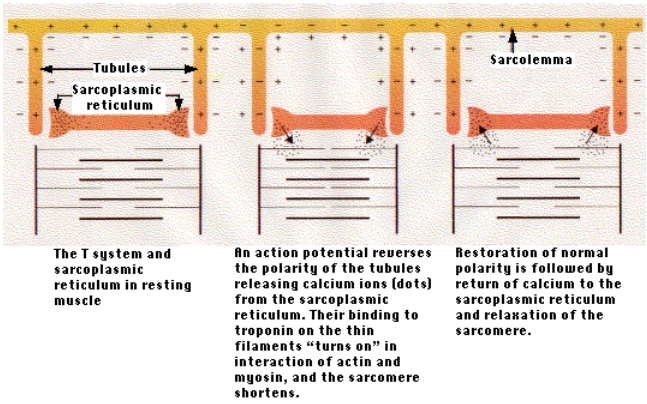


Figure 15.10.2.8 Sacrolemma

- The arrival of the action potential at the ends of the T-tubules triggers the release of Ca^{2+}.
- The Ca^{2+} diffuses among the thick and thin filaments where it
- binds to **troponin** on the thin filaments.
- This turns on the interaction between actin and myosin and the sarcomere contracts.
- Because of the speed of the action potential (milliseconds), the action potential arrives virtually simultaneously at the ends of all the T-tubules, ensuring that all sarcomeres contract in unison.
- When the process is over, the calcium is pumped back into the sarcoplasmic reticulum using a **Ca^{2+} ATPase**.

Isotonic versus Isometric Contractions

If a stimulated muscle is held so that it cannot shorten, it simply exerts tension. This is called an **isometric** ("same length") contraction. If the muscle is allowed to shorten, the contraction is called **isotonic** ("same tension").

Motor Units

All motor neurons leading to skeletal muscles have branching axons, each of which terminates in a neuromuscular junction with a single muscle fiber. Nerve impulses passing down a single motor neuron will thus trigger contraction in all the muscle fibers at which the branches of that neuron terminate. This minimum unit of contraction is called the **motor unit**.

The size of the motor unit is small in muscles over which we have precise control. Examples:

- a single motor neuron triggers fewer than 10 fibers in the muscles controlling eye movements
- the motor units of the muscles controlling the larynx are as small as 2–3 fibers per motor neuron
- In contrast, a single motor unit for a muscle like the gastrocnemius (calf) muscle may include 1000–2000 fibers (scattered uniformly through the muscle).

Although the response of a motor unit is all-or-none, the strength of the response of the entire muscle is determined by the **number of motor units** activated. Even at rest, most of our skeletal muscles are in a state of partial contraction called **tonus**. Tonus is maintained by the activation of a few motor units at all times even in resting muscle. As one set of motor units relaxes, another set takes over.

Fueling Muscle Contraction

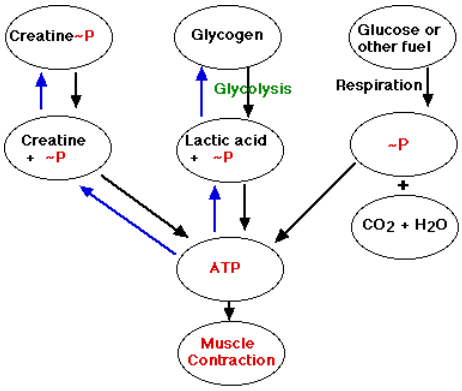


Figure 15.10.2.9 Creatine

ATP is the immediate source of energy for muscle contraction. Although a muscle fiber contains only enough ATP to power a few twitches, its ATP "pool" is replenished as needed. There are three sources of high-energy phosphate to keep the ATP pool filled.

- **creatine phosphate**
- **glycogen**
- **cellular respiration** in the mitochondria of the fibers.

Creatine phosphate

The phosphate group in creatine phosphate is attached by a "high-energy" bond like that in ATP. Creatine phosphate derives its high-energy phosphate from ATP and can donate it back to ADP to form ATP.

Creatine phosphate + ADP ↔ creatine + ATP

The pool of creatine phosphate in the fiber is about 10 times larger than that of ATP and thus serves as a modest reservoir of ATP.

Glycogen

Skeletal muscle fibers contain about 1% **glycogen**. The muscle fiber can degrade this glycogen by glycogenolysis producing glucose-1-phosphate. This enters the glycolytic pathway to yield two molecules of ATP for each pair of lactic acid molecules produced. Not much, but enough to keep the muscle functioning if it fails to receive sufficient oxygen to meet its ATP needs by respiration.

However, this source is limited and eventually the muscle must depend on cellular respiration.

Cellular respiration

Cellular respiration not only is required to meet the ATP needs of a muscle engaged in prolonged activity (thus causing more rapid and deeper breathing), but is also required afterwards to enable the body to resynthesize glycogen from the lactic acid produced earlier (deep breathing continues for a time after exercise is stopped). The body must repay its **oxygen debt**.

Type I vs. Type II Fibers

Several different types of muscle fiber can be found in most skeletal muscles: Type I and and 3 subtypes of Type II fibers. Each type differs in the myosin it uses and also in its structure and biochemistry.

Type I Fibers

- loaded with mitochondria
- depend on cellular respiration for ATP production
- fatty acids the major energy source
- resistant to fatigue
- rich in myoglobin and hence red in color (the "dark" meat of the turkey)
- activated by small-diameter, thus slow-conducting, motor neurons
- also known as "slow-twitch" fibers

- dominant in muscles used in activities requiring endurance (leg muscles) and those that depend on tonus, e.g., those responsible for posture

Type IIb Fibers

- few mitochondria
- rich in glycogen
- depend on creatine phosphate and glycolysis for ATP production
- fatigue easily with the production of lactic acid
- low in myoglobin hence whitish in color (the white meat of the turkey)
- activated by large-diameter, thus fast-conducting, motor neurons
- also known as "fast-twitch" fibers
- dominant in muscles used for rapid movement, e.g., those moving the eyeballs.

The other subtypes of Type II fibers have properties intermediate between those of Type IIb and Type I.

Most skeletal muscles contain some mixture of Type I and Type II fibers, but a single motor unit always contains one type or the other, never both.

In mice, the number of Type I vs Type II fibers can be changed with exercise and drug treatment. Whether the same holds true for humans remains to be seen. Perhaps training in humans does not alter the **number** of fibers of a particular type but may increase the diameter of one type (e.g., Type I in marathoners, Type IIb in weight lifters) at the expense of the other types.

Cardiac Muscle

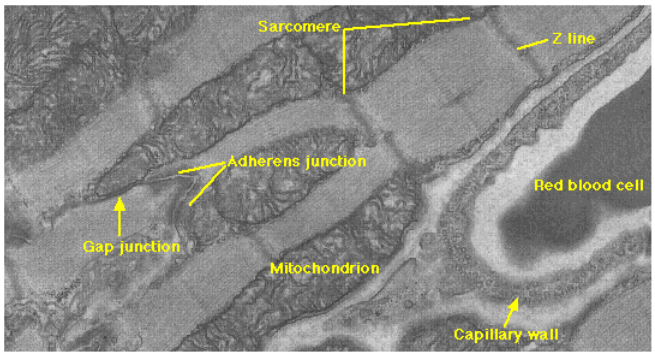


Figure 15.10.2.10 Cardiac muscle

Cardiac or heart muscle resembles skeletal muscle in some ways: it is striated and each cell contains sarcomeres with sliding filaments of actin and myosin. However, cardiac muscle has a number of unique features that reflect its function of pumping blood.

- The myofibrils of each cell (and cardiac muscle is made of single cells — each with a single nucleus) are branched.
- The branches interlock with those of adjacent fibers by adherens junctions. These strong junctions enable the heart to contract forcefully without ripping the fibers apart.

  This electron micrograph (reproduced with permission from Keith R. Porter and Mary A. Bonneville, *An Introduction to the Fine Structure of Cells and Tissues*, 4th ed., Lea & Febiger, Philadelphia, 1973) shows an adherens junction and several of the other features listed here.

- The action potential that triggers the heartbeat is generated within the heart itself. Motor nerves (of the autonomic nervous system) do run to the heart, but their effect is simply to modulate — increase or decrease — the intrinsic rate and the strength of the heartbeat. Even if the nerves are destroyed (as they are in a transplanted heart), the heart continues to beat.
- The action potential that drives contraction of the heart passes from fiber to fiber through gap junctions.
  - Significance: all the fibers contract in a synchronous wave that sweeps from the atria down through the ventricles and pumps blood out of the heart. Anything that interferes with this synchronous wave (such as damage to part of the heart muscle from a heart attack) may cause the fibers of the heart to beat at random — called **fibrillation**. Fibrillation is the ultimate cause of most deaths, and its reversal is the function of defibrillators that are part of the equipment in ambulances, hospital emergency rooms, and even on U.S. air lines.

- The **refractory period** in heart muscle is **longer** than the period it takes for the muscle to contract (systole) and relax (diastole). Thus **tetanus** is not possible (a good thing, too!).
- Cardiac muscle has a much richer supply of mitochondria than skeletal muscle. This reflects its greater dependence on cellular respiration for ATP.
- Cardiac muscle has little glycogen and gets little benefit from glycolysis when the supply of oxygen is limited.
    - Thus anything that interrupts the flow of oxygenated blood to the heart leads quickly to damage - even death - of the affected part. This is what happens in heart attacks.

Smooth Muscle

Smooth muscle is made of single, spindle-shaped cells. It gets its name because no striations are visible in them. Nonetheless, each smooth muscle cell contains **thick** (myosin) and **thin** (actin) filaments that slide against each other to produce contraction of the cell. The thick and thin filaments are anchored near the plasma membrane (with the help of intermediate filaments).

Smooth muscle (like cardiac muscle) does not depend on motor neurons to be stimulated. However, motor neurons (of the autonomic system) reach smooth muscle and can stimulate it or relax it depending on the neurotransmitter they release (e.g. noradrenaline or nitric oxide, NO).

Smooth muscle can also be made to contract

- by other substances released in the vicinity (paracrine stimulation)
    - Example: release of **histamine** causes contraction of the smooth muscle lining our air passages (triggering an attack of **asthma**)
- by hormones circulating in the blood
    - Example: oxytocin reaching the uterus stimulates it to contract to begin childbirth.

The contraction of smooth muscle tends to be slower than that of striated muscle. It also is often sustained for long periods. This, too, is called **tonus** but the mechanism is not like that in skeletal muscle.

Muscle Diseases

The Muscular Dystrophies (MD)

Together myosin, actin, tropomyosin, and troponin make up over three-quarters of the protein in muscle fibers. Some two dozen other proteins make up the rest. These serve such functions as attaching and organizing the filaments in the sarcomere and connecting the sarcomeres to the plasma membrane and the extracellular matrix. Mutations in the genes encoding these proteins may produce defective proteins and resulting defects in the muscles.

Among the most common of the muscular dystrophies are those caused by mutations in the gene for **dystrophin**. The gene for dystrophin is huge, containing 79 exons spread out over 2.4 million base pairs of DNA. Thus this single gene represents about 0.1% of the entire human genome (3×10^9 bp) and is almost half the size of the entire genome of E. coli!

- **Duchenne muscular dystrophy** (**DMD**)

  Deletions or nonsense mutations that cause a **frameshift** usually introduce premature termination codons (PTCs) in the resulting mRNA. Thus at best only a fragment of dystrophin is synthesized and DMD, a very severe form of the disease, results.

- **Becker muscular dystrophy** (**BMD**).

  If the deletion simply removes certain exons but preserves the correct reading frame, a slightly-shortened protein results that produces BMD, a milder form of the disease.

The gene for dystrophin is on the X chromosome, so these two diseases strike males in a typical X-linked pattern of inheritance.

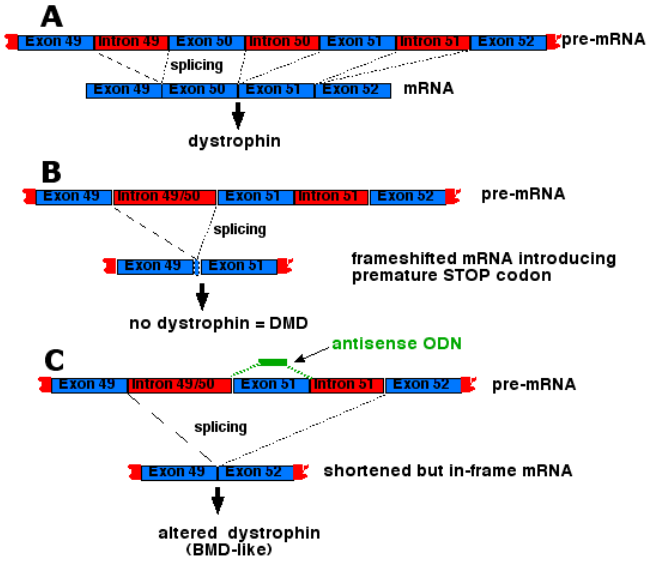


Figure 15.10.2.11 Exon skipping

Deletions of one or more exons in the huge dystrophin gene are the cause of most of the cases of DMD. Exon 50 is a particularly notorious offender. When it is deleted, splicing of the pre-mRNA introduces a frameshift which then introduces a premature termination codon resulting in no functional dystrophin synthesized ("**B**"). However, an antisense oligonucleotide targeted to exon 51 causes the splicing mechanism to skip over it resulting in the stitching together of exons 49 and 52. This restores the correct reading frame so that only a slightly-altered version of dystrophin is produced, i.e., a BMD-type dystrophin ("**C**"). Seventeen weeks of weekly injections of 12 young DMD patients in the Netherlands with the oligonucleotide caused their muscles to synthesize sufficient amounts of dystrophin to enable 8 of them to walk better than before. (See Goemans, N., et al., in the 21 April 2011 issue of **The New England Journal of Medicine**.

Three research groups have used the CRISPR-Cas9 genome editing system to remove a mutated exon in DMD mice. The treatment restored dystrophin synthesis and improved skeletal and cardiac muscle function in the mice.

Myasthenia Gravis

Myasthenia gravis is an autoimmune disorder affecting the neuromuscular junction. Patients have smaller end plate potentials (EPPs) than normal. With repeated stimulation, the EPPs become too small to trigger further action potentials and the fiber ceases to contract. Administration of an inhibitor of acetylcholinesterase temporarily can restore contractility by allowing more ACh to remain at the site.

Patients with myasthenia gravis have only 20% or so of the number of ACh receptors found in normal neuromuscular junctions. This loss appears to be caused by antibodies directed against the receptors. Some evidence:

- A disease resembling myasthenia gravis can be induced in experimental animals by immunizing them with purified ACh receptors.
- Anti-ACh receptor antibodies are found in the serum of human patients.
- Experimental animals injected with serum from human patients develop the signs of myasthenia gravis.
- Newborns of mothers with myasthenia gravis often show mild signs of the disease for a short time after their birth. This is the result of the transfer of the mother's antibodies across the placenta during gestation.

The reason some people develop autoimmune antibodies against the ACh receptor is unknown.

The Cardiac Myopathies

Cardiac muscle, like skeletal muscle, contains many proteins in addition to actin and myosin. Mutations in the genes for these may cause the wall of the heart to become weakened and, in due course, enlarged. Among the genes that have been implicated in these diseases are those encoding:

- actin
- two types of myosin
- troponin
- tropomyosin
- myosin-binding protein C (which links myosin to titin)

The severity of the disease varies with the particular mutation causing it (over 100 have been identified so far) . Some mutations are sufficiently dangerous that they can lead to sudden catastrophic heart failure in seemingly healthy and active young adults.

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41.5: Nerve Tissue

Skills to Develop

- List and describe the functions of the structural components of a neuron
- List and describe the four main types of neurons
- Compare the functions of different types of glial cells

Nervous systems throughout the animal kingdom vary in structure and complexity, as illustrated by the variety of animals shown in Figure **41.5.1**. Some organisms, like sea sponges, lack a true nervous system. Others, like jellyfish, lack a true brain and instead have a system of separate but connected nerve cells (neurons) called a "nerve net." Echinoderms such as sea stars have nerve cells that are bundled into fibers called nerves. Flatworms of the phylum Platyhelminthes have both a central nervous system (CNS), made up of a small "brain" and two nerve cords, and a peripheral nervous system (PNS) containing a system of nerves that extend throughout the body. The insect nervous system is more complex but also fairly decentralized. It contains a brain, ventral nerve cord, and ganglia (clusters of connected neurons). These ganglia can control movements and behaviors without input from the brain. Octopi may have the most complicated of invertebrate nervous systems—they have neurons that are organized in specialized lobes and eyes that are structurally similar to vertebrate species.

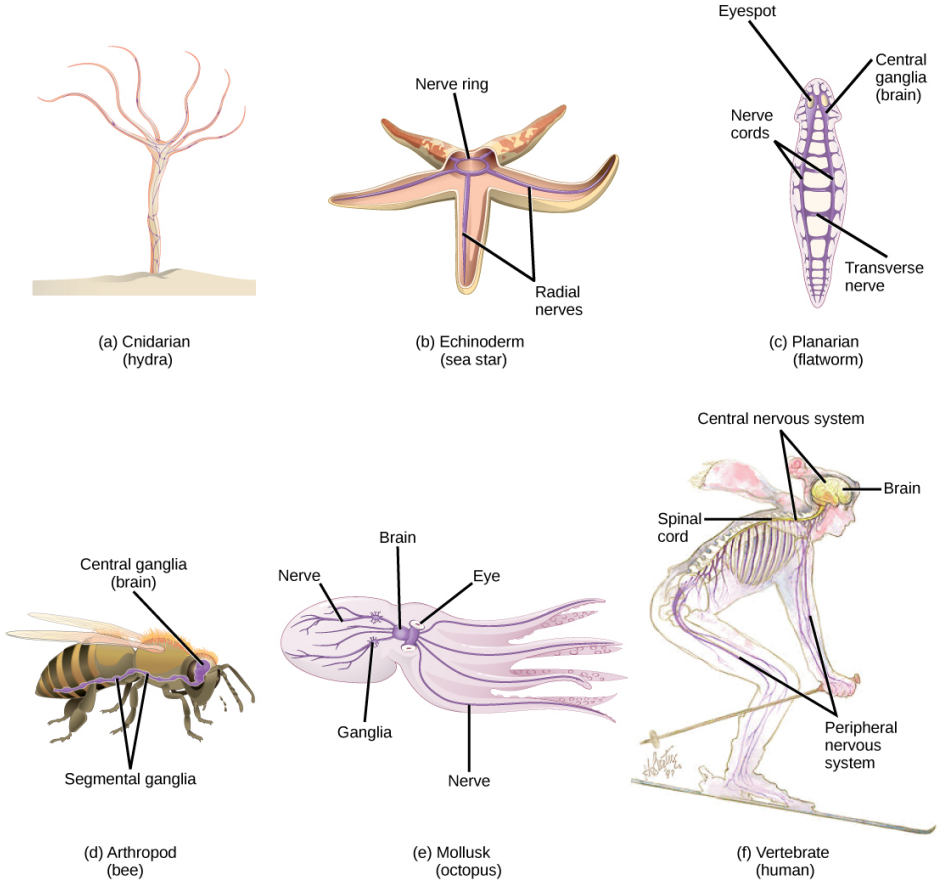


Figure **41.5.1**: Nervous systems vary in structure and complexity. In (a) cnidarians, nerve cells form a decentralized nerve net. In (b) echinoderms, nerve cells are bundled into fibers called nerves. In animals exhibiting bilateral symmetry such as (c) planarians, neurons cluster into an anterior brain that processes information. In addition to a brain, (d) arthropods have clusters of nerve cell bodies, called peripheral ganglia, located along the ventral nerve cord. Mollusks such as squid and (e) octopi, which must hunt to survive, have complex brains containing millions of neurons. In (f) vertebrates, the brain and spinal cord comprise the central nervous system, while neurons extending into the rest of the body comprise the peripheral nervous system. (credit e: modification of work by Michael Vecchione, Clyde F.E. Roper, and Michael J. Sweeney, NOAA; credit f: modification of work by NIH).

Compared to invertebrates, vertebrate nervous systems are more complex, centralized, and specialized. While there is great diversity among different vertebrate nervous systems, they all share a basic structure: a CNS that contains a brain and spinal cord

and a PNS made up of peripheral sensory and motor nerves. One interesting difference between the nervous systems of invertebrates and vertebrates is that the nerve cords of many invertebrates are located ventrally whereas the vertebrate spinal cords are located dorsally. There is debate among evolutionary biologists as to whether these different nervous system plans evolved separately or whether the invertebrate body plan arrangement somehow "flipped" during the evolution of vertebrates.

Link to Learning



Watch this video of biologist Mark Kirschner discussing the "flipping" phenomenon of vertebrate evolution.

The nervous system is made up of neurons, specialized cells that can receive and transmit chemical or electrical signals, and glia, cells that provide support functions for the neurons by playing an information processing role that is complementary to neurons. A neuron can be compared to an electrical wire—it transmits a signal from one place to another. Glia can be compared to the workers at the electric company who make sure wires go to the right places, maintain the wires, and take down wires that are broken. Although glia have been compared to workers, recent evidence suggests that also usurp some of the signaling functions of neurons.

There is great diversity in the types of neurons and glia that are present in different parts of the nervous system. There are four major types of neurons, and they share several important cellular components.

Neurons

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors—from basic reflexes to more complicated behaviors like finding food and courting mates. The ability of neurons to communicate with each other as well as with other types of cells underlies all of these behaviors.

Most neurons share the same cellular components. But neurons are also highly specialized—different types of neurons have different sizes and shapes that relate to their functional roles.

Parts of a Neuron

Like other cells, each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components. Neurons also contain unique structures, illustrated in Figure **41.5.2** for receiving and sending the electrical signals that make neuronal communication possible. Dendrites are tree-like structures that extend away from the cell body to receive messages from other neurons at specialized junctions called synapses. Although some neurons do not have any dendrites, some types of neurons have multiple dendrites. Dendrites can have small protrusions called dendritic spines, which further increase surface area for possible synaptic connections.

Once a signal is received by the dendrite, it then travels passively to the cell body. The cell body contains a specialized structure, the axon hillock that integrates signals from multiple synapses and serves as a junction between the cell body and an axon. An axon is a tube-like structure that propagates the integrated signal to specialized endings called axon terminals. These terminals in turn synapse on other neurons, muscle, or target organs. Chemicals released at axon terminals allow signals to be communicated to

these other cells. Neurons usually have one or two axons, but some neurons, like amacrine cells in the retina, do not contain any axons. Some axons are covered with myelin, which acts as an insulator to minimize dissipation of the electrical signal as it travels down the axon, greatly increasing the speed on conduction. This insulation is important as the axon from a human motor neuron can be as long as a meter—from the base of the spine to the toes. The myelin sheath is not actually part of the neuron. Myelin is produced by glial cells. Along the axon there are periodic gaps in the myelin sheath. These gaps are called nodes of Ranvier and are sites where the signal is "recharged" as it travels along the axon.

It is important to note that a single neuron does not act alone—neuronal communication depends on the connections that neurons make with one another (as well as with other cells, like muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

Art Connection

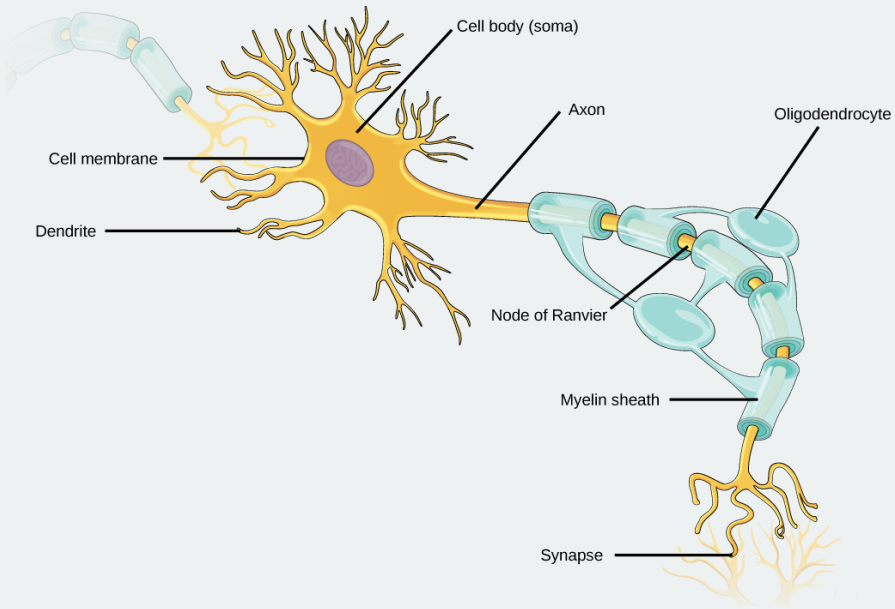


Figure **41.5.2**: Neurons contain organelles common to many other cells, such as a nucleus and mitochondria. They also have more specialized structures, including dendrites and axons.

Which of the following statements is false?

A. The soma is the cell body of a nerve cell.
B. Myelin sheath provides an insulating layer to the dendrites.
C. Axons carry the signal from the soma to the target.
D. Dendrites carry the signal to the soma.

Types of Neurons

There are different types of neurons, and the functional role of a given neuron is intimately dependent on its structure. There is an amazing diversity of neuron shapes and sizes found in different parts of the nervous system (and across species), as illustrated by the neurons shown in Figure **41.5.3**.

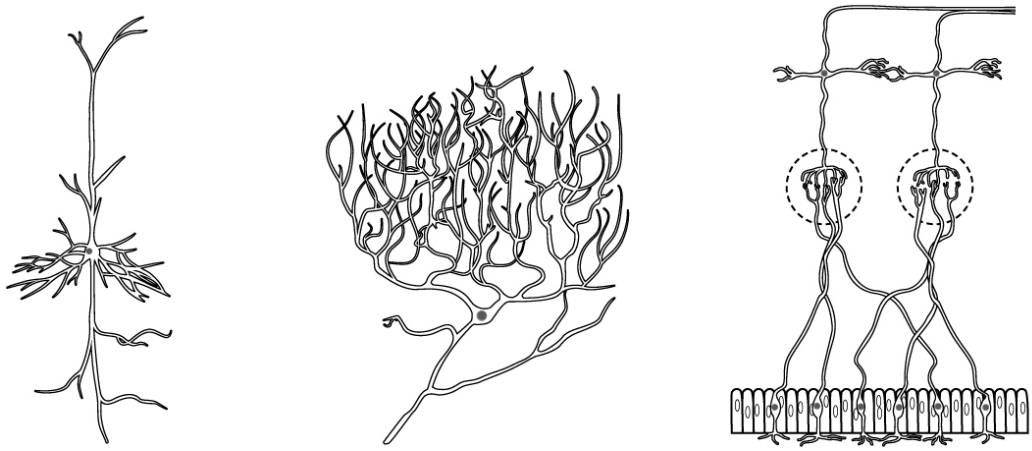


Figure 41.5.3: There is great diversity in the size and shape of neurons throughout the nervous system. Examples include (a) a pyramidal cell from the cerebral cortex, (b) a Purkinje cell from the cerebellar cortex, and (c) olfactory cells from the olfactory epithelium and olfactory bulb.

While there are many defined neuron cell subtypes, neurons are broadly divided into four basic types: unipolar, bipolar, multipolar, and pseudounipolar. Figure 41.5.4 illustrates these four basic neuron types. Unipolar neurons have only one structure that extends away from the soma. These neurons are not found in vertebrates but are found in insects where they stimulate muscles or glands. A bipolar neuron has one axon and one dendrite extending from the soma. An example of a bipolar neuron is a retinal bipolar cell, which receives signals from photoreceptor cells that are sensitive to light and transmits these signals to ganglion cells that carry the signal to the brain. Multipolar neurons are the most common type of neuron. Each multipolar neuron contains one axon and multiple dendrites. Multipolar neurons can be found in the central nervous system (brain and spinal cord). An example of a multipolar neuron is a Purkinje cell in the cerebellum, which has many branching dendrites but only one axon. Pseudounipolar cells share characteristics with both unipolar and bipolar cells. A pseudounipolar cell has a single process that extends from the soma, like a unipolar cell, but this process later branches into two distinct structures, like a bipolar cell. Most sensory neurons are pseudounipolar and have an axon that branches into two extensions: one connected to dendrites that receive sensory information and another that transmits this information to the spinal cord.

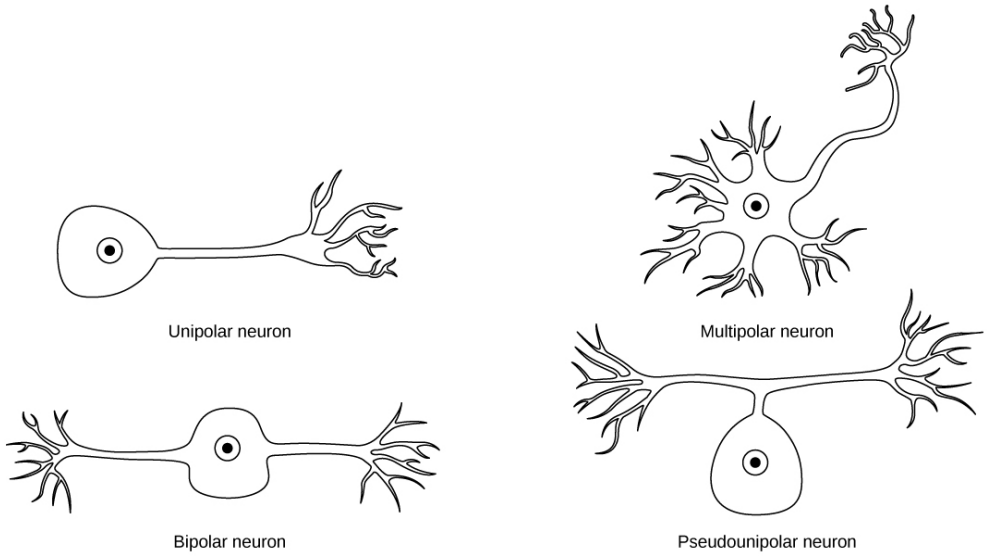


Figure 41.5.4: Neurons are broadly divided into four main types based on the number and placement of axons: (1) unipolar, (2) bipolar, (3) multipolar, and (4) pseudounipolar.

Everyday Connection: Neurogenesis

At one time, scientists believed that people were born with all the neurons they would ever have. Research performed during the last few decades indicates that neurogenesis, the birth of new neurons, continues into adulthood. Neurogenesis was first discovered in songbirds that produce new neurons while learning songs. For mammals, new neurons also play an important role in learning: about 1000 new neurons develop in the hippocampus (a brain structure involved in learning and memory) each day. While most of the new neurons will die, researchers found that an increase in the number of surviving new neurons in the hippocampus correlated with how well rats learned a new task. Interestingly, both exercise and some antidepressant medications also promote neurogenesis in the hippocampus. Stress has the opposite effect. While neurogenesis is quite limited compared to regeneration in other tissues, research in this area may lead to new treatments for disorders such as Alzheimer's, stroke, and epilepsy.

How do scientists identify new neurons? A researcher can inject a compound called bromodeoxyuridine (BrdU) into the brain of an animal. While all cells will be exposed to BrdU, BrdU will only be incorporated into the DNA of newly generated cells that are in S phase. A technique called immunohistochemistry can be used to attach a fluorescent label to the incorporated BrdU, and a researcher can use fluorescent microscopy to visualize the presence of BrdU, and thus new neurons, in brain tissue. Figure **41.5.5** is a micrograph which shows fluorescently labeled neurons in the hippocampus of a rat.

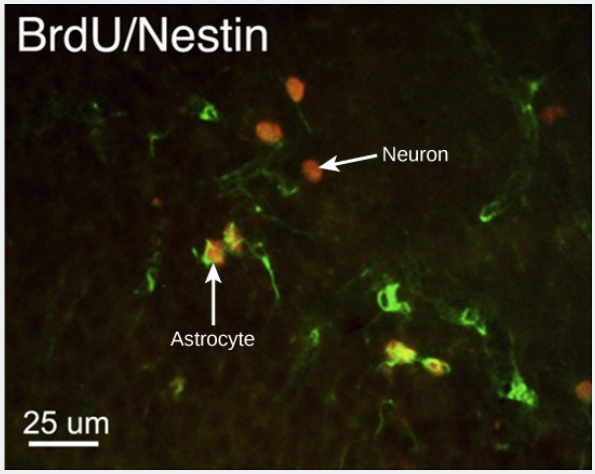


Figure **41.5.5**: This micrograph shows fluorescently labeled new neurons in a rat hippocampus. Cells that are actively dividing have bromodoxyuridine (BrdU) incorporated into their DNA and are labeled in red. Cells that express glial fibrillary acidic protein (GFAP) are labeled in green. Astrocytes, but not neurons, express GFAP. Thus, cells that are labeled both red and green are actively dividing astrocytes, whereas cells labeled red only are actively dividing neurons. (credit: modification of work by Dr. Maryam Faiz, et. al., University of Barcelona; scale-bar data from Matt Russell)

Link to Learning

This site contains more information about neurogenesis, including an interactive laboratory simulation and a video that explains how BrdU labels new cells.

Glia

While glia are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of ten. Neurons would be unable to function without the vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons, and provide myelin sheaths around axons. Scientists have recently discovered that they also play a role in responding to nerve activity and modulating communication between nerve cells. When glia do not function properly, the result can be disastrous—most brain tumors are caused by mutations in glia.

Types of Glia

There are several different types of glia with different functions, two of which are shown in Figure **41.5.6**. Astrocytes, shown in Figure **41.5.7** make contact with both capillaries and neurons in the CNS. They provide nutrients and other substances to neurons, regulate the concentrations of ions and chemicals in the extracellular fluid, and provide structural support for synapses. Astrocytes also form the blood-brain barrier—a structure that blocks entrance of toxic substances into the brain. Astrocytes, in particular, have been shown through calcium imaging experiments to become active in response to nerve activity, transmit calcium waves between astrocytes, and modulate the activity of surrounding synapses.

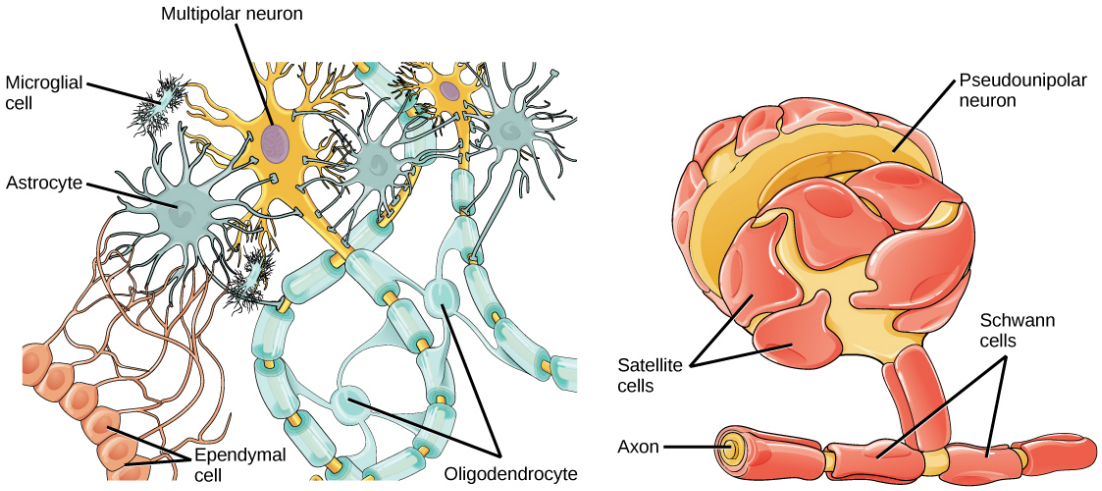
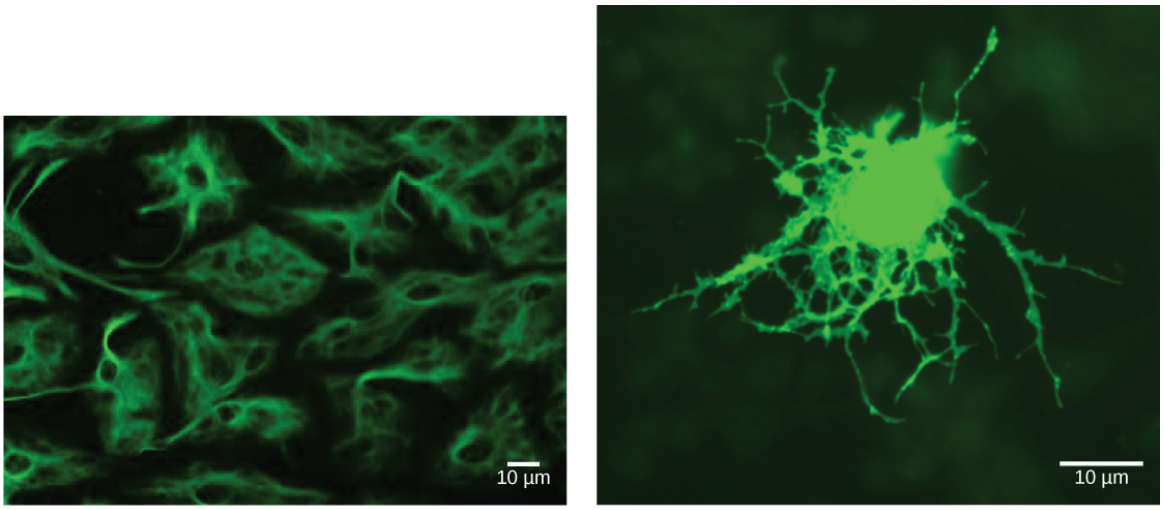


Figure **41.5.6**: Glial cells support neurons and maintain their environment. Glial cells of the (a) central nervous system include oligodendrocytes, astrocytes, ependymal cells, and microglial cells. Oligodendrocytes form the myelin sheath around axons. Astrocytes provide nutrients to neurons, maintain their extracellular environment, and provide structural support. Microglia scavenge pathogens and dead cells. Ependymal cells produce cerebrospinal fluid that cushions the neurons. Glial cells of the (b) peripheral nervous system include Schwann cells, which form the myelin sheath, and satellite cells, which provide nutrients and structural support to neurons.

Satellite glia provide nutrients and structural support for neurons in the PNS. Microglia scavenge and degrade dead cells and protect the brain from invading microorganisms. Oligodendrocytes, shown in Figure **41.5.7** form myelin sheaths around axons in the CNS. One axon can be myelinated by several oligodendrocytes, and one oligodendrocyte can provide myelin for multiple neurons. This is distinctive from the PNS where a single Schwann cell provides myelin for only one axon as the entire Schwann cell surrounds the axon. Radial glia serve as scaffolds for developing neurons as they migrate to their end destinations. Ependymal cells line fluid-filled ventricles of the brain and the central canal of the spinal cord. They are involved in the production of cerebrospinal fluid, which serves as a cushion for the brain, moves the fluid between the spinal cord and the brain, and is a component for the choroid plexus.



(a) Astrocyte (b) Oligodendrocyte

Figure **41.5.7**: (a) Astrocytes and (b) oligodendrocytes are glial cells of the central nervous system. (credit a: modification of work by Uniformed Services University; credit b: modification of work by Jurjen Broeke; scale-bar data from Matt Russell)

Summary

The nervous system is made up of neurons and glia. Neurons are specialized cells that are capable of sending electrical as well as chemical signals. Most neurons contain dendrites, which receive these signals, and axons that send signals to other neurons or tissues. There are four main types of neurons: unipolar, bipolar, multipolar, and pseudounipolar neurons. Glia are non-neuronal cells in the nervous system that support neuronal development and signaling. There are several types of glia that serve different functions.

Art Connections

Figure **41.5.2**: Which of the following statements is false?

A. The soma is the cell body of a nerve cell.
B. Myelin sheath provides an insulating layer to the dendrites.
C. Axons carry the signal from the soma to the target.
D. Dendrites carry the signal to the soma.

Answer

B

Glossary

astrocyte
glial cell in the central nervous system that provide nutrients, extracellular buffering, and structural support for neurons; also makes up the blood-brain barrier

axon
tube-like structure that propagates a signal from a neuron’s cell body to axon terminals

axon hillock
electrically sensitive structure on the cell body of a neuron that integrates signals from multiple neuronal connections

axon terminal
structure on the end of an axon that can form a synapse with another neuron

dendrite
structure that extends away from the cell body to receive messages from other neurons

ependymal
cell that lines fluid-filled ventricles of the brain and the central canal of the spinal cord; involved in production of cerebrospinal fluid

glia
(also, glial cells) cells that provide support functions for neurons

microglia
glia that scavenge and degrade dead cells and protect the brain from invading microorganisms

myelin
fatty substance produced by glia that insulates axons

neuron
specialized cell that can receive and transmit electrical and chemical signals

nodes of Ranvier
gaps in the myelin sheath where the signal is recharged

oligodendrocyte
glial cell that myelinates central nervous system neuron axons

radial glia
glia that serve as scaffolds for developing neurons as they migrate to their final destinations

satellite glia
glial cell that provides nutrients and structural support for neurons in the peripheral nervous system

Schwann cell
glial cell that creates myelin sheath around a peripheral nervous system neuron axon

synapse
junction between two neurons where neuronal signals are communicated

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CHAPTER OVERVIEW

41.6: Overview of Vertebrate Organ Systems

Vertebrates are among the most recognizable organisms of the animal kingdom. More than 62,000 vertebrate species have been identified. The vertebrate species now living represent only a small portion of the vertebrates that have existed. The best-known extinct vertebrates are the dinosaurs, a unique group of reptiles, which reached sizes not seen before or after in terrestrial animals. They were the dominant terrestrial animals for 150 million years, until they died out in a mass extinction near the end of the Cretaceous period. Although it is not known with certainty what caused their extinction, a great deal is known about the anatomy of the dinosaurs, given the preservation of skeletal elements in the fossil record.

41.6.1: Prelude to Vertebrates

41.6.2: Chordates

41.6.3: Fishes

41.6.4: Amphibians

41.6.5: Reptiles

41.6.6: Birds

41.6.7: Mammals

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41.6.1: Prelude to Vertebrates



(a) (b) (c)

Figure **41.6.1.1**: Examples of critically endangered vertebrate species include (a) the Siberian tiger (*Panthera tigris*), (b) the mountain gorilla (*Gorilla beringei*), and (c) the Philippine eagle (*Pithecophega jefferyi*). (credit a: modification of work by Dave Pape; credit b: modification of work by Dave Proffer; credit c: modification of work by "cuatrok77"/Flickr)

Vertebrates are among the most recognizable organisms of the animal kingdom. More than 62,000 vertebrate species have been identified. The vertebrate species now living represent only a small portion of the vertebrates that have existed. The best-known extinct vertebrates are the dinosaurs, a unique group of reptiles, which reached sizes not seen before or after in terrestrial animals. They were the dominant terrestrial animals for 150 million years, until they died out in a mass extinction near the end of the Cretaceous period. Although it is not known with certainty what caused their extinction, a great deal is known about the anatomy of the dinosaurs, given the preservation of skeletal elements in the fossil record.

Currently, a number of vertebrate species face extinction primarily due to habitat loss and pollution. According to the International Union for the Conservation of Nature, more than 6,000 vertebrate species are classified as threatened. Amphibians and mammals are the classes with the greatest percentage of threatened species, with 29 percent of all amphibians and 21 percent of all mammals classified as threatened. Attempts are being made around the world to prevent the extinction of threatened species. For example, the Biodiversity Action Plan is an international program, ratified by 188 countries, which is designed to protect species and habitats.

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41.6.2: Chordates

Skills to Develop

- Describe the distinguishing characteristics of chordates
- Identify the derived character of craniates that sets them apart from other chordates
- Describe the developmental fate of the notochord in vertebrates

Vertebrates are members of the kingdom Animalia and the phylum Chordata (Figure **41.6.2.1**). Recall that animals that possess bilateral symmetry can be divided into two groups—protostomes and deuterostomes—based on their patterns of embryonic development. The deuterostomes, whose name translates as "second mouth," consist of two phyla: Chordata and Echinodermata. Echinoderms are invertebrate marine animals that have pentaradial symmetry and a spiny body covering, a group that includes sea stars, sea urchins, and sea cucumbers. The most conspicuous and familiar members of Chordata are vertebrates, but this phylum also includes two groups of invertebrate chordates.

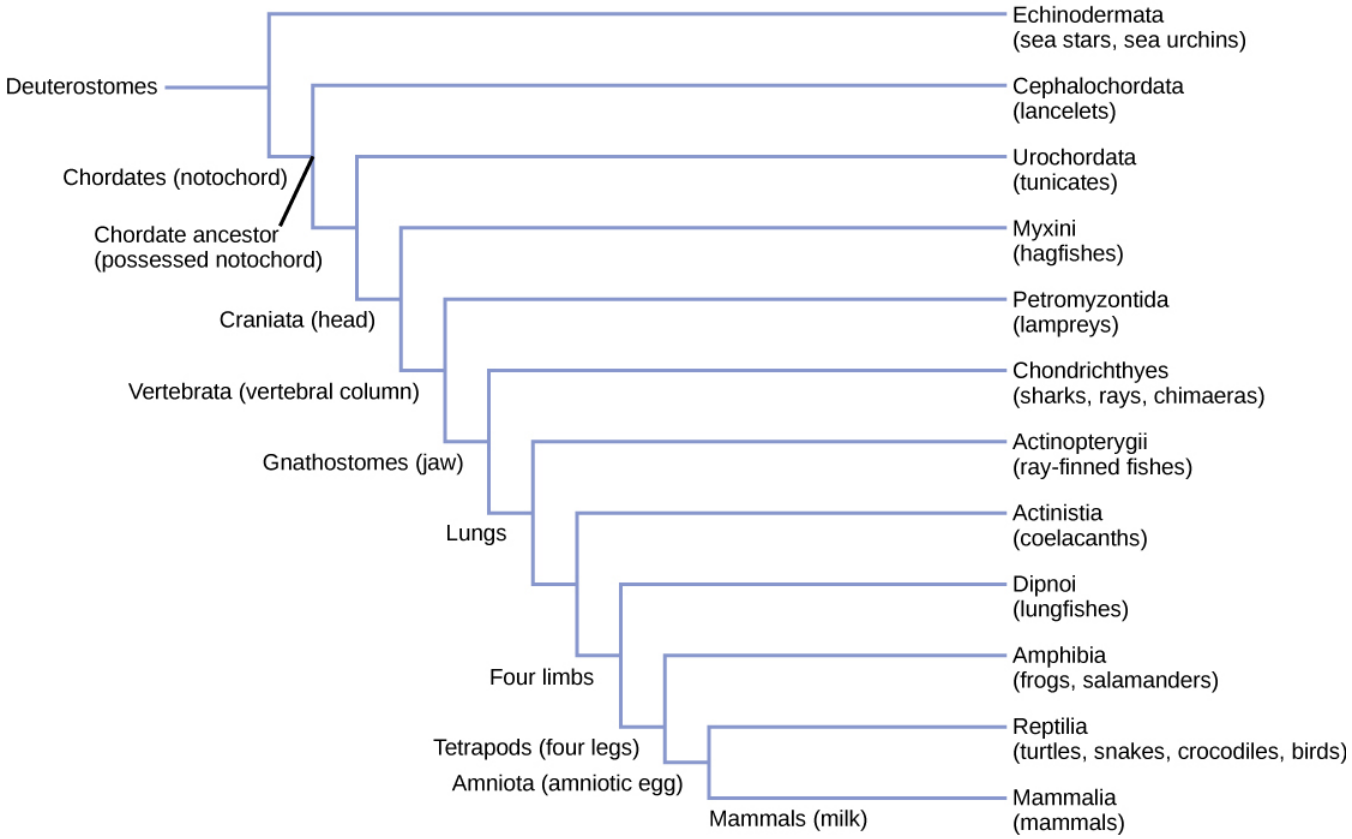


Figure **41.6.2.1**: All chordates are deuterostomes possessing a notochord.

Characteristics of Chordata

Animals in the phylum Chordata share four key features that appear at some stage during their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail (Figure **41.6.2.2**). In some groups, some of these are present only during embryonic development.

The chordates are named for the notochord, which is a flexible, rod-shaped structure that is found in the embryonic stage of all chordates and in the adult stage of some chordate species. It is located between the digestive tube and the nerve cord, and provides skeletal support through the length of the body. In some chordates, the notochord acts as the primary axial support of the body throughout the animal's lifetime. In vertebrates, the notochord is present during embryonic development, at which time it induces

the development of the neural tube and serves as a support for the developing embryonic body. The notochord, however, is not found in the postnatal stage of vertebrates; at this point, it has been replaced by the vertebral column (that is, the spine).

Art Connection

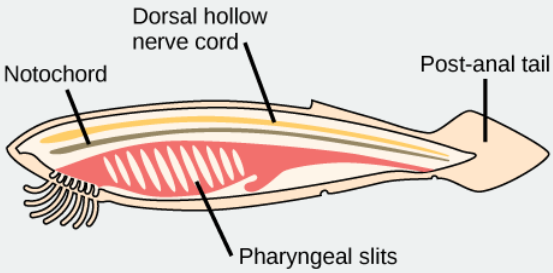


Figure 41.6.2.2: In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

Which of the following statements about common features of chordates is true?

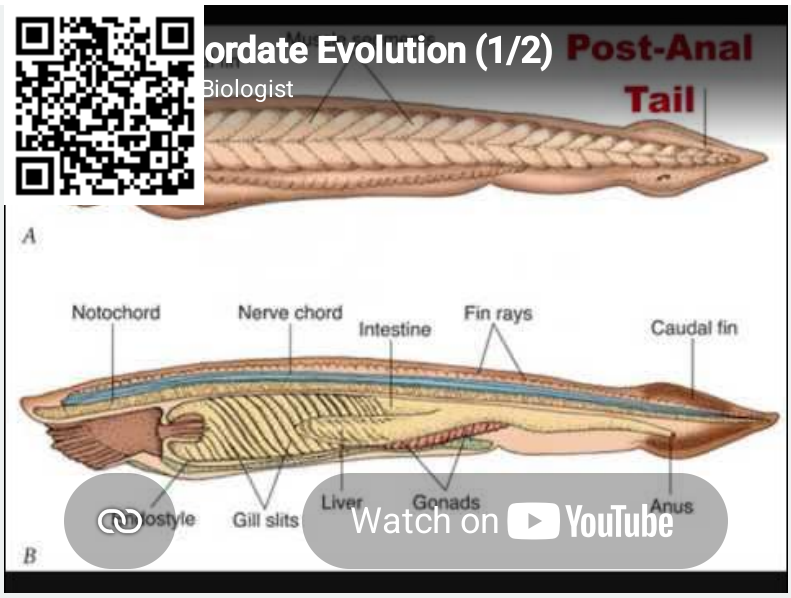
A. The dorsal hollow nerve cord is part of the chordate central nervous system.
B. In vertebrate fishes, the pharyngeal slits become the gills.
C. Humans are not chordates because humans do not have a tail.
D. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

The dorsal hollow nerve cord derives from ectoderm that rolls into a hollow tube during development. In chordates, it is located dorsal to the notochord. In contrast, other animal phyla are characterized by solid nerve cords that are located either ventrally or laterally. The nerve cord found in most chordate embryos develops into the brain and spinal cord, which compose the central nervous system.

Pharyngeal slits are openings in the pharynx (the region just posterior to the mouth) that extend to the outside environment. In organisms that live in aquatic environments, pharyngeal slits allow for the exit of water that enters the mouth during feeding. Some invertebrate chordates use the pharyngeal slits to filter food out of the water that enters the mouth. In vertebrate fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, into jaw supports. In tetrapods, the slits are modified into components of the ear and tonsils. Tetrapod literally means “four-footed,” which refers to the phylogenetic history of various groups that evolved accordingly, even though some now possess fewer than two pairs of walking appendages. Tetrapods include amphibians, reptiles, birds, and mammals.

The post-anal tail is a posterior elongation of the body, extending beyond the anus. The tail contains skeletal elements and muscles, which provide a source of locomotion in aquatic species, such as fishes. In some terrestrial vertebrates, the tail also helps with balance, courting, and signaling when danger is near. In humans, the post-anal tail is vestigial, that is, reduced in size and nonfunctional.

Link to Learning



Click for a video discussing the evolution of chordates and five characteristics that they share.

Chordates and the Evolution of Vertebrates

Chordata also contains two clades of invertebrates: Urochordata and Cephalochordata. Members of these groups also possess the four distinctive features of chordates at some point during their development.

Urochordata

Members of Urochordata are also known as tunicates (Figure **41.6.2.3**). The name tunicate derives from the cellulose-like carbohydrate material, called the tunic, which covers the outer body of tunicates. Although adult tunicates are classified as chordates, they do not have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits. The larval form, however, possesses all four structures. Most tunicates are hermaphrodites. Tunicate larvae hatch from eggs inside the adult tunicate's body. After hatching, a tunicate larva swims for a few days until it finds a suitable surface on which it can attach, usually in a dark or shaded location. It then attaches via the head to the surface and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear.

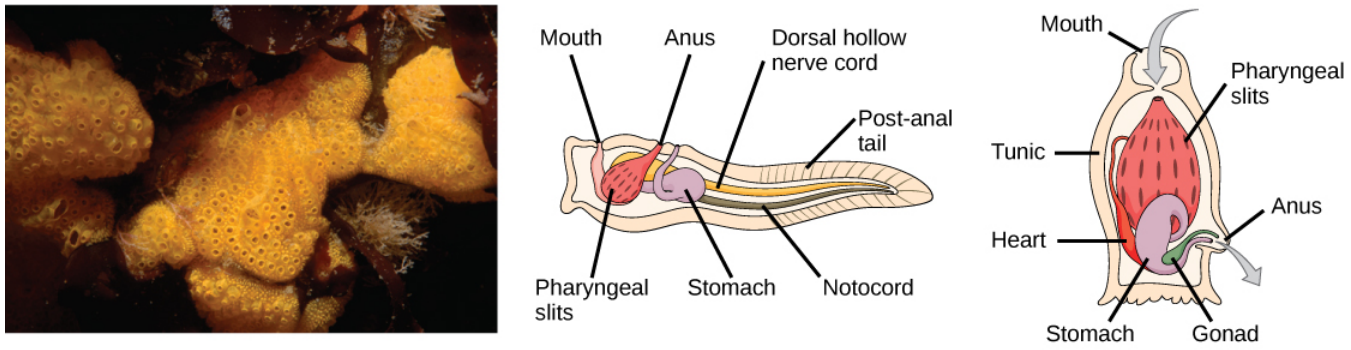


Figure **41.6.2.3**: (a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. (c) In the adult stage, the notochord, nerve cord, and tail disappear. (credit: modification of work by Dann Blackwood, USGS)

Most tunicates live a sessile existence on the ocean floor and are suspension feeders. The primary foods of tunicates are plankton and detritus. Seawater enters the tunicate's body through its incurrent siphon. Suspended material is filtered out of this water by a mucous net (pharyngeal slits) and is passed into the intestine via the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water. Tunicates are found in shallow ocean waters around the world.

Cephalochordata

Members of Cephalochordata possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage (Figure **41.6.2.4**). The notochord extends into the head, which gives the subphylum its name. Extinct members of this subphylum include *Pikaia*, which is the oldest known cephalochordate. *Pikaia* fossils were recovered from the Burgess shales of Canada and dated to the middle of the Cambrian age, making them more than 500 million years old.

Extant members of Cephalochordata are the lancelets, named for their blade-like shape. Lancelets are only a few centimeters long and are usually found buried in sand at the bottom of warm temperate and tropical seas. Like tunicates, they are suspension feeders.

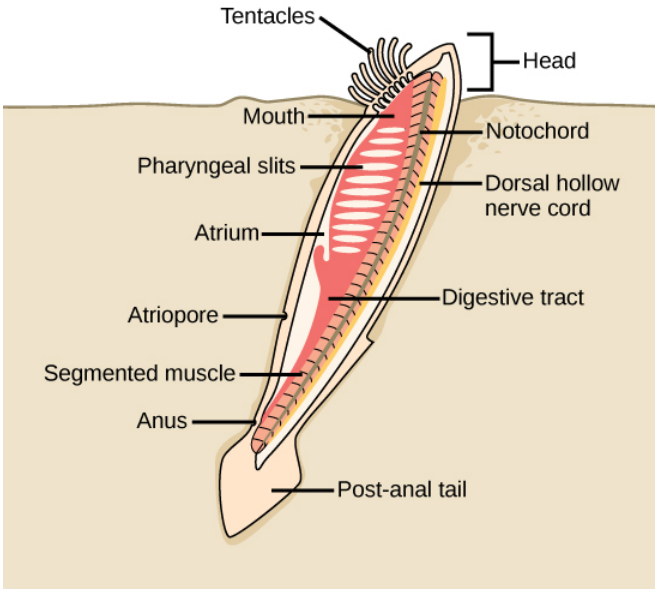


Figure **41.6.2.4**: The lancelet, like all cephalochordates, has a head. Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Water from the mouth enters the pharyngeal slits, which filter out food particles. The filtered water then collects in the atrium and exits through the atriopore.

Craniata and Vertebrata

A cranium is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones (Figure **41.6.2.5**). Most bilaterally symmetrical animals have a head; of these, those that have a cranium compose the clade Craniata. Craniata includes the hagfishes (Myxini), which have a cranium but lack a backbone, and all of the organisms called “vertebrates.”

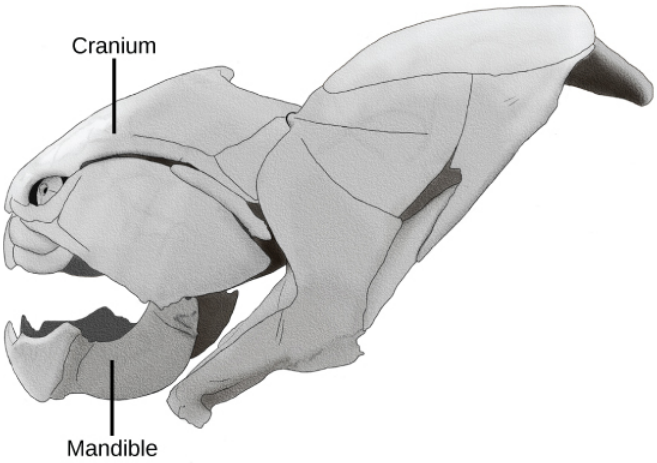


Figure **41.6.2.5**: Craniata, including this fish (*Dunkleosteus* sp.), are characterized by the presence of a cranium, mandible, and other facial bones. (credit: “Steveoc 86”/Wikimedia Commons)

Vertebrates are members of the clade Vertebrata. Vertebrates display the four characteristic features of the chordates; however, members of this group also share derived characteristics that distinguish them from invertebrate chordates. Vertebrata is named for

the vertebral column, composed of vertebrae, a series of separate bones joined together as a backbone (Figure **41.6.2.6**). In adult vertebrates, the vertebral column replaces the notochord, which is only seen in the embryonic stage.

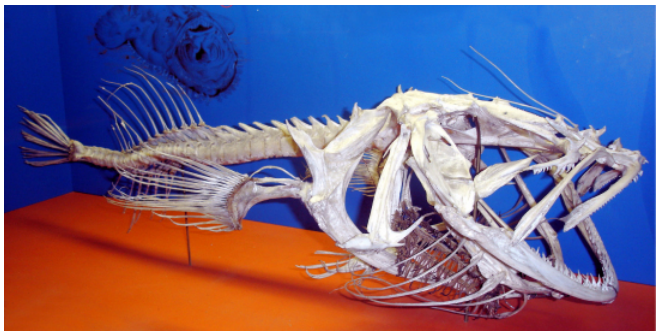


Figure **41.6.2.6**: Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium. (credit: Ernest V. More; taken at Smithsonian Museum of Natural History, Washington, D.C.)

Based on molecular analysis, vertebrates appear to be more closely related to lancelets (cephalochordates) than to tunicates (urochordates) among the invertebrate chordates. This evidence suggests that the cephalochordates diverged from Urochordata and the vertebrates subsequently diverged from the cephalochordates. This hypothesis is further supported by the discovery of a fossil in China from the genus *Haikouella*. This organism seems to be an intermediate form between cephalochordates and vertebrates. The *Haikouella* fossils are about 530 million years old and appear similar to modern lancelets. These organisms had a brain and eyes, as do vertebrates, but lack the skull found in craniates.[1] This evidence suggests that vertebrates arose during the Cambrian explosion. Recall that the "Cambrian explosion" is the name given to a relatively brief span of time during the Cambrian period during which many animal groups appeared and rapidly diversified. Most modern animal phyla originated during the Cambrian explosion.

Vertebrates are the largest group of chordates, with more than 62,000 living species. Vertebrates are grouped based on anatomical and physiological traits. More than one classification and naming scheme is used for these animals. Here we will consider the traditional groups Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia, which constitute classes in the subphylum Vertebrata. Many modern authors classify birds within Reptilia, which correctly reflects their evolutionary heritage. We consider them separately only for convenience. Further, we will consider hagfishes and lampreys together as jawless fishes, the agnathans, although emerging classification schemes separate them into chordate jawless fishes (the hagfishes) and vertebrate jawless fishes (the lampreys).

Animals that possess jaws are known as gnathostomes, which means "jawed mouth." Gnathostomes include fishes and tetrapods—amphibians, reptiles, birds, and mammals. Tetrapods can be further divided into two groups: amphibians and amniotes. Amniotes are animals whose eggs are adapted for terrestrial living, and this group includes mammals, reptiles, and birds. Amniotic embryos, developing in either an externally shed egg or an egg carried by the female, are provided with a water-retaining environment and are protected by amniotic membranes.

Summary

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms. Vertebrata is named for the vertebral column, which is a feature of almost all members of this clade.

Art Connections

Figure **41.6.2.2**: Which of the following statements about common features of chordates is true?

A. The dorsal hollow nerve cord is part of the chordate central nervous system.
B. In vertebrate fishes, the pharyngeal slits become the gills.
C. Humans are not chordates because humans do not have a tail.

D. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

Answer

A

Footnotes

1. 1 Chen, J. Y., Huang, D. Y., and Li, C. W., “An early Cambrian craniate-like chordate,” *Nature* 402 (1999): 518–522, doi:10.1038/990080.

Glossary

Cephalochordata
chordate clade whose members possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage

Chordata
phylum of animals distinguished by their possession of a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail at some point during their development

Craniata
clade composed of chordates that possess a cranium; includes Vertebrata together with hagfishes

cranium
bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones

dorsal hollow nerve cord
hollow, tubular structure derived from ectoderm, which is located dorsal to the notochord in chordates

lancelet
member of Cephalochordata; named for its blade-like shape

notochord
flexible, rod-shaped support structure that is found in the embryonic stage of all chordates and in the adult stage of some chordates

pharyngeal slit
opening in the pharynx

post-anal tail
muscular, posterior elongation of the body extending beyond the anus in chordates

tetrapod
phylogenetic reference to an organism with a four-footed evolutionary history; includes amphibians, reptiles, birds, and mammals

tunicate
sessile chordate that is a member of Urochordata

Urochordata
clade composed of tunicates

vertebral column
series of separate bones joined together as a backbone

Vertebrata

members of the phylum Chordata that possess a backbone

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41.6.3: Fishes

Skills to Develop

- Describe the difference between jawless and jawed fishes
- Discuss the distinguishing features of sharks and rays compared to other modern fishes

Modern fishes include an estimated 31,000 species. Fishes were the earliest vertebrates, with jawless species being the earliest and jawed species evolving later. They are active feeders, rather than sessile, suspension feeders. Jawless fishes—the hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, distinguishing them from the invertebrate chordates.

Jawless Fishes

Jawless fishes are craniates that represent an ancient vertebrate lineage that arose over one half-billion years ago. In the past, the hagfishes and lampreys were classified together as agnathans. Today, hagfishes and lampreys are recognized as separate clades, primarily because lampreys are true vertebrates, whereas hagfishes are not. A defining feature is the lack of paired lateral appendages (fins). Some of the earliest jawless fishes were the ostracoderms (which translates to “shell-skin”). Ostracoderms were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

Myxini: Hagfishes

The clade Myxini includes at least 20 species of hagfishes. Hagfishes are eel-like scavengers that live on the ocean floor and feed on dead invertebrates, other fishes, and marine mammals (Figure **41.6.3.1**). Hagfishes are entirely marine and are found in oceans around the world, except for the polar regions. A unique feature of these animals is the slime glands beneath the skin that release mucus through surface pores. This mucus allows the hagfish to escape from the grip of predators. Hagfish can also twist their bodies in a knot to feed and sometimes eat carcasses from the inside out.

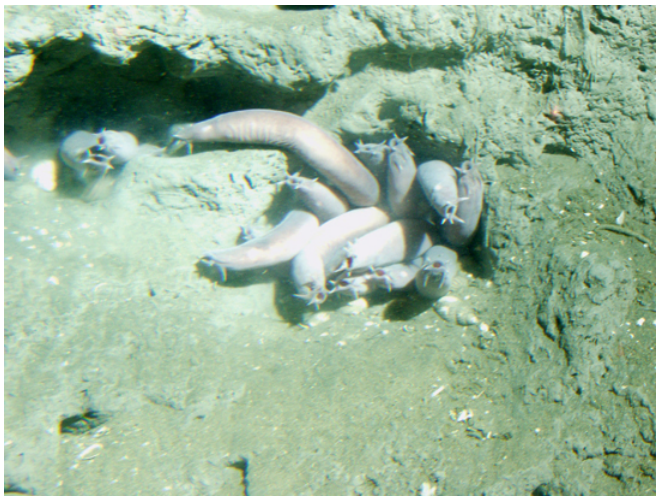


Figure **41.6.3.1**: Pacific hagfish are scavengers that live on the ocean floor. (credit: Linda Snook, NOAA/CBNMS)

The skeleton of a hagfish is composed of cartilage, which includes a cartilaginous notochord that runs the length of the body. This notochord provides support to the hagfish’s body. Hagfishes do not replace the notochord with a vertebral column during development, as do true vertebrates.

Petromyzontidae: Lampreys

The clade Petromyzontidae includes approximately 35–40 or more species of lampreys. Lampreys are similar to hagfishes in size and shape; however, lampreys possess some vertebral elements. Lampreys lack paired appendages and bone, as do the hagfishes. As adults, lampreys are characterized by a toothed, funnel-like sucking mouth. Many species have a parasitic stage of their life cycle during which they are ectoparasites of fishes (Figure **41.6.3.2**).



Figure **41.6.3.2**: These parasitic sea lampreys attach to their lake trout host by suction and use their rough tongues to rasp away flesh in order to feed on the trout's blood. (credit: USGS)

Lampreys live primarily in coastal and fresh waters, and have a worldwide distribution, except for in the tropics and polar regions. Some species are marine, but all species spawn in fresh water. Eggs are fertilized externally, and the larvae distinctly differ from the adult form, spending 3 to 15 years as suspension feeders. Once they attain sexual maturity, the adults reproduce and die within days.

Lampreys possess a notochord as adults; however, this notochord is surrounded by a cartilaginous structure called an arcualia, which may resemble an evolutionarily early form of the vertebral column.

Gnathostomes: Jawed Fishes

Gnathostomes or "jaw-mouths" are vertebrates that possess jaws. One of the most significant developments in early vertebrate evolution was the development of the jaw, which is a hinged structure attached to the cranium that allows an animal to grasp and tear its food. The evolution of jaws allowed early gnathostomes to exploit food resources that were unavailable to jawless fishes.

Early gnathostomes also possessed two sets of paired fins, allowing the fishes to maneuver accurately. Pectoral fins are typically located on the anterior body, and pelvic fins on the posterior. Evolution of the jaw and paired fins permitted gnathostomes to expand from the sedentary suspension feeding of jawless fishes to become mobile predators. The ability of gnathostomes to exploit new nutrient sources likely is one reason that they replaced most jawless fishes during the Devonian period. Two early groups of gnathostomes were the acanthodians and placoderms (Figure **41.6.3.3**), which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes.



Figure **41.6.3.3**: *Dunkleosteous* was an enormous placoderm from the Devonian period, 380–360 million years ago. It measured up to 10 meters in length and weighed up to 3.6 tons. (credit: Nobu Tamura)

Chondrichthyes: Cartilaginous Fishes

The clade Chondrichthyes is diverse, consisting of sharks (Figure **41.6.3.4**), rays, and skates, together with sawfishes and a few dozen species of fishes called *chimaeras*, or "ghost" sharks." Chondrichthyes are jawed fishes that possess paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the early or middle Devonian. They are thought to be descended from the placoderms, which had skeletons made of bone; thus, the cartilaginous skeleton of Chondrichthyes is a later development. Parts of shark skeleton are strengthened by granules of calcium carbonate, but this is not the same as bone.

Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for a part or all of their lives. Most sharks are carnivores that feed on live prey, either swallowing it whole or using their jaws and teeth to tear it into smaller pieces. Shark teeth likely evolved from the jagged scales that cover their skin, called placoid scales. Some species of sharks and rays are suspension feeders that feed on plankton.

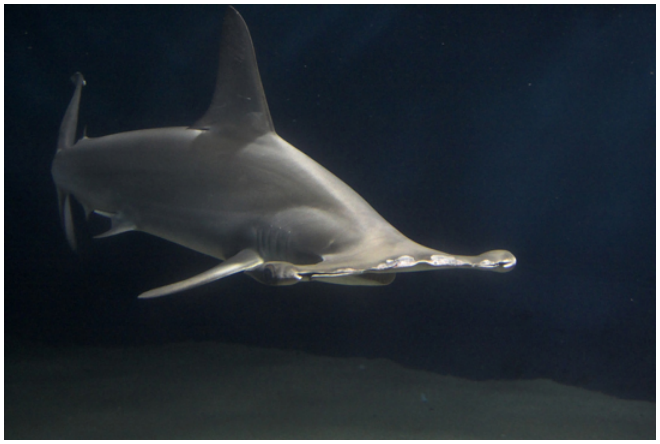


Figure **41.6.3.4**: Hammerhead sharks tend to school during the day and hunt prey at night. (credit: Masashi Sugawara)

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and electroreception, with the latter perhaps the most sensitive of any animal. Organs called ampullae of Lorenzini allow sharks to detect the electromagnetic fields that are produced by all living things, including their prey. Electroreception has only been observed in aquatic or amphibious animals. Sharks, together with most fishes and aquatic and larval amphibians, also have a sense organ called the lateral line, which is used to detect movement and vibration in the surrounding water, and is often considered homologous to "hearing" in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of a fish's body.

Sharks reproduce sexually, and eggs are fertilized internally. Most species are ovoviviparous: The fertilized egg is retained in the oviduct of the mother's body and the embryo is nourished by the egg yolk. The eggs hatch in the uterus, and young are born alive and fully functional. Some species of sharks are oviparous: They lay eggs that hatch outside of the mother's body. Embryos are protected by a shark egg case or "mermaid's purse" (Figure **41.6.3.5**) that has the consistency of leather. The shark egg case has tentacles that snag in seaweed and give the newborn shark cover. A few species of sharks are viviparous: The young develop within the mother's body and she gives live birth.

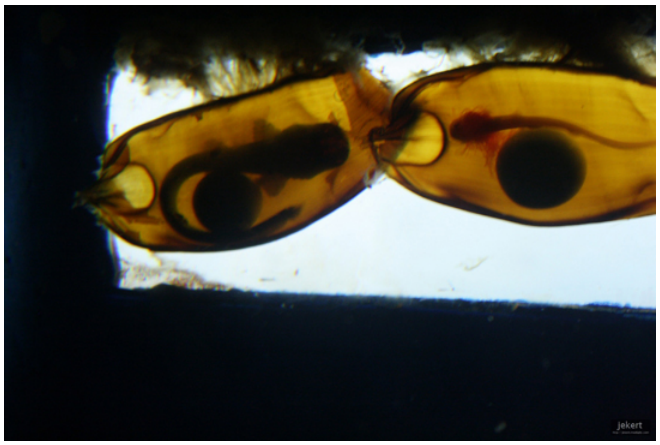


Figure **41.6.3.5**: Shark embryos are clearly visible through these transparent egg cases. The round structure is the yolk that nourishes the growing embryo. (credit: Jek Bacarisas)

Rays and skates comprise more than 500 species and are closely related to sharks. They can be distinguished from sharks by their flattened bodies, pectoral fins that are enlarged and fused to the head, and gill slits on their ventral surface (Figure **41.6.3.6**). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.



Figure **41.6.3.6**: This stingray blends into the sandy bottom of the ocean floor. (credit: "Sailn1"/Flickr)

Osteichthyes: Bony Fishes

Members of the clade Osteichthyes, also called bony fishes, are characterized by a bony skeleton. The vast majority of present-day fishes belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fishes have an ossified skeleton with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. This characteristic has only reversed in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered by overlapping scales, and glands in the skin secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fishes have a lateral line system that detects vibrations in water.

All bony fishes use gills to breathe. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Many bony fishes also have a swim bladder, a gas-filled organ that helps to control the buoyancy of the fish. Bony fishes are further divided into two extant clades: Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes).

Actinopterygii, the ray-finned fishes, include many familiar fishes—tuna, bass, trout, and salmon (Figure 41.6.3.7), among others. Ray-finned fishes are named for their fins that are webs of skin supported by bony spines called rays. In contrast, the fins of Sarcopterygii are fleshy and lobed, supported by bone (Figure 41.6.3.7). Living members of this clade include the less-familiar lungfishes and coelacanths.

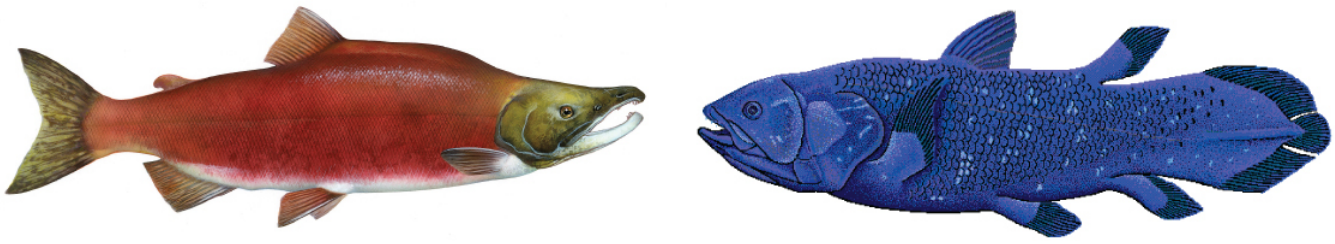


Figure 41.6.3.7: The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish, was thought to have gone extinct in the Late Cretaceous period, 100 million years ago, until one was discovered in 1938 near the Comoros Islands between Africa and Madagascar. (credit a: modification of work by Timothy Knepp, USFWS; credit b: modification of work by Robbie Cada)

Summary

The earliest vertebrates that diverged from the invertebrate chordates were the jawless fishes. Fishes with jaws (gnathostomes) evolved later. Jaws allowed early gnathostomes to exploit new food sources. Agnathans include the hagfishes and lampreys. Hagfishes are eel-like scavengers that feed on dead invertebrates and other fishes. Lampreys are characterized by a toothed, funnel-like sucking mouth, and most species are parasitic on other fishes. Gnathostomes include the cartilaginous fishes and the bony fishes, as well as all other tetrapods. Cartilaginous fishes include sharks, rays, skates, and ghost sharks. Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for part or all of their lives. The vast majority of present-day fishes belong to the clade Osteichthyes, which consists of approximately 30,000 species. Bony fishes can be divided into two clades: Actinopterygii (ray-finned fishes, virtually all extant species) and Sarcopterygii (lobe-finned fishes, comprising fewer than 10 extant species but which are the ancestors of tetrapods).

Glossary

Actinopterygii
ray-finned fishes

ampulla of Lorenzini
sensory organ that allows sharks to detect electromagnetic fields produced by living things

Chondrichthyes
jawed fish with paired fins and a skeleton made of cartilage

gnathostome
jawed fish

hagfish
eel-like jawless fish that live on the ocean floor and are scavengers

lamprey
jawless fish characterized by a toothed, funnel-like, sucking mouth

lateral line
sense organ that runs the length of a fish's body; used to detect vibration in the water

Myxini

hagfishes

Osteichthyes
bony fish

ostracoderm
one of the earliest jawless fish covered in bone

Petromyzontidae
clade of lampreys

Sarcopterygii
lobe-finned fish

swim bladder
in fishes, a gas filled organ that helps to control the buoyancy of the fish

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41.6.4: Amphibians

Skills to Develop

- Describe the important difference between the life cycle of amphibians and the life cycles of other vertebrates
- Distinguish between the characteristics of Urodela, Anura, and Apoda
- Describe the evolutionary history of amphibians

Amphibians are vertebrate tetrapods. Amphibia includes frogs, salamanders, and caecilians. The term amphibian loosely translates from the Greek as “dual life,” which is a reference to the metamorphosis that many frogs and salamanders undergo and their mixture of aquatic and terrestrial environments in their life cycle. Amphibians evolved during the Devonian period and were the earliest terrestrial tetrapods.

Link to Learning

Watch this series of Animal Planet videos on tetrapod evolution:

1: The evolution from fish to earliest tetrapod

2: Fish to Earliest Tetrapod

3: The discovery of coelacanth and *Acanthostega* fossils

4: The number of fingers on “legs”

Characteristics of Amphibians

As tetrapods, most amphibians are characterized by four well-developed limbs. Some species of salamanders and all caecilians are functionally limbless; their limbs are vestigial. An important characteristic of extant amphibians is a moist, permeable skin that is achieved via mucus glands that keep the skin moist; thus, exchange of oxygen and carbon dioxide with the environment can take place through it (cutaneous respiration). Additional characteristics of amphibians include pedicellate teeth—teeth in which the root and crown are calcified, separated by a zone of noncalcified tissue—and a papilla amphibiorum and papilla basilaris, structures of the inner ear that are sensitive to frequencies below and above 10,00 hertz, respectively. Amphibians also have an auricular operculum, which is an extra bone in the ear that transmits sounds to the inner ear. All extant adult amphibians are carnivorous, and some terrestrial amphibians have a sticky tongue that is used to capture prey.

Evolution of Amphibians

The fossil record provides evidence of the first tetrapods: now-extinct amphibian species dating to nearly 400 million years ago. Evolution of tetrapods from fishes represented a significant change in body plan from one suited to organisms that respired and swam in water, to organisms that breathed air and moved onto land; these changes occurred over a span of 50 million years during the Devonian period. One of the earliest known tetrapods is from the genus *Acanthostega*. *Acanthostega* was aquatic; fossils show that it had gills similar to fishes. However, it also had four limbs, with the skeletal structure of limbs found in present-day tetrapods, including amphibians. Therefore, it is thought that *Acanthostega* lived in shallow waters and was an intermediate form between lobe-finned fishes and early, fully terrestrial tetrapods. What preceded *Acanthostega*?

In 2006, researchers published news of their discovery of a fossil of a “tetrapod-like fish,” *Tiktaalik roseae*, which seems to be an intermediate form between fishes having fins and tetrapods having limbs (Figure **41.6.4.1**). *Tiktaalik* likely lived in a shallow water

environment about 375 million years ago.[1]

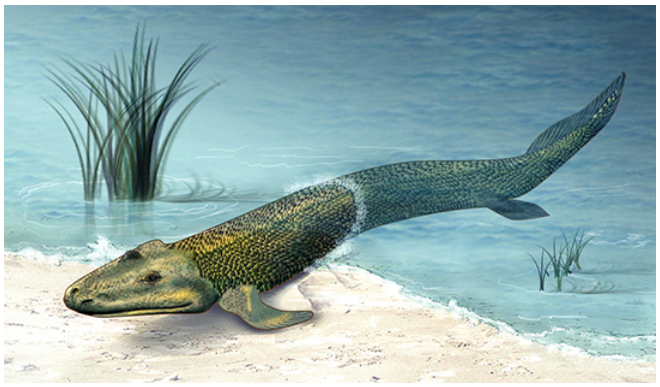


Figure 41.6.4.1: The recent fossil discovery of *Tiktaalik roseae* suggests evidence for an animal intermediate to finned fish and legged tetrapods. (credit: Zina Deretsky, National Science Foundation)

The early tetrapods that moved onto land had access to new nutrient sources and relatively few predators. This led to the widespread distribution of tetrapods during the early Carboniferous period, a period sometimes called the "age of the amphibians."

Modern Amphibians

Amphibia comprises an estimated 6,770 extant species that inhabit tropical and temperate regions around the world. Amphibians can be divided into three clades: Urodela ("tailed-ones"), the salamanders; Anura ("tail-less ones"), the frogs; and Apoda ("legless ones"), the caecilians.

Urodela: Salamanders

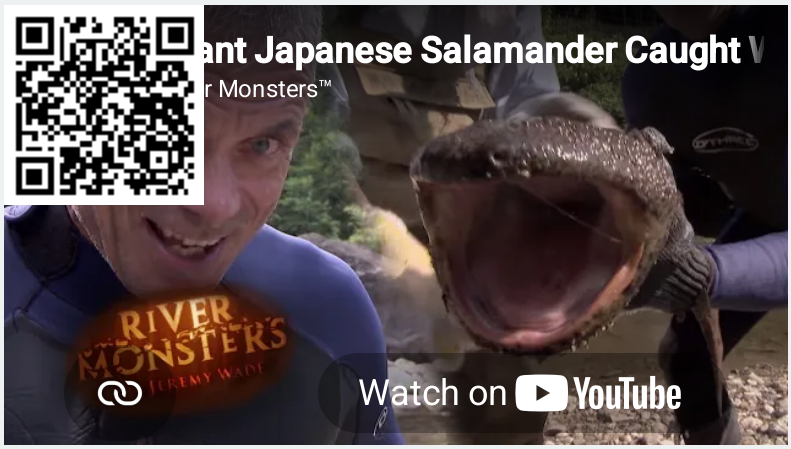
Salamanders are amphibians that belong to the order Urodela. Living salamanders (Figure 41.6.4.1) include approximately 620 species, some of which are aquatic, other terrestrial, and some that live on land only as adults. Adult salamanders usually have a generalized tetrapod body plan with four limbs and a tail. They move by bending their bodies from side to side, called lateral undulation, in a fish-like manner while "walking" their arms and legs fore and aft. It is thought that their gait is similar to that used by early tetrapods. Respiration differs among different species. The majority of salamanders are lungless, and respiration occurs through the skin or through external gills. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs.

Unlike frogs, virtually all salamanders rely on internal fertilization of the eggs. The only male amphibians that possess copulatory structures are the caecilians, so fertilization among salamanders typically involves an elaborate and often prolonged courtship. Such a courtship allows the successful transfer of sperm from male to female via a spermatophore. Development in many of the most highly evolved salamanders, which are fully terrestrial, occurs during a prolonged egg stage, with the eggs guarded by the mother. During this time, the gilled larval stage is found only within the egg capsule, with the gills being resorbed, and metamorphosis being completed, before hatching. Hatchlings thus resemble tiny adults.



Figure 41.6.4.2: Most salamanders have legs and a tail, but respiration varies among species. (credit: Valentina Storti)

Link to Learning



View River Monsters: Fish With Arms and Hands? to see a video about an unusually large salamander species.

Anura: Frogs

Frogs are amphibians that belong to the order Anura (Figure **41.6.4.3**). Anurans are among the most diverse groups of vertebrates, with approximately 5,965 species that occur on all of the continents except Antarctica. Anurans have a body plan that is more specialized for movement. Adult frogs use their hind limbs to jump on land. Frogs have a number of modifications that allow them to avoid predators, including skin that acts as camouflage. Many species of frogs and salamanders also release defensive chemicals from glands in the skin that are poisonous to predators.



Figure **41.6.4.3**: The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source.

Frog eggs are fertilized externally, and like other amphibians, frogs generally lay their eggs in moist environments. A moist environment is required as eggs lack a shell and thus dehydrate quickly in dry environments. Frogs demonstrate a great diversity of parental behaviors, with some species laying many eggs and exhibiting little parental care, to species that carry eggs and tadpoles on their hind legs or backs. The life cycle of frogs, as other amphibians, consists of two distinct stages: the larval stage followed by metamorphosis to an adult stage. The larval stage of a frog, the tadpole, is often a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, and lack limbs. At the end of the tadpole stage, frogs undergo metamorphosis into the adult form (Figure **41.6.4.4**). During this stage, the gills, tail, and lateral line system disappear, and four limbs develop. The jaws become larger and are suited for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop. These changes during metamorphosis allow the larvae to move onto land in the adult stage.



Figure **41.6.4.4**: A juvenile frog metamorphoses into a frog. Here, the frog has started to develop limbs, but its tadpole tail is still evident.

Apoda: Caecilians

An estimated 185 species comprise caecilians, a group of amphibians that belong to the order Apoda. Although they are vertebrates, a complete lack of limbs leads to their resemblance to earthworms in appearance. They are adapted for a soil-burrowing or aquatic lifestyle, and they are nearly blind. These animals are found in the tropics of South America, Africa, and Southern Asia. They have vestigial limbs, evidence that they evolved from a legged ancestor.

Evolution Connection: The Paleozoic Era and the Evolution of Vertebrates

The climate and geography of Earth was vastly different during the Paleozoic Era, when vertebrates arose, as compared to today. The Paleozoic spanned from approximately 542 to 251 million years ago. The landmasses on Earth were very different from those of today. Laurentia and Gondwana were continents located near the equator that subsumed much of the current day landmasses in a different configuration (Figure **41.6.4.5**). At this time, sea levels were very high, probably at a level that hasn't been reached since. As the Paleozoic progressed, glaciations created a cool global climate, but conditions warmed near the end of the first half of the Paleozoic. During the latter half of the Paleozoic, the landmasses began moving together, with the initial formation of a large northern block called Laurasia. This contained parts of what is now North America, along with Greenland, parts of Europe, and Siberia. Eventually, a single supercontinent, called Pangaea, was formed, starting in the latter third of the Paleozoic. Glaciations then began to affect Pangaea's climate, affecting the distribution of vertebrate life.

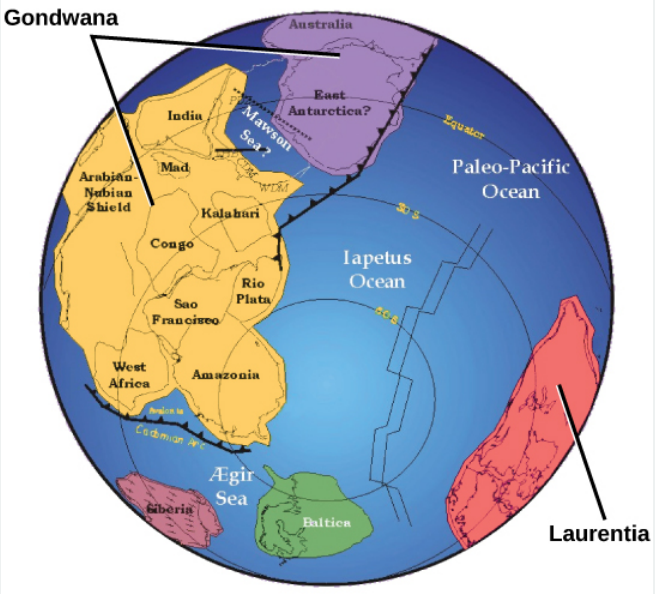


Figure **41.6.4.5**: During the Paleozoic Era, around 550 million years ago, the continent Gondwana formed. Both Gondwana and the continent Laurentia were located near the equator.

During the early Paleozoic, the amount of carbon dioxide in the atmosphere was much greater than it is today. This may have begun to change later, as land plants became more common. As the roots of land plants began to infiltrate rock and soil began to form, carbon dioxide was drawn out of the atmosphere and became trapped in the rock. This reduced the levels of carbon dioxide and increased the levels of oxygen in the atmosphere, so that by the end of the Paleozoic, atmospheric conditions were similar to those of today.

As plants became more common through the latter half of the Paleozoic, microclimates began to emerge and ecosystems began to change. As plants and ecosystems continued to grow and become more complex, vertebrates moved from the water to land. The presence of shoreline vegetation may have contributed to the movement of vertebrates onto land. One hypothesis suggests that the fins of aquatic vertebrates were used to maneuver through this vegetation, providing a precursor to the movement of fins on land and the development of limbs. The late Paleozoic was a time of diversification of vertebrates, as amniotes emerged and became two different lines that gave rise, on one hand, to mammals, and, on the other hand, to reptiles and birds. Many marine vertebrates became extinct near the end of the Devonian period, which ended about 360 million years ago, and both marine and terrestrial vertebrates were decimated by a mass extinction in the early Permian period about 250 million years ago.

Link to Learning



View Earth's Paleogeography: Continental Movements Through Time to see changes in Earth as life evolved.

Summary

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians are limbless. The most important characteristic of extant amphibians is a moist, permeable skin used for cutaneous respiration. The fossil record provides evidence of amphibian species, now extinct, that arose over 400 million years ago as the first tetrapods. Amphibia can be divided into three clades: salamanders (Urodela), frogs (Anura), and caecilians (Apoda). The life cycle of frogs, like the majority of amphibians, consists of two distinct stages: the larval stage and metamorphosis to an adult stage. Some species in all orders bypass a free-living larval stage.

Footnotes

1. 1 Daeschler, E. B., Shubin, N. H., and Jenkins, F. J. "A Devonian tetrapod-like fish and the evolution of the tetrapod body plan," *Nature* 440 (2006): 757–763, doi:10.1038/nature04639, http://www.nature.com/nature/journal/v440/n7085/abs/nature04639.html.

Glossary

Acanthostega
: one of the earliest known tetrapods

Amphibia
: frogs, salamanders, and caecilians

Anura
: frogs

Apoda
: caecilians

caecilian
: legless amphibian that belongs to the clade Apoda

cutaneous respiration
: gas exchange through the skin

frog

tail-less amphibian that belongs to the clade Anura

salamander

tailed amphibian that belongs to the clade Urodela

tadpole

larval stage of a frog

Urodela

salamanders

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41.6.5: Reptiles

Skills to Develop

- Describe the main characteristics of amniotes
- Explain the difference between anapsids, synapsids, and diapsids, and give an example of each
- Identify the characteristics of reptiles
- Discuss the evolution of reptiles

The amniotes —reptiles, birds, and mammals—are distinguished from amphibians by their terrestrially adapted egg, which is protected by amniotic membranes. The evolution of amniotic membranes meant that the embryos of amniotes were provided with their own aquatic environment, which led to less dependence on water for development and thus allowed the amniotes to branch out into drier environments. This was a significant development that distinguished them from amphibians, which were restricted to moist environments due their shell-less eggs. Although the shells of various amniotic species vary significantly, they all allow retention of water. The shells of bird eggs are composed of calcium carbonate and are hard, but fragile. The shells of reptile eggs are leathery and require a moist environment. Most mammals do not lay eggs (except for monotremes). Instead, the embryo grows within the mother's body; however, even with this internal gestation, amniotic membranes are still present.

Characteristics of Amniotes

The amniotic egg is the key characteristic of amniotes. In amniotes that lay eggs, the shell of the egg provides protection for the developing embryo while being permeable enough to allow for the exchange of carbon dioxide and oxygen. The albumin, or egg white, provides the embryo with water and protein, whereas the fattier egg yolk is the energy supply for the embryo, as is the case with the eggs of many other animals, such as amphibians. However, the eggs of amniotes contain three additional extra-embryonic membranes: the chorion, amnion, and allantois (Figure **41.6.5.1**). Extra-embryonic membranes are membranes present in amniotic eggs that are not a part of the body of the developing embryo. While the inner amniotic membrane surrounds the embryo itself, the chorion surrounds the embryo and yolk sac. The chorion facilitates exchange of oxygen and carbon dioxide between the embryo and the egg's external environment. The amnion protects the embryo from mechanical shock and supports hydration. The allantois stores nitrogenous wastes produced by the embryo and also facilitates respiration. In mammals, membranes that are homologous to the extra-embryonic membranes in eggs are present in the placenta.

Art Connection

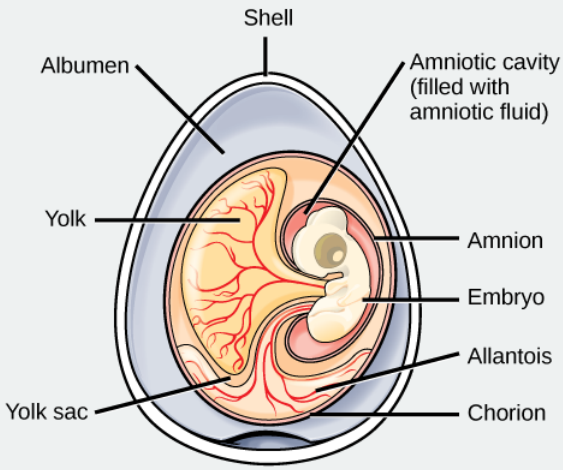


Figure **41.6.5.1**: The key features of an amniotic egg are shown.

Which of the following statements about the parts of an egg are false?

A. The allantois stores nitrogenous waste and facilitates respiration.
B. The chorion facilitates gas exchange.
C. The yolk provides food for the growing embryo.

D. The amniotic cavity is filled with albumen.

Additional derived characteristics of amniotes include waterproof skin, due to the presence of lipids, and costal (rib) ventilation of the lungs.

Evolution of Amniotes

The first amniotes evolved from amphibian ancestors approximately 340 million years ago during the Carboniferous period. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids and sauropsids. Synapsids include all mammals, including extinct mammalian species. Synapsids also include therapsids, which were mammal-like reptiles from which mammals evolved. Sauropsids include reptiles and birds, and can be further divided into anapsids and diapsids. The key differences between the synapsids, anapsids, and diapsids are the structures of the skull and the number of temporal fenestrae behind each eye (Figure **41.6.5.2**). Temporal fenestrae are post-orbital openings in the skull that allow muscles to expand and lengthen. Anapsids have no temporal fenestrae, synapsids have one, and diapsids have two. Anapsids include extinct organisms and may, based on anatomy, include turtles. However, this is still controversial, and turtles are sometimes classified as diapsids based on molecular evidence. The diapsids include birds and all other living and extinct reptiles.

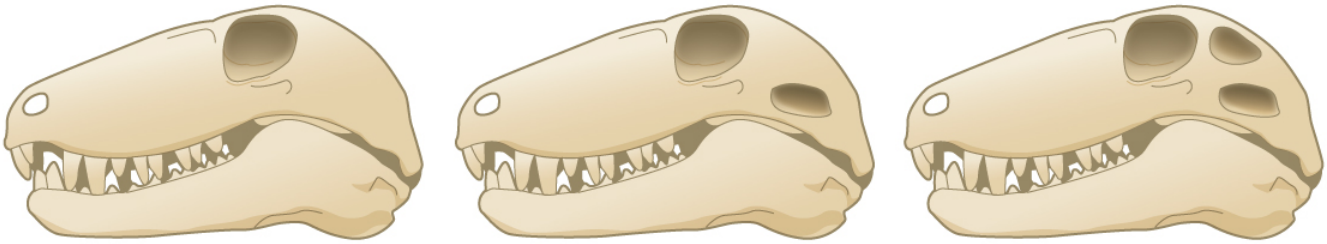


Figure **41.6.5.2**: Compare the skulls and temporal fenestrae of anapsids, synapsids, and diapsids. Anapsids have no openings, synapsids have one opening, and diapsids have two openings.

The diapsids diverged into two groups, the Archosauromorpha (“ancient lizard form”) and the Lepidosauromorpha (“scaly lizard form”) during the Mesozoic period (Figure **41.6.5.3**). The lepidosaurs include modern lizards, snakes, and tuataras. The archosaurs include modern crocodiles and alligators, and the extinct pterosaurs (“winged lizard”) and dinosaurs (“terrible lizard”). Clade Dinosauria includes birds, which evolved from a branch of dinosaurs.

Art Connection

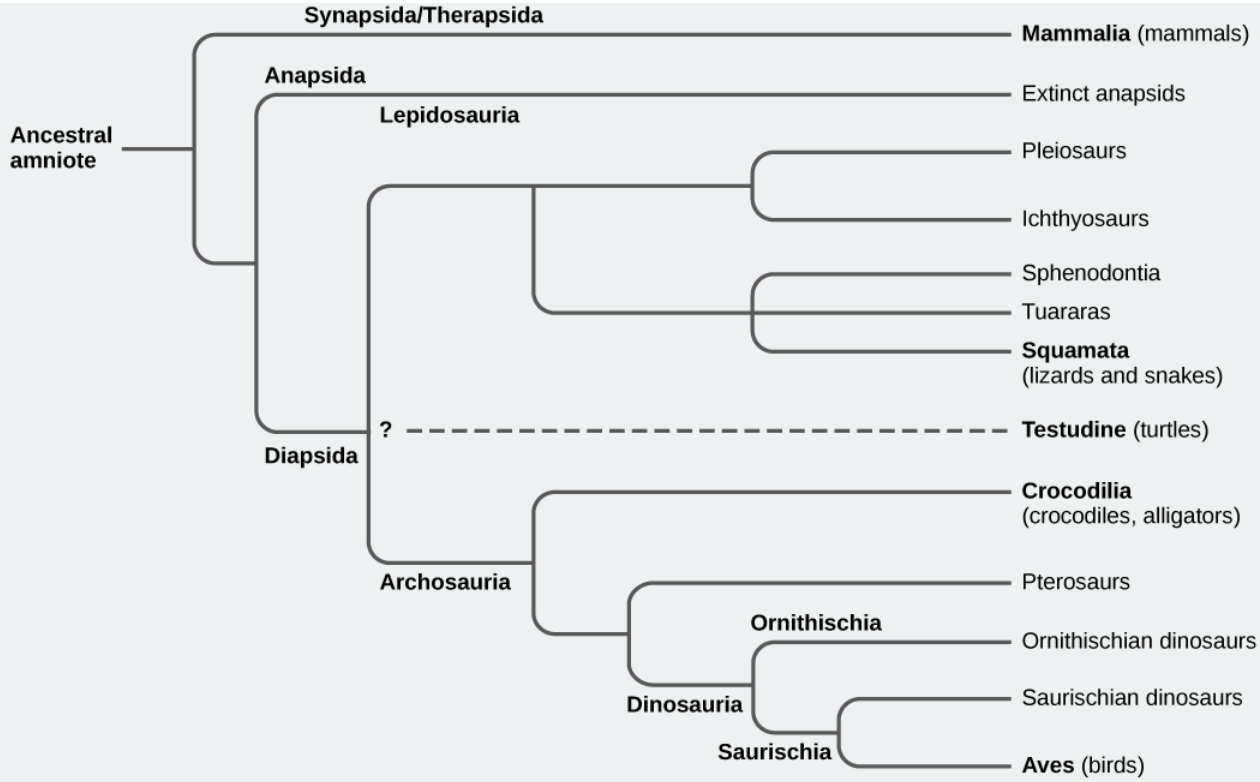


Figure **41.6.5.3**: This chart shows the evolution of amniotes. The placement of Testudines (turtles) is currently still debated.

Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

In the past, the most common division of amniotes has been into the classes Mammalia, Reptilia, and Aves. Birds are descended, however, from dinosaurs, so this classical scheme results in groups that are not true clades. We will consider birds as a group distinct from reptiles for the purpose of this discussion with the understanding that this does not completely reflect phylogenetic history and relationships.

Characteristics of Reptiles

Reptiles are tetrapods. Limbless reptiles—snakes and other squamates—have vestigial limbs and, like caecilians, are classified as tetrapods because they are descended from four-limbed ancestors. Reptiles lay eggs enclosed in shells on land. Even aquatic reptiles return to the land to lay eggs. They usually reproduce sexually with internal fertilization. Some species display ovoviviparity, with the eggs remaining in the mother's body until they are ready to hatch. Other species are viviparous, with the offspring born alive.

One of the key adaptations that permitted reptiles to live on land was the development of their scaly skin, containing the protein keratin and waxy lipids, which reduced water loss from the skin. This occlusive skin means that reptiles cannot use their skin for respiration, like amphibians, and thus all breathe with lungs.

Reptiles are ectotherms, animals whose main source of body heat comes from the environment. This is in contrast to endotherms, which use heat produced by metabolism to regulate body temperature. In addition to being ectothermic, reptiles are categorized as poikilotherms, or animals whose body temperatures vary rather than remain stable. Reptiles have behavioral adaptations to help regulate body temperature, such as basking in sunny places to warm up and finding shady spots or going underground to cool down. The advantage of ectothermy is that metabolic energy from food is not required to heat the body; therefore, reptiles can survive on about 10 percent of the calories required by a similarly sized endotherm. In cold weather, some reptiles such as the garter snake brumate. Brumation is similar to hibernation in that the animal becomes less active and can go for long periods without eating, but differs from hibernation in that brumating reptiles are not asleep or living off fat reserves. Rather, their metabolism is slowed in response to cold temperatures, and the animal is very sluggish.

Evolution of Reptiles

Reptiles originated approximately 300 million years ago during the Carboniferous period. One of the oldest known amniotes is Casineria, which had both amphibian and reptilian characteristics. One of the earliest undisputed reptiles was Hylonomus. Soon after the first amniotes appeared, they diverged into three groups—synapsids, anapsids, and diapsids—during the Permian period. The Permian period also saw a second major divergence of diapsid reptiles into archosaurs (predecessors of crocodilians and dinosaurs) and lepidosaurs (predecessors of snakes and lizards). These groups remained inconspicuous until the Triassic period, when the archosaurs became the dominant terrestrial group due to the extinction of large-bodied anapsids and synapsids during the Permian-Triassic extinction. About 250 million years ago, archosaurs radiated into the dinosaurs and the pterosaurs.

Although they are sometimes mistakenly called dinosaurs, the pterosaurs were distinct from true dinosaurs (Figure **41.6.5.4**). Pterosaurs had a number of adaptations that allowed for flight, including hollow bones (birds also exhibit hollow bones, a case of convergent evolution). Their wings were formed by membranes of skin that attached to the long, fourth finger of each arm and extended along the body to the legs.



Figure **41.6.5.4**: Pterosaurs, which existed from the late Triassic to the Cretaceous period (210 to 65.5 million years ago), possessed wings but are not believed to have been capable of powered flight. Instead, they may have been able to soar after launching from cliffs. (credit: Mark Witton, Darren Naish)

The dinosaurs were a diverse group of terrestrial reptiles with more than 1,000 species identified to date. Paleontologists continue to discover new species of dinosaurs. Some dinosaurs were quadrupeds (Figure **41.6.5.5**); others were bipeds. Some were carnivorous, whereas others were herbivorous. Dinosaurs laid eggs, and a number of nests containing fossilized eggs have been found. It is not known whether dinosaurs were endotherms or ectotherms. However, given that modern birds are endothermic, the dinosaurs that served as ancestors to birds likely were endothermic as well. Some fossil evidence exists for dinosaurian parental care, and comparative biology supports this hypothesis since the archosaur birds and crocodilians display parental care.

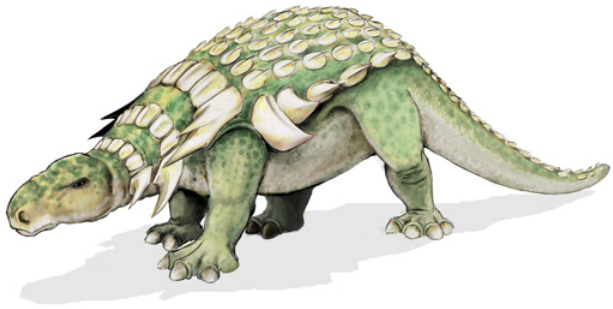


Figure **41.6.5.5**: *Edmontonia* was an armored dinosaur that lived in the late Cretaceous period, 145.5 to 65.6 million years ago. (credit: Mariana Ruiz Villareal)

Dinosaurs dominated the Mesozoic Era, which was known as the “age of reptiles.” The dominance of dinosaurs lasted until the end of the Cretaceous, the last period of the Mesozoic Era. The Cretaceous-Tertiary extinction resulted in the loss of most of the large-bodied animals of the Mesozoic Era. Birds are the only living descendants of one of the major clades of dinosaurs.

Link to Learning

Visit this site to see a video discussing the hypothesis that an asteroid caused the Cretaceous-Triassic (KT) extinction.

Modern Reptiles

Class Reptilia includes many diverse species that are classified into four living clades. These are the 25 species of Crocodilia, 2 species of Sphenodontia, approximately 9,200 Squamata species, and the Testudines, with about 325 species.

Crocodilia

Crocodilia (“small lizard”) arose with a distinct lineage by the middle Triassic; extant species include alligators, crocodiles, and caimans. Crocodilians (Figure 41.6.5.6) live throughout the tropics and subtropics of Africa, South America, Southern Florida, Asia, and Australia. They are found in freshwater, saltwater, and brackish habitats, such as rivers and lakes, and spend most of their time in water. Some species are able to move on land due to their semi-erect posture.



Figure 41.6.5.6: Crocodilians, such as this Siamese crocodile (*Crocodylus siamensis*), provide parental care for their offspring. (credit: Keshav Mukund Kandhadai)

Sphenodontia

Sphenodontia (“wedge tooth”) arose in the Mesozoic era and includes only one living genus, *Tuatara*, comprising two species that are found in New Zealand (Figure 41.6.5.7). Tuataras measure up to 80 centimeters and weigh about 1 kilogram. Although quite lizard-like in gross appearance, several unique features of the skull and jaws clearly define them and distinguish the group from the squamates.



Figure 41.6.5.7: This tuatara from New Zealand may resemble a lizard but belongs to a distinct lineage, the Sphenodontidae family. (credit: Sid Mosdell)

Squamata

Squamata ("scaly") arose in the late Permian, and extant species include lizards and snakes. Both are found on all continents except Antarctica. Lizards and snakes are most closely related to tuataras, both groups having evolved from a lepidosaurian ancestor. Squamata is the largest extant clade of reptiles (Figure 41.6.5.8). Most lizards differ from snakes by having four limbs, although these have been variously lost or significantly reduced in at least 60 lineages. Snakes lack eyelids and external ears, which are present in lizards. Lizard species range in size from chameleons and geckos, which are a few centimeters in length, to the Komodo dragon, which is about 3 meters in length. Most lizards are carnivorous, but some large species, such as iguanas, are herbivores.



Figure 41.6.5.8: This Jackson's chameleon (*Trioceros jacksonii*) blends in with its surroundings.

Snakes are thought to have descended from either burrowing lizards or aquatic lizards over 100 million years ago (Figure 41.6.5.9). Snakes comprise about 3,000 species and are found on every continent except Antarctica. They range in size from 10 centimeter-long thread snakes to 10 meter-long pythons and anacondas. All snakes are carnivorous and eat small animals, birds, eggs, fish, and insects. The snake body form is so specialized that, in its general morphology, a "snake is a snake." Their specializations all point to snakes having evolved to feed on relatively large prey (even though some current species have reversed this trend). Although variations exist, most snakes have a skull that is very flexible, involving eight rotational joints. They also differ from other squamates by having mandibles (lower jaws) without either bony or ligamentous attachment anteriorly. Having this connection via skin and muscle allows for great expansion of the gape and independent motion of the two sides—both advantages in swallowing big items.



Figure **41.6.5.9**: The garter snake belongs to the genus *Thamnophis*, the most widely distributed reptile genus in North America. (credit: Steve Jurvetson)

Testudines

Turtles are members of the clade Testudines (“having a shell”) (Figure **41.6.5.10**). Turtles are characterized by a bony or cartilaginous shell. The shell consists of the ventral surface called the plastron and the dorsal surface called the carapace, which develops from the ribs. The plastron is made of scutes or plates; the scutes can be used to differentiate species of turtles. The two clades of turtles are most easily recognized by how they retract their necks. The dominant group, which includes all North American species, retracts its neck in a vertical S-curve. Turtles in the less speciose clade retract the neck with a horizontal curve.

Turtles arose approximately 200 million years ago, predating crocodiles, lizards, and snakes. Similar to other reptiles, turtles are ectotherms. They lay eggs on land, although many species live in or near water. None exhibit parental care. Turtles range in size from the speckled padloper tortoise at 8 centimeters (3.1 inches) to the leatherback sea turtle at 200 centimeters (over 6 feet). The term “turtle” is sometimes used to describe only those species of Testudines that live in the sea, with the terms “tortoise” and “terrapin” used to refer to species that live on land and in fresh water, respectively.



Figure **41.6.5.10**: The African spurred tortoise (*Geochelone sulcata*) lives at the southern edge of the Sahara Desert. It is the third largest tortoise in the world. (credit: Jim Bowen)

Summary

The amniotes are distinguished from amphibians by the presence of a terrestrially adapted egg protected by amniotic membranes. The amniotes include reptiles, birds, and mammals. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids (mammals) and sauropsids. Sauropsids can be further divided into anapsids (turtles) and

diapsids (birds and reptiles). Reptiles are tetrapods either having four limbs or descending from such. Limbless reptiles (snakes) are classified as tetrapods, as they are descended from four-limbed organisms. One of the key adaptations that permitted reptiles to live on land was the development of scaly skin containing the protein keratin, which prevented water loss from the skin. Reptilia includes four living clades: Crocodilia (crocodiles and alligators), Sphenodontia (tuataras), Squamata (lizards and snakes), and Testudines (turtles).

Art Connections

Figure 41.6.5.1: Which of the following statements about the parts of an egg are false?

A. The allantois stores nitrogenous waste and facilitates respiration.
B. The chorion facilitates gas exchange.
C. The yolk provides food for the growing embryo.
D. The amniotic cavity is filled with albumen.

Answer

D

Figure 41.6.5.3: Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

Answer

The ancestor of modern Testudines may at one time have had a second opening in the skull, but over time this might have been lost.

Glossary

amniote
animal that produces a terrestrially adapted egg protected by amniotic membranes

allantois
membrane of the egg that stores nitrogenous wastes produced by the embryo; also facilitates respiration

amnion
membrane of the egg that protects the embryo from mechanical shock and prevents dehydration

anapsid
animal having no temporal fenestrae in the cranium

archosaur
modern crocodilian or bird, or an extinct pterosaur or dinosaur

brumation
period of much reduced metabolism and torpor that occurs in any ectotherm in cold weather

Casineria
one of the oldest known amniotes; had both amphibian and reptilian characteristics

chorion
membrane of the egg that surrounds the embryo and yolk sac

Crocodilia

crocodiles and alligators

diapsid
animal having two temporal fenestrae in the cranium

Hylonomus
one of the earliest reptiles

lepidosaur
modern lizards, snakes, and tuataras

sauropsid
reptile or bird

Sphenodontia
clade of tuataras

Squamata
clade of lizards and snakes

synapsid
mammal having one temporal fenestra

temporal fenestra
non-orbital opening in the skull that may allow muscles to expand and lengthen

Testudines
order of turtles

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41.6.6: Birds

Skills to Develop

- Describe the evolutionary history of birds
- Describe the derived characteristics in birds that facilitate flight

The most obvious characteristic that sets birds apart from other modern vertebrates is the presence of feathers, which are modified scales. While vertebrates like bats fly without feathers, birds rely on feathers and wings, along with other modifications of body structure and physiology, for flight.

Characteristics of Birds

Birds are endothermic, and because they fly, they require large amounts of energy, necessitating a high metabolic rate. Like mammals, which are also endothermic, birds have an insulating covering that keeps heat in the body: feathers. Specialized feathers called down feathers are especially insulating, trapping air in spaces between each feather to decrease the rate of heat loss. Certain parts of a bird's body are covered in down feathers, and the base of other feathers have a downy portion, whereas newly hatched birds are covered in down.

Feathers not only act as insulation but also allow for flight, enabling the lift and thrust necessary to become airborne. The feathers on a wing are flexible, so the collective feathers move and separate as air moves through them, reducing the drag on the wing. Flight feathers are asymmetrical, which affects airflow over them and provides some of the lifting and thrusting force required for flight (Figure **41.6.6.1**). Two types of flight feathers are found on the wings, primary feathers and secondary feathers. Primary feathers are located at the tip of the wing and provide thrust. Secondary feathers are located closer to the body, attach to the forearm portion of the wing and provide lift. Contour feathers are the feathers found on the body, and they help reduce drag produced by wind resistance during flight. They create a smooth, aerodynamic surface so that air moves smoothly over the bird's body, allowing for efficient flight.

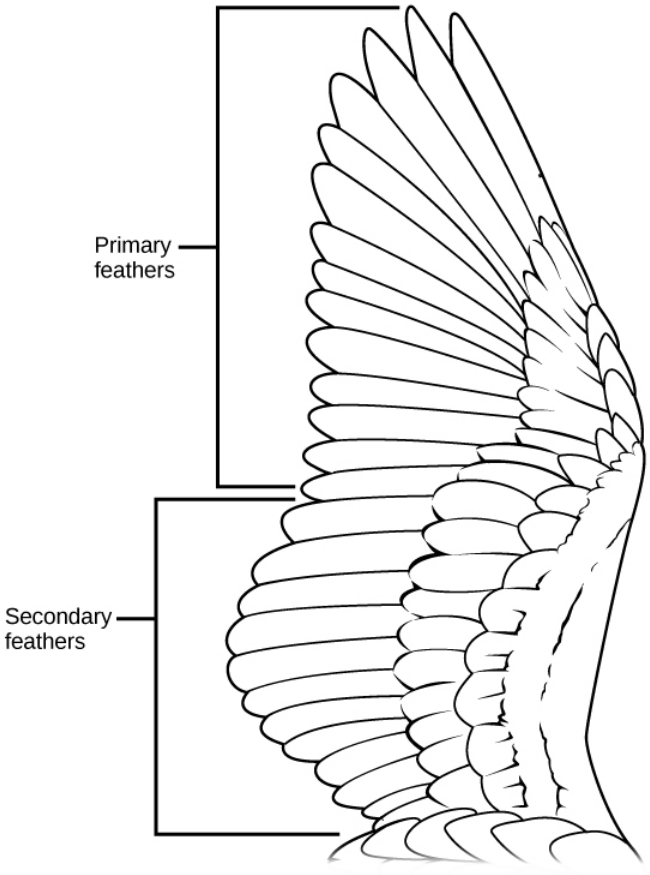


Figure **41.6.6.1**: Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift.

Flapping of the entire wing occurs primarily through the actions of the chest muscles, the pectoralis and the supracoracoideus. These muscles are highly developed in birds and account for a higher percentage of body mass than in most mammals. These attach to a blade-shaped keel, like that of a boat, located on the sternum. The sternum of birds is larger than that of other vertebrates, which accommodates the large muscles required to generate enough upward force to generate lift with the flapping of the wings. Another skeletal modification found in most birds is the fusion of the two clavicles (collarbones), forming the furcula or wishbone. The furcula is flexible enough to bend and provide support to the shoulder girdle during flapping.

An important requirement of flight is a low body weight. As body weight increases, the muscle output required for flying increases. The largest living bird is the ostrich, and while it is much smaller than the largest mammals, it is flightless. For birds that do fly, reduction in body weight makes flight easier. Several modifications are found in birds to reduce body weight, including pneumatization of bones. Pneumatic bones are bones that are hollow, rather than filled with tissue (Figure **41.6.6.2**). They contain air spaces that are sometimes connected to air sacs, and they have struts of bone to provide structural reinforcement. Pneumatic bones are not found in all birds, and they are more extensive in large birds than in small birds. Not all bones of the skeleton are pneumatic, although the skulls of almost all birds are.



Figure **41.6.6.2**: Many birds have hollow, pneumatic bones, which make flight easier.

Other modifications that reduce weight include the lack of a urinary bladder. Birds possess a cloaca, a structure that allows water to be reabsorbed from waste back into the bloodstream. Uric acid is not expelled as a liquid but is concentrated into urate salts, which are expelled along with fecal matter. In this way, water is not held in the urinary bladder, which would increase body weight. Most bird species only possess one ovary rather than two, further reducing body mass.

The air sacs that extend into bones to form pneumatic bones also join with the lungs and function in respiration. Unlike mammalian lungs in which air flows in two directions, as it is breathed in and out, airflow through bird lungs travels in one direction (Figure **41.6.6.3**). Air sacs allow for this unidirectional airflow, which also creates a cross-current exchange system with the blood. In a cross-current or counter-current system, the air flows in one direction and the blood flows in the opposite direction, creating a very efficient means of gas exchange.

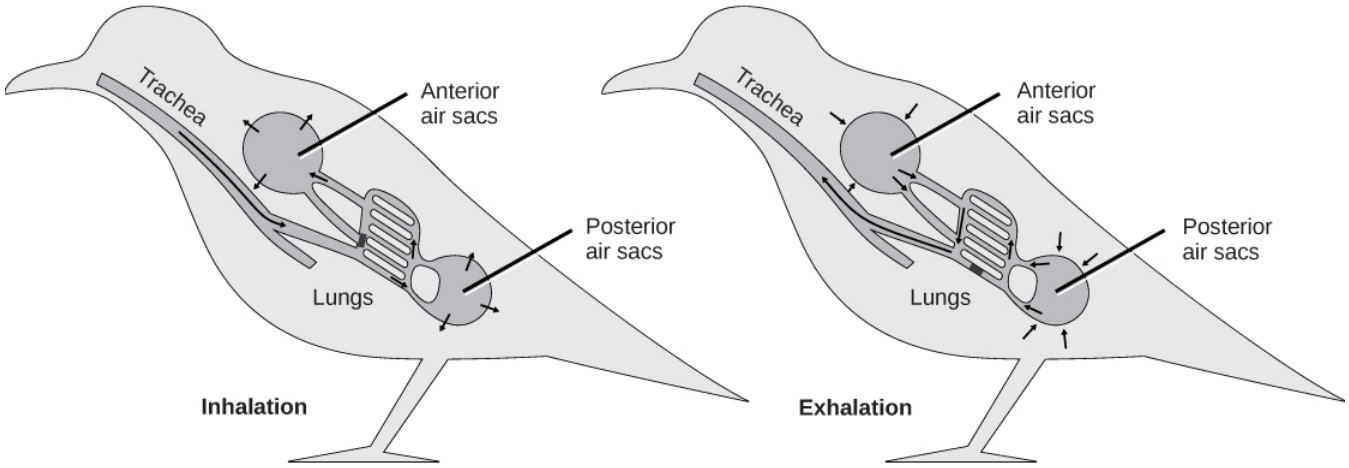


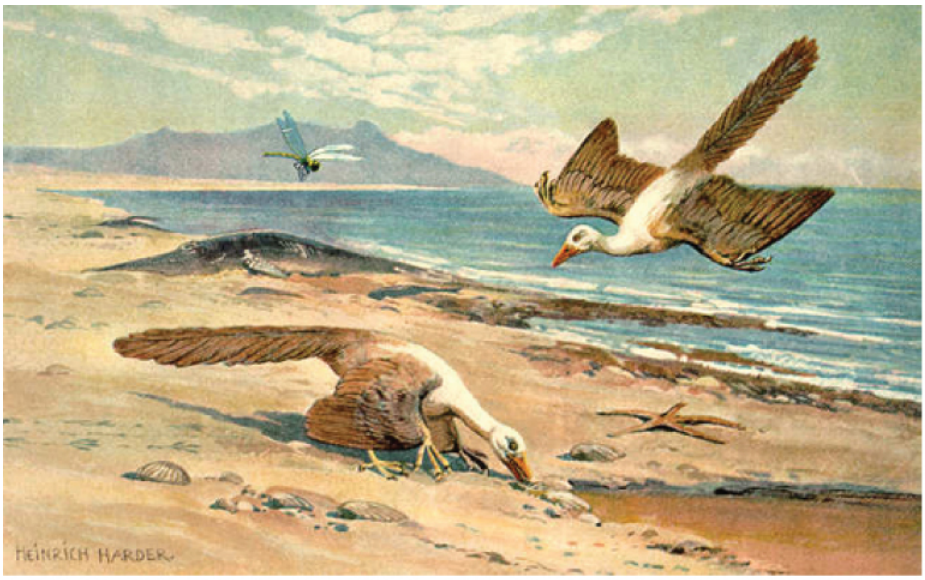
Figure **41.6.6.3**: Avian respiration is an efficient system of gas exchange with air flowing unidirectionally. During inhalation, air passes from the trachea into posterior air sacs, then through the lungs to anterior air sacs. The air sacs are connected to the hollow interior of bones. During exhalation, air from air sacs passes into the lungs and out the trachea. (credit: modification of work by L. Shyamal)

Evolution of Birds

The evolutionary history of birds is still somewhat unclear. Due to the fragility of bird bones, they do not fossilize as well as other vertebrates. Birds are diapsids, meaning they have two fenestrations or openings in their skulls. Birds belong to a group of diapsids called the archosaurs, which also includes crocodiles and dinosaurs. It is commonly accepted that birds evolved from dinosaurs.

Dinosaurs (including birds) are further subdivided into two groups, the Saurischia ("lizard like") and the Ornithischia ("bird like"). Despite the names of these groups, it was not the bird-like dinosaurs that gave rise to modern birds. Rather, Saurischia diverged into two groups: One included the long-necked herbivorous dinosaurs, such as Apatosaurus. The second group, bipedal predators called theropods, includes birds. This course of evolution is suggested by similarities between theropod fossils and birds, specifically in the structure of the hip and wrist bones, as well as the presence of the wishbone, formed by the fusing of the clavicles.

One important fossil of an animal intermediate to dinosaurs and birds is *Archaeopteryx*, which is from the Jurassic period (Figure **41.6.6.4**). *Archaeopteryx* is important in establishing the relationship between birds and dinosaurs, because it is an intermediate fossil, meaning it has characteristics of both dinosaurs and birds. Some scientists propose classifying it as a bird, but others prefer to classify it as a dinosaur. The fossilized skeleton of *Archaeopteryx* looks like that of a dinosaur, and it had teeth whereas birds do not, but it also had feathers modified for flight, a trait associated only with birds among modern animals. Fossils of older feathered dinosaurs exist, but the feathers do not have the characteristics of flight feathers.



(a)



(b)

Figure **41.6.6.4**: (a) *Archaeopteryx* lived in the late Jurassic Period around 150 million years ago. It had teeth like a dinosaur, but had (b) flight feathers like modern birds, which can be seen in this fossil.

It is still unclear exactly how flight evolved in birds. Two main theories exist, the arboreal (“tree”) hypothesis and the terrestrial (“land”) hypothesis. The arboreal hypothesis posits that tree-dwelling precursors to modern birds jumped from branch to branch using their feathers for gliding before becoming fully capable of flapping flight. In contrast to this, the terrestrial hypothesis holds that running was the stimulus for flight, as wings could be used to improve running and then became used for flapping flight. Like the question of how flight evolved, the question of how endothermy evolved in birds still is unanswered. Feathers provide insulation, but this is only beneficial if body heat is being produced internally. Similarly, internal heat production is only viable if insulation is present to retain that heat. It has been suggested that one or the other—feathers or endothermy—evolved in response to some other selective pressure.

During the Cretaceous period, a group known as the Enantiornithes was the dominant bird type (Figure **41.6.6.5**). Enantiornithes means “opposite birds,” which refers to the fact that certain bones of the feet are joined differently than the way the bones are joined in modern birds. These birds formed an evolutionary line separate from modern birds, and they did not survive past the Cretaceous. Along with the Enantiornithes, Ornithurae birds (the evolutionary line that includes modern birds) were also present in the Cretaceous. After the extinction of Enantiornithes, modern birds became the dominant bird, with a large radiation occurring during the Cenozoic Era. Referred to as Neornithes (“new birds”), modern birds are now classified into two groups, the Paleognathae (“old jaw”) or ratites, a group of flightless birds including ostriches, emus, rheas, and kiwis, and the Neognathae (“new jaw”), which includes all other birds.



Figure **41.6.6.5**: *Shanweiniao cooperorum* was a species of Enantiornithes that did not survive past the Cretaceous period. (credit: Nobu Tamura)

Career Connection: Veterinarian

Veterinarians treat diseases, disorders, and injuries in animals, primarily vertebrates. They treat pets, livestock, and animals in zoos and laboratories. Veterinarians usually treat dogs and cats, but also treat birds, reptiles, rabbits, and other animals that are kept as pets. Veterinarians that work with farms and ranches treat pigs, goats, cows, sheep, and horses.

Veterinarians are required to complete a degree in veterinary medicine, which includes taking courses in animal physiology, anatomy, microbiology, and pathology, among many other courses. The physiology and biochemistry of different vertebrate species differ greatly.

Veterinarians are also trained to perform surgery on many different vertebrate species, which requires an understanding of the vastly different anatomies of various species. For example, the stomach of ruminants like cows has four compartments versus one compartment for non-ruminants. Birds also have unique anatomical adaptations that allow for flight.

Some veterinarians conduct research in academic settings, broadening our knowledge of animals and medical science. One area of research involves understanding the transmission of animal diseases to humans, called zoonotic diseases. For example, one area of great concern is the transmission of the avian flu virus to humans. One type of avian flu virus, H5N1, is a highly pathogenic strain that has been spreading in birds in Asia, Europe, Africa, and the Middle East. Although the virus does not cross over easily to humans, there have been cases of bird-to-human transmission. More research is needed to understand how this virus can cross the species barrier and how its spread can be prevented.

Summary

Birds are endothermic, meaning they produce their own body heat and regulate their internal temperature independently of the external temperature. Feathers not only act as insulation but also allow for flight, providing lift with secondary feathers and thrust with primary feathers. Pneumatic bones are bones that are hollow rather than filled with tissue, containing air spaces that are sometimes connected to air sacs. Airflow through bird lungs travels in one direction, creating a cross-current exchange with the blood. Birds are diapsids and belong to a group called the archosaurs. Birds are thought to have evolved from theropod dinosaurs. The oldest known fossil of a bird is that of *Archaeopteryx*, which is from the Jurassic period. Modern birds are now classified into two groups, Paleognathae and Neognathae.

Glossary

Archaeopteryx
transition species from dinosaur to bird from the Jurassic period

contour feather
feather that creates an aerodynamic surface for efficient flight

down feather
feather specialized for insulation

Enantiornithes
dominant bird group during the Cretaceous period

flight feather
feather specialized for flight

furcula
wishbone formed by the fusing of the clavicles

Neognathae

birds other than the Paleognathae

Neornithes
modern birds

Paleognathae
ratites; flightless birds, including ostriches and emus

pneumatic bone
air-filled bone

primary feather
feather located at the tip of the wing that provides thrust

secondary feather
feather located at the base of the wing that provides lift

theropod
dinosaur group ancestral to birds

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41.6.7: Mammals

Skills to Develop

- Name and describe the distinguishing features of the three main groups of mammals
- Describe the proposed line of descent that produced mammals
- List some derived features that may have arisen in response to mammals' need for constant, high-level metabolism

Mammals are vertebrates that possess hair and mammary glands. Several other characteristics are distinctive to mammals, including certain features of the jaw, skeleton, integument, and internal anatomy. Modern mammals belong to three clades: monotremes, marsupials, and eutherians (or placental mammals).

Characteristics of Mammals

The presence of hair is one of the most obvious signs of a mammal. Although it is not very extensive on certain species, such as whales, hair has many important functions for mammals. Mammals are endothermic, and hair provides insulation to retain heat generated by metabolic work. Hair traps a layer of air close to the body, retaining heat. Along with insulation, hair can serve as a sensory mechanism via specialized hairs called vibrissae, better known as whiskers. These attach to nerves that transmit information about sensation, which is particularly useful to nocturnal or burrowing mammals. Hair can also provide protective coloration or be part of social signaling, such as when an animal's hair stands "on end."

Mammalian integument, or skin, includes secretory glands with various functions. Sebaceous glands produce a lipid mixture called sebum that is secreted onto the hair and skin for water resistance and lubrication. Sebaceous glands are located over most of the body. Eccrine glands produce sweat, or perspiration, which is mainly composed of water. In most mammals, eccrine glands are limited to certain areas of the body, and some mammals do not possess them at all. However, in primates, especially humans, sweat figures prominently in thermoregulation, regulating the body through evaporative cooling. Sweat glands are located over most of the body surface in primates. Apocrine glands, or scent glands, secrete substances that are used for chemical communication, such as in skunks. Mammary glands produce milk that is used to feed newborns. While male monotremes and eutherians possess mammary glands, male marsupials do not. Mammary glands likely are modified sebaceous or eccrine glands, but their evolutionary origin is not entirely clear.

The skeletal system of mammals possesses many unique features. The lower jaw of mammals consists of only one bone, the dentary. The jaws of other vertebrates are composed of more than one bone. In mammals, the dentary bone joins the skull at the squamosal bone, while in other vertebrates, the quadrate bone of the jaw joins with the articular bone of the skull. These bones are present in mammals, but they have been modified to function in hearing and form bones in the middle ear (Figure **41.6.7.1**). Other vertebrates possess only one middle ear bone, the stapes. Mammals have three: the malleus, incus, and stapes. The malleus originated from the articular bone, whereas the incus originated from the quadrate bone. This arrangement of jaw and ear bones aids in distinguishing fossil mammals from fossils of other synapsids.

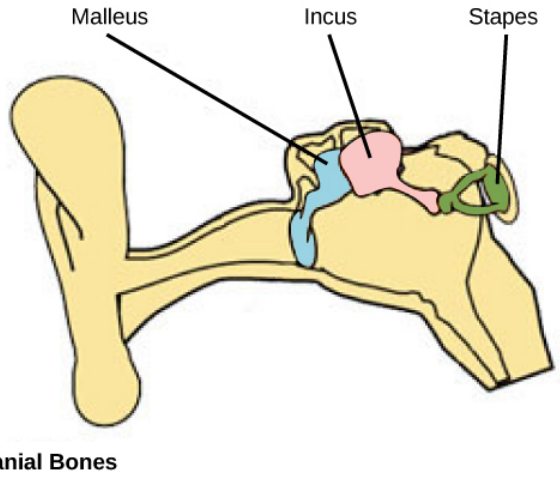


Figure **41.6.7.1**: Bones of the mammalian inner ear are modified from bones of the jaw and skull. (credit: NCI)

The adductor muscle that closes the jaw is composed of two muscles in mammals: the temporalis and the masseter. These allow side-to-side movement of the jaw, making chewing possible, which is unique to mammals. Most mammals have heterodont teeth, meaning that they have different types and shapes of teeth rather than just one type and shape of tooth. Most mammals are diphyodonts, meaning that they have two sets of teeth in their lifetime: deciduous or “baby” teeth, and permanent teeth. Other vertebrates are polyphyodonts, that is, their teeth are replaced throughout their entire life.

Mammals, like birds, possess a four-chambered heart. Mammals also have a specialized group of cardiac fibers located in the walls of their right atrium called the sinoatrial node, or pacemaker, which determines the rate at which the heart beats. Mammalian erythrocytes (red blood cells) do not have nuclei, whereas the erythrocytes of other vertebrates are nucleated.

The kidneys of mammals have a portion of the nephron called the loop of Henle or nephritic loop, which allows mammals to produce urine with a high concentration of solutes, higher than that of the blood. Mammals lack a renal portal system, which is a system of veins that moves blood from the hind or lower limbs and region of the tail to the kidneys. Renal portal systems are present in all other vertebrates except jawless fishes. A urinary bladder is present in all mammals.

Mammalian brains have certain characteristics that differ from other vertebrates. In some, but not all mammals, the cerebral cortex, the outermost part of the cerebrum, is highly folded, allowing for a greater surface area than is possible with a smooth cortex. The optic lobes, located in the midbrain, are divided into two parts in mammals, whereas other vertebrates possess a single, undivided lobe. Eutherian mammals also possess a specialized structure that links the two cerebral hemispheres, called the corpus callosum.

Evolution of Mammals

Mammals are synapsids, meaning they have a single opening in the skull. They are the only living synapsids, as earlier forms became extinct by the Jurassic period. The early non-mammalian synapsids can be divided into two groups, the pelycosaurs and the therapsids. Within the therapsids, a group called the cynodonts are thought to be the ancestors of mammals (Figure **41.6.7.2**).



Figure **41.6.7.2**: Cynodonts, which first appeared in the Late Permian period 260 million years ago, are thought to be the ancestors of modern mammals. (credit: Nobu Tamura)

A key characteristic of synapsids is endothermy, rather than the ectothermy seen in most other vertebrates. The increased metabolic rate required to internally modify body temperature went hand in hand with changes to certain skeletal structures. The later synapsids, which had more evolved characteristics unique to mammals, possess cheeks for holding food and heterodont teeth, which are specialized for chewing, mechanically breaking down food to speed digestion and releasing the energy needed to produce heat. Chewing also requires the ability to chew and breathe at the same time, which is facilitated by the presence of a secondary palate. A secondary palate separates the area of the mouth where chewing occurs from the area above where respiration occurs, allowing breathing to proceed uninterrupted during chewing. A secondary palate is not found in pelycosaurs but is present in cynodonts and mammals. The jawbone also shows changes from early synapsids to later ones. The zygomatic arch, or cheekbone, is present in mammals and advanced therapsids such as cynodonts, but is not present in pelycosaurs. The presence of the zygomatic arch suggests the presence of the masseter muscle, which closes the jaw and functions in chewing.

In the appendicular skeleton, the shoulder girdle of therian mammals is modified from that of other vertebrates in that it does not possess a procoracoid bone or an interclavicle, and the scapula is the dominant bone.

Mammals evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period, some 205 million years ago. Early mammals were small, about the size of a small rodent. Mammals first began to diversify in the Mesozoic Era, from the Jurassic to the Cretaceous periods, although most of these mammals were extinct by the end of the

Mesozoic. During the Cretaceous period, another radiation of mammals began and continued through the Cenozoic Era, about 65 million years ago.

Living Mammals

The eutherians, or placental mammals, and the marsupials together comprise the clade of therian mammals. Monotremes, or metatherians, form their sister clade.

There are three living species of monotremes: the platypus and two species of echidnas, or spiny anteaters. The leathery-beaked platypus belongs to the family Ornithorhynchidae ("bird beak"), whereas echidnas belong to the family Tachyglossidae ("sticky tongue") (Figure **41.6.7.3**). The platypus and one species of echidna are found in Australia, and the other species of echidna is found in New Guinea. Monotremes are unique among mammals as they lay eggs, rather than giving birth to live young. The shells of their eggs are not like the hard shells of birds, but are a leathery shell, similar to the shells of reptile eggs. Monotremes have no teeth.



Figure **41.6.7.3**: (a) The platypus, a monotreme, possesses a leathery beak and lays eggs rather than giving birth to live young. (b) The echidna is another monotreme. (credit b: modification of work by Barry Thomas)

Marsupials are found primarily in Australia, though the opossum is found in North America. Australian marsupials include the kangaroo, koala, bandicoot, Tasmanian devil (Figure **41.6.7.4**), and several other species. Most species of marsupials possess a pouch in which the very premature young reside after birth, receiving milk and continuing to develop. Marsupials differ from eutherians in that there is a less complex placental connection: The young are born at an extremely early age and latch onto the nipple within the pouch.



Figure **41.6.7.4**: The Tasmanian devil is one of several marsupials native to Australia. (credit: Wayne McLean)

Eutherians are the most widespread of the mammals, occurring throughout the world. There are 18 to 20 orders of placental mammals. Some examples are Insectivora, the insect eaters; Edentata, the toothless anteaters; Rodentia, the rodents; Cetacea, the aquatic mammals including whales; Carnivora, carnivorous mammals including dogs, cats, and bears; and Primates, which includes humans. Eutherian mammals are sometimes called placental mammals because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. While other mammals possess a less complex placenta or briefly have a placenta, all eutherians possess a complex placenta during gestation.

Summary

Mammals in general are vertebrates that possess hair and mammary glands. The mammalian integument includes various secretory glands, including sebaceous glands, eccrine glands, apocrine glands, and mammary glands. Mammals are synapsids, meaning that they have a single opening in the skull. A key characteristic of synapsids is endothermy rather than the ectothermy seen in other vertebrates. Mammals probably evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period. There are three groups of mammals living today: monotremes, marsupials, and eutherians. Monotremes are unique among mammals as they lay eggs, rather than giving birth to young. Eutherian mammals are sometimes called placental mammals, because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange.

Glossary

apocrine gland
: scent gland that secretes substances that are used for chemical communication

dentary
: single bone that comprises the lower jaw of mammals

diphyodont
: refers to the possession of two sets of teeth in a lifetime

eccrine gland
: sweat gland

eutherian mammal
: mammal that possesses a complex placenta, which connects a fetus to the mother; sometimes called placental mammals

heterodont tooth
: different types of teeth that are modified for different purposes

mammal

one of the groups of endothermic vertebrates that possesses hair and mammary glands

mammary gland
in female mammals, a gland that produces milk for newborns

marsupial
one of the groups of mammals that includes the kangaroo, koala, bandicoot, Tasmanian devil, and several other species; young develop within a pouch

monotreme
egg-laying mammal

Ornithorhynchidae
clade that includes the duck-billed platypus

sebaceous gland
in mammals, a skin gland that produce a lipid mixture called *sebum*

Tachyglossidae
clade that includes the echidna or spiny anteater

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41.7: Homeostasis

Skills to Develop

- Define homeostasis
- Describe the factors affecting homeostasis
- Discuss positive and negative feedback mechanisms used in homeostasis
- Describe thermoregulation of endothermic and ectothermic animals

Animal organs and organ systems constantly adjust to internal and external changes through a process called homeostasis (“steady state”). These changes might be in the level of glucose or calcium in blood or in external temperatures. Homeostasis means to maintain dynamic equilibrium in the body. It is dynamic because it is constantly adjusting to the changes that the body’s systems encounter. It is equilibrium because body functions are kept within specific ranges. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium.

Homeostatic Process

The goal of homeostasis is the maintenance of equilibrium around a point or value called a set point. While there are normal fluctuations from the set point, the body’s systems will usually attempt to go back to this point. A change in the internal or external environment is called a stimulus and is detected by a receptor; the response of the system is to adjust the deviation parameter toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If the blood’s glucose rises after a meal, adjustments are made to lower the blood glucose level by getting the nutrient into tissues that need it or to store it for later use.

Control of Homeostasis

When a change occurs in an animal’s environment, an adjustment must be made. The receptor senses the change in the environment, then sends a signal to the control center (in most cases, the brain) which in turn generates a response that is signaled to an effector. The effector is a muscle (that contracts or relaxes) or a gland that secretes. Homeostatsis is maintained by negative feedback loops. Positive feedback loops actually push the organism further out of homeostasis, but may be necessary for life to occur. Homeostasis is controlled by the nervous and endocrine system of mammals.

Negative Feedback Mechanisms

Any homeostatic process that changes the direction of the stimulus is a negative feedback loop. It may either increase or decrease the stimulus, but the stimulus is not allowed to continue as it did before the receptor sensed it. In other words, if a level is too high, the body does something to bring it down, and conversely, if a level is too low, the body does something to make it go up. Hence the term negative feedback. An example is animal maintenance of blood glucose levels. When an animal has eaten, blood glucose levels rise. This is sensed by the nervous system. Specialized cells in the pancreas sense this, and the hormone insulin is released by the endocrine system. Insulin causes blood glucose levels to decrease, as would be expected in a negative feedback system, as illustrated in Figure **41.7.1**. However, if an animal has not eaten and blood glucose levels decrease, this is sensed in another group of cells in the pancreas, and the hormone glucagon is released causing glucose levels to increase. This is still a negative feedback loop, but not in the direction expected by the use of the term “negative.” Another example of an increase as a result of the feedback loop is the control of blood calcium. If calcium levels decrease, specialized cells in the parathyroid gland sense this and release parathyroid hormone (PTH), causing an increased absorption of calcium through the intestines and kidneys and, possibly, the breakdown of bone in order to liberate calcium. The effects of PTH are to raise blood levels of the element. Negative feedback loops are the predominant mechanism used in homeostasis.

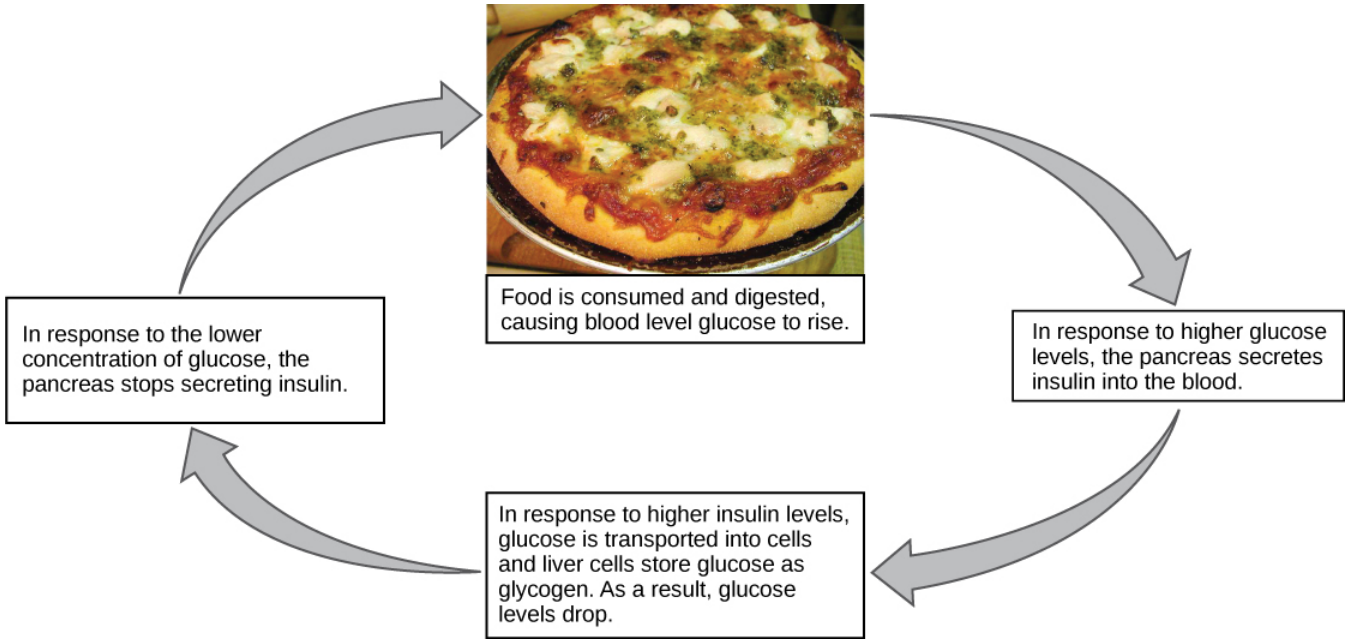


Figure **41.7.1**: Blood sugar levels are controlled by a negative feedback loop. (credit: modification of work by Jon Sullivan)

Positive Feedback Loop

A positive feedback loop maintains the direction of the stimulus, possibly accelerating it. Few examples of positive feedback loops exist in animal bodies, but one is found in the cascade of chemical reactions that result in blood clotting, or coagulation. As one clotting factor is activated, it activates the next factor in sequence until a fibrin clot is achieved. The direction is maintained, not changed, so this is positive feedback. Another example of positive feedback is uterine contractions during childbirth, as illustrated in Figure **41.7.2**. The hormone oxytocin, made by the endocrine system, stimulates the contraction of the uterus. This produces pain sensed by the nervous system. Instead of lowering the oxytocin and causing the pain to subside, more oxytocin is produced until the contractions are powerful enough to produce childbirth.

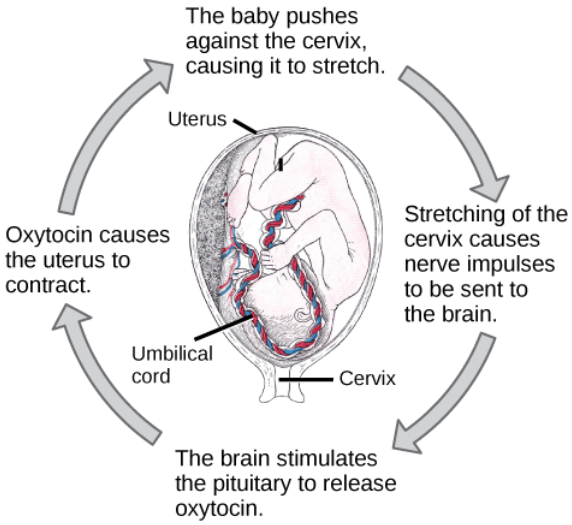


Figure **41.7.2**: The birth of a human infant is the result of positive feedback.

Exercise

State whether each of the following processes is regulated by a positive feedback loop or a negative feedback loop.

A. A person feels satiated after eating a large meal.
B. The blood has plenty of red blood cells. As a result, erythropoietin, a hormone that stimulates the production of new red blood cells, is no longer released from the kidney.

Answer

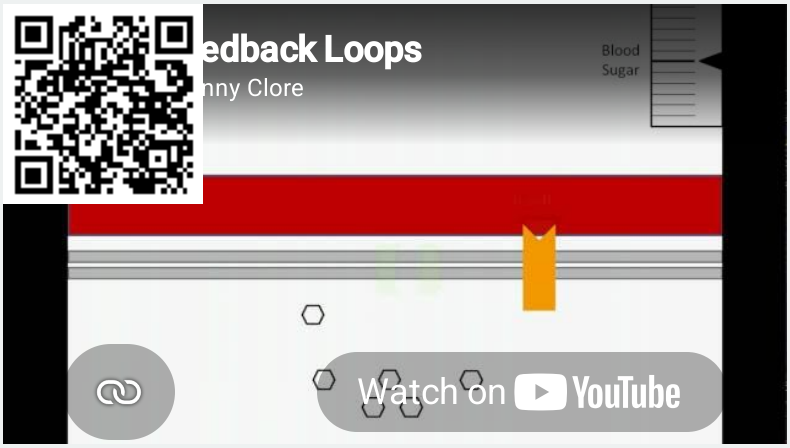
Both processes are the result of negative feedback loops. Negative feedback loops, which tend to keep a system at equilibrium, are more common than positive feedback loops.

Set Point

It is possible to adjust a system's set point. When this happens, the feedback loop works to maintain the new setting. An example of this is blood pressure: over time, the normal or set point for blood pressure can increase as a result of continued increases in blood pressure. The body no longer recognizes the elevation as abnormal and no attempt is made to return to the lower set point. The result is the maintenance of an elevated blood pressure that can have harmful effects on the body. Medication can lower blood pressure and lower the set point in the system to a more healthy level. This is called a process of alteration of the set point in a feedback loop.

Changes can be made in a group of body organ systems in order to maintain a set point in another system. This is called acclimatization. This occurs, for instance, when an animal migrates to a higher altitude than it is accustomed to. In order to adjust to the lower oxygen levels at the new altitude, the body increases the number of red blood cells circulating in the blood to ensure adequate oxygen delivery to the tissues. Another example of acclimatization is animals that have seasonal changes in their coats: a heavier coat in the winter ensures adequate heat retention, and a light coat in summer assists in keeping body temperature from rising to harmful levels.

Link to Learning



Feedback mechanisms can be understood in terms of driving a race car along a track: watch a short video lesson on positive and negative feedback loops.

Homeostasis: Thermoregulation

Body temperature affects body activities. Generally, as body temperature rises, enzyme activity rises as well. For every ten degree centigrade rise in temperature, enzyme activity doubles, up to a point. Body proteins, including enzymes, begin to denature and lose their function with high heat (around 50^{o}C for mammals). Enzyme activity will decrease by half for every ten degree centigrade drop in temperature, to the point of freezing, with a few exceptions. Some fish can withstand freezing solid and return to normal with thawing.

Link to Learning



Watch this Discovery Channel video on thermoregulation to see illustrations of this process in a variety of animals.

Endotherms and Ectotherms

Animals can be divided into two groups: some maintain a constant body temperature in the face of differing environmental temperatures, while others have a body temperature that is the same as their environment and thus varies with the environment. Animals that do not control their body temperature are ectotherms. This group has been called cold-blooded, but the term may not apply to an animal in the desert with a very warm body temperature. In contrast to ectotherms, which rely on external temperatures to set their body temperatures, poikilotherms are animals with constantly varying internal temperatures. An animal that maintains a constant body temperature in the face of environmental changes is called a homeotherm. Endotherms are animals that rely on internal sources for body temperature but which can exhibit extremes in temperature. These animals are able to maintain a level of activity at cooler temperature, which an ectotherm cannot due to differing enzyme levels of activity.

Heat can be exchanged between an animal and its environment through four mechanisms: radiation, evaporation, convection, and conduction (Figure **41.7.3**). Radiation is the emission of electromagnetic “heat” waves. Heat comes from the sun in this manner and radiates from dry skin the same way. Heat can be removed with liquid from a surface during evaporation. This occurs when a mammal sweats. Convection currents of air remove heat from the surface of dry skin as the air passes over it. Heat will be conducted from one surface to another during direct contact with the surfaces, such as an animal resting on a warm rock.



(a) Radiation (b) Evaporation



(c) Convection (d) Conduction

Figure **41.7.3**: Heat can be exchanged by four mechanisms: (a) radiation, (b) evaporation, (c) convection, or (d) conduction. (credit b: modification of work by “Kullez”/Flickr; credit c: modification of work by Chad Rosenthal; credit d: modification of work by “stacey.d”/Flickr)

Heat Conservation and Dissipation

Animals conserve or dissipate heat in a variety of ways. In certain climates, endothermic animals have some form of insulation, such as fur, fat, feathers, or some combination thereof. Animals with thick fur or feathers create an insulating layer of air between their skin and internal organs. Polar bears and seals live and swim in a subfreezing environment and yet maintain a constant, warm, body temperature. The arctic fox, for example, uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals have a residual effect from shivering and increased muscle activity: arrector pili muscles cause “goose bumps,” causing small hairs to stand up when the individual is cold; this has the intended effect of increasing body temperature. Mammals use layers of fat to achieve the same end. Loss of significant amounts of body fat will compromise an individual’s ability to conserve heat.

Endotherms use their circulatory systems to help maintain body temperature. Vasodilation brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, which helps to cool the body. Vasoconstriction reduces blood flow in peripheral blood vessels, forcing blood toward the core and the vital organs found there, and conserving heat. Some animals have adaptions to their circulatory system that enable them to transfer heat from arteries to veins, warming blood returning to the heart. This is called a countercurrent heat exchange; it prevents the cold venous blood from cooling the heart and other internal organs. This adaption can be shut down in some animals to prevent overheating the internal organs. The countercurrent adaption is found in many animals, including dolphins, sharks, bony fish, bees, and hummingbirds. In contrast, similar adaptations can help cool endotherms when needed, such as dolphin flukes and elephant ears.

Some ectothermic animals use changes in their behavior to help regulate body temperature. For example, a desert ectothermic animal may simply seek cooler areas during the hottest part of the day in the desert to keep from getting too warm. The same animals may climb onto rocks to capture heat during a cold desert night. Some animals seek water to aid evaporation in cooling them, as seen with reptiles. Other ectotherms use group activity such as the activity of bees to warm a hive to survive winter.

Many animals, especially mammals, use metabolic waste heat as a heat source. When muscles are contracted, most of the energy from the ATP used in muscle actions is wasted energy that translates into heat. Severe cold elicits a shivering reflex that generates heat for the body. Many species also have a type of adipose tissue called brown fat that specializes in generating heat.

Neural Control of Thermoregulation

The nervous system is important to thermoregulation, as illustrated in Figure **41.7.4**. The processes of homeostasis and temperature control are centered in the hypothalamus of the advanced animal brain.

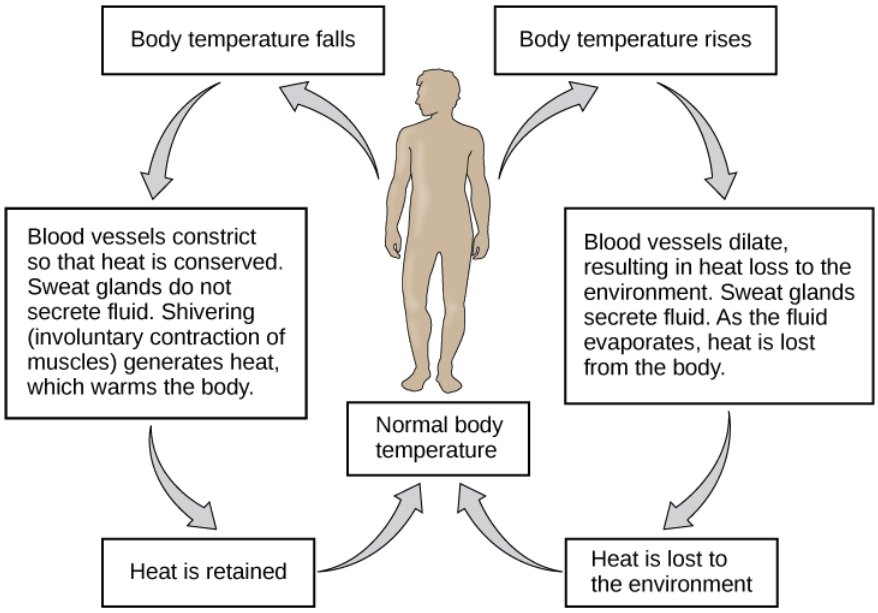


Figure **41.7.4**: The body is able to regulate temperature in response to signals from the nervous system.

Exercise

When bacteria are destroyed by leuckocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

Answer

Pyrogens increase body temperature by causing the blood vessels to constrict, inducing shivering, and stopping sweat glands from secreting fluid.

The hypothalamus maintains the set point for body temperature through reflexes that cause vasodilation and sweating when the body is too warm, or vasoconstriction and shivering when the body is too cold. It responds to chemicals from the body. When a bacterium is destroyed by phagocytic leukocytes, chemicals called endogenous pyrogens are released into the blood. These pyrogens circulate to the hypothalamus and reset the thermostat. This allows the body's temperature to increase in what is commonly called a fever. An increase in body temperature causes iron to be conserved, which reduces a nutrient needed by bacteria. An increase in body heat also increases the activity of the animal's enzymes and protective cells while inhibiting the enzymes and activity of the invading microorganisms. Finally, heat itself may also kill the pathogen. A fever that was once thought to be a complication of an infection is now understood to be a normal defense mechanism.

Summary

Homeostasis is a dynamic equilibrium that is maintained in body tissues and organs. It is dynamic because it is constantly adjusting to the changes that the systems encounter. It is in equilibrium because body functions are kept within a normal range, with some fluctuations around a set point for the processes.

Glossary

acclimatization
alteration in a body system in response to environmental change

alteration
change of the set point in a homeostatic system

homeostasis
dynamic equilibrium maintaining appropriate body functions

negative feedback loop
feedback to a control mechanism that increases or decreases a stimulus instead of maintaining it

positive feedback loop
feedback to a control mechanism that continues the direction of a stimulus

set point
midpoint or target point in homeostasis

thermoregulation
regulation of body temperature

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41.8: Regulating Body Temperature

Skills to Develop

- Describe the various types of body plans that occur in animals
- Describe limits on animal size and shape
- Relate bioenergetics to body size, levels of activity, and the environment

Animals vary in form and function. From a sponge to a worm to a goat, an organism has a distinct body plan that limits its size and shape. Animals' bodies are also designed to interact with their environments, whether in the deep sea, a rainforest canopy, or the desert. Therefore, a large amount of information about the structure of an organism's body (anatomy) and the function of its cells, tissues and organs (physiology) can be learned by studying that organism's environment.

Body Plans

Animal body plans follow set patterns related to symmetry. They are asymmetrical, radial, or bilateral in form as illustrated in Figure **41.8.1**. Asymmetrical animals are animals with no pattern or symmetry; an example of an asymmetrical animal is a sponge. Radial symmetry, as illustrated in Figure **41.8.1**, describes when an animal has an up-and-down orientation: any plane cut along its longitudinal axis through the organism produces equal halves, but not a definite right or left side. This plan is found mostly in aquatic animals, especially organisms that attach themselves to a base, like a rock or a boat, and extract their food from the surrounding water as it flows around the organism. Bilateral symmetry is illustrated in the same figure by a goat. The goat also has an upper and lower component to it, but a plane cut from front to back separates the animal into definite right and left sides. Additional terms used when describing positions in the body are anterior (front), posterior (rear), dorsal (toward the back), and ventral (toward the stomach). Bilateral symmetry is found in both land-based and aquatic animals; it enables a high level of mobility.

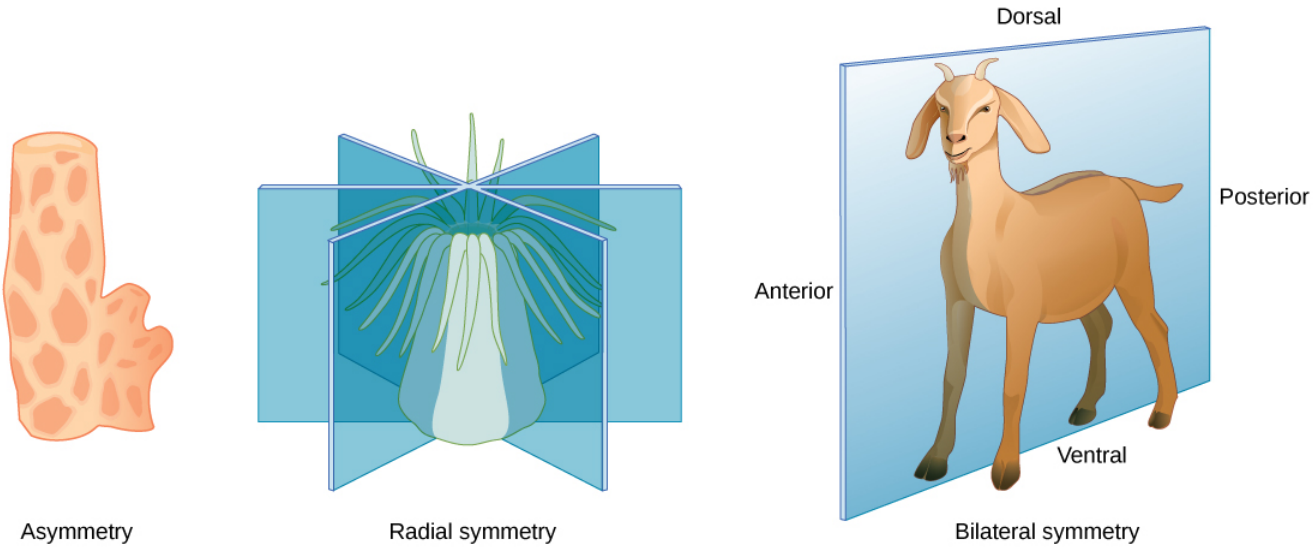


Figure **41.8.1**: Animals exhibit different types of body symmetry. The sponge is asymmetrical, the sea anemone has radial symmetry, and the goat has bilateral symmetry.

Limits on Animal Size and Shape

Animals with bilateral symmetry that live in water tend to have a fusiform shape: this is a tubular shaped body that is tapered at both ends. This shape decreases the drag on the body as it moves through water and allows the animal to swim at high speeds. The table below lists the maximum speed of various animals. Certain types of sharks can swim at fifty kilometers an hour and some dolphins at 32 to 40 kilometers per hour. Land animals frequently travel faster, although the tortoise and snail are significantly slower than cheetahs. Another difference in the adaptations of aquatic and land-dwelling organisms is that aquatic organisms are constrained in shape by the forces of drag in the water since water has higher viscosity than air. On the other hand, land-dwelling

organisms are constrained mainly by gravity, and drag is relatively unimportant. For example, most adaptations in birds are for gravity not for drag.

Table 41.8.1: Maximum Speed of Assorted Land and Marine Animals

Animal	Speed (kmh)	Speed (mph)
Cheetah	113	70
Quarter horse	77	48
Fox	68	42
Shortfin mako shark	50	31
Domestic house cat	48	30
Human	45	28
Dolphin	32–40	20–25
Mouse	13	8
Snail	0.05	0.03

Most animals have an exoskeleton, including insects, spiders, scorpions, horseshoe crabs, centipedes, and crustaceans. Scientists estimate that, of insects alone, there are over 30 million species on our planet. The exoskeleton is a hard covering or shell that provides benefits to the animal, such as protection against damage from predators and from water loss (for land animals); it also provides for the attachments of muscles.

As the tough and resistant outer cover of an arthropod, the exoskeleton may be constructed of a tough polymer such as chitin and is often biomineralized with materials such as calcium carbonate. This is fused to the animal's epidermis. Ingrowths of the exoskeleton, called apodemes, function as attachment sites for muscles, similar to tendons in more advanced animals (Figure 41.8.2). In order to grow, the animal must first synthesize a new exoskeleton underneath the old one and then shed or molt the original covering. This limits the animal's ability to grow continually, and may limit the individual's ability to mature if molting does not occur at the proper time. The thickness of the exoskeleton must be increased significantly to accommodate any increase in weight. It is estimated that a doubling of body size increases body weight by a factor of eight. The increasing thickness of the chitin necessary to support this weight limits most animals with an exoskeleton to a relatively small size. The same principles apply to endoskeletons, but they are more efficient because muscles are attached on the outside, making it easier to compensate for increased mass.

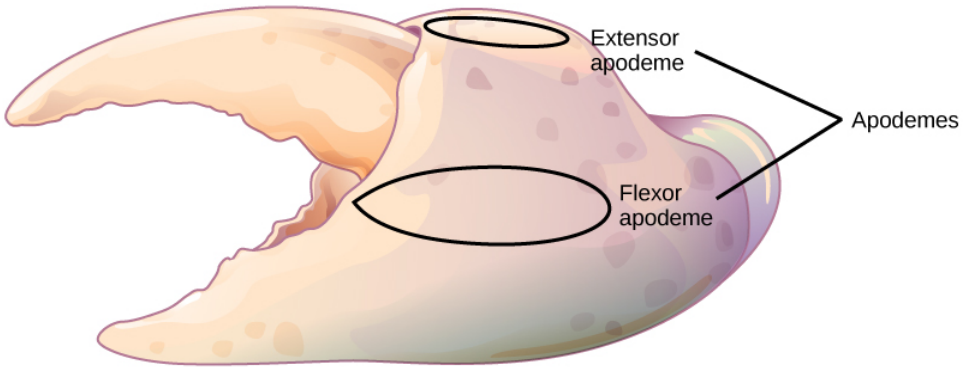


Figure 41.8.2: Apodemes are ingrowths on arthropod exoskeletons to which muscles attach. The apodemes on this crab leg are located above and below the fulcrum of the claw. Contraction of muscles attached to the apodemes pulls the claw closed.

An animal with an endoskeleton has its size determined by the amount of skeletal system it needs in order to support the other tissues and the amount of muscle it needs for movement. As the body size increases, both bone and muscle mass increase. The speed achievable by the animal is a balance between its overall size and the bone and muscle that provide support and movement.

Limiting Effects of Diffusion on Size and Development

The exchange of nutrients and wastes between a cell and its watery environment occurs through the process of diffusion. All living cells are bathed in liquid, whether they are in a single-celled organism or a multicellular one. Diffusion is effective over a specific distance and limits the size that an individual cell can attain. If a cell is a single-celled microorganism, such as an amoeba, it can satisfy all of its nutrient and waste needs through diffusion. If the cell is too large, then diffusion is ineffective and the center of the cell does not receive adequate nutrients nor is it able to effectively dispel its waste.

An important concept in understanding how efficient diffusion is as a means of transport is the surface to volume ratio. Recall that any three-dimensional object has a surface area and volume; the ratio of these two quantities is the surface-to-volume ratio. Consider a cell shaped like a perfect sphere: it has a surface area of $4\pi r^2$, and a volume of $(4/3)\pi r^3$. The surface-to-volume ratio of a sphere is 3/r; as the cell gets bigger, its surface to volume ratio decreases, making diffusion less efficient. The larger the size of the sphere, or animal, the less surface area for diffusion it possesses.

The solution to producing larger organisms is for them to become multicellular. Specialization occurs in complex organisms, allowing cells to become more efficient at doing fewer tasks. For example, circulatory systems bring nutrients and remove waste, while respiratory systems provide oxygen for the cells and remove carbon dioxide from them. Other organ systems have developed further specialization of cells and tissues and efficiently control body functions. Moreover, surface-to-volume ratio applies to other areas of animal development, such as the relationship between muscle mass and cross-sectional surface area in supporting skeletons, and in the relationship between muscle mass and the generation of dissipation of heat.

Animal Bioenergetics

All animals must obtain their energy from food they ingest or absorb. These nutrients are converted to adenosine triphosphate (ATP) for short-term storage and use by all cells. Some animals store energy for slightly longer times as glycogen, and others store energy for much longer times in the form of triglycerides housed in specialized adipose tissues. No energy system is one hundred percent efficient, and an animal's metabolism produces waste energy in the form of heat. If an animal can conserve that heat and maintain a relatively constant body temperature, it is classified as a warm-blooded animal and called an endotherm. The insulation used to conserve the body heat comes in the forms of fur, fat, or feathers. The absence of insulation in ectothermic animals increases their dependence on the environment for body heat.

The amount of energy expended by an animal over a specific time is called its metabolic rate. The rate is measured variously in joules, calories, or kilocalories (1000 calories). Carbohydrates and proteins contain about 4.5 to 5 kcal/g, and fat contains about 9 kcal/g. Metabolic rate is estimated as the basal metabolic rate (BMR) in endothermic animals at rest and as the standard metabolic rate (SMR) in ectotherms. Human males have a BMR of 1600 to 1800 kcal/day, and human females have a BMR of 1300 to 1500 kcal/day. Even with insulation, endothermal animals require extensive amounts of energy to maintain a constant body temperature. An ectotherm such as an alligator has an SMR of 60 kcal/day.

Energy Requirements Related to Body Size

Smaller endothermic animals have a greater surface area for their mass than larger ones (Figure **41.8.3**). Therefore, smaller animals lose heat at a faster rate than larger animals and require more energy to maintain a constant internal temperature. This results in a smaller endothermic animal having a higher BMR, per body weight, than a larger endothermic animal.

Species		
Mass	35 g	4,500,000 g
Metabolic rate	890 mm^3 0_2/g body mass/hr	75 mm^3 0_2/g body mass/hr

Figure **41.8.3**: The mouse has a much higher metabolic rate than the elephant. (credit "mouse": modification of work by Magnus Kjaergaard; credit "elephant": modification of work by "TheLizardQueen"/Flickr)

Energy Requirements Related to Levels of Activity

The more active an animal is, the more energy is needed to maintain that activity, and the higher its BMR or SMR. The average daily rate of energy consumption is about two to four times an animal's BMR or SMR. Humans are more sedentary than most animals and have an average daily rate of only 1.5 times the BMR. The diet of an endothermic animal is determined by its BMR. For example: the type of grasses, leaves, or shrubs that an herbivore eats affects the number of calories that it takes in. The relative caloric content of herbivore foods, in descending order, is tall grasses > legumes > short grasses > forbs (any broad-leaved plant, not a grass) > subshrubs > annuals/biennials.

Energy Requirements Related to Environment

Animals adapt to extremes of temperature or food availability through torpor. Torpor is a process that leads to a decrease in activity and metabolism and allows animals to survive adverse conditions. Torpor can be used by animals for long periods, such as entering a state of hibernation during the winter months, in which case it enables them to maintain a reduced body temperature. During hibernation, ground squirrels can achieve an abdominal temperature of 0° C (32° F), while a bear's internal temperature is maintained higher at about 37° C (99° F).

If torpor occurs during the summer months with high temperatures and little water, it is called estivation. Some desert animals use this to survive the harshest months of the year. Torpor can occur on a daily basis; this is seen in bats and hummingbirds. While endothermy is limited in smaller animals by surface to volume ratio, some organisms can be smaller and still be endotherms because they employ daily torpor during the part of the day that is coldest. This allows them to conserve energy during the colder parts of the day, when they consume more energy to maintain their body temperature.

Animal Body Planes and Cavities

A standing vertebrate animal can be divided by several planes. A sagittal plane divides the body into right and left portions. A midsagittal plane divides the body exactly in the middle, making two equal right and left halves. A frontal plane (also called a coronal plane) separates the front from the back. A transverse plane (or, horizontal plane) divides the animal into upper and lower portions. This is sometimes called a cross section, and, if the transverse cut is at an angle, it is called an oblique plane. Figure **41.8.4** illustrates these planes on a goat (a four-legged animal) and a human being.

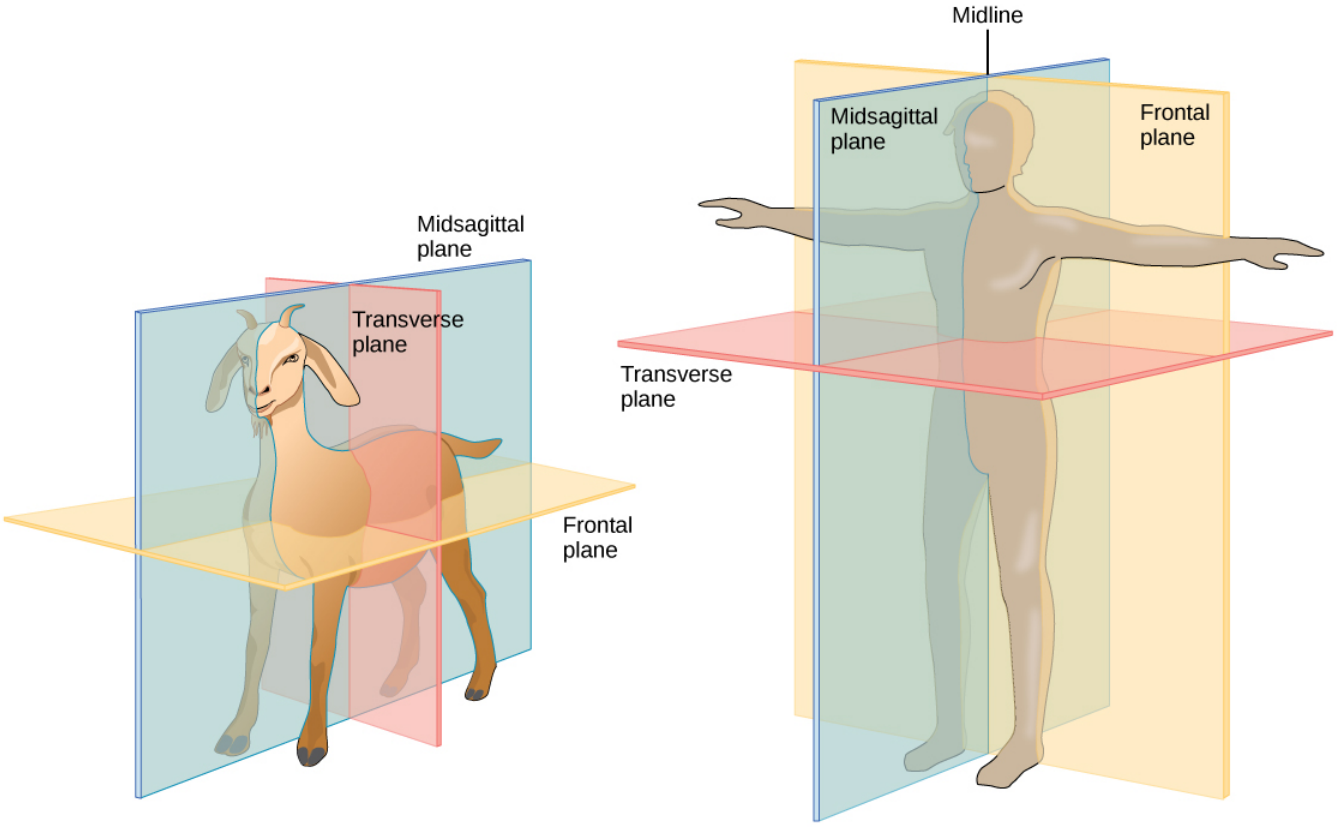


Figure **41.8.4**: Shown are the planes of a quadruped goat and a bipedal human. The midsagittal plane divides the body exactly in half, into right and left portions. The frontal plane divides the front and back, and the transverse plane divides the body into upper and lower portions.

Vertebrate animals have a number of defined body cavities, as illustrated in Figure **41.8.5**. Two of these are major cavities that contain smaller cavities within them. The dorsal cavity contains the cranial and the vertebral (or spinal) cavities. The ventral cavity contains the thoracic cavity, which in turn contains the pleural cavity around the lungs and the pericardial cavity, which surrounds the heart. The ventral cavity also contains the abdominopelvic cavity, which can be separated into the abdominal and the pelvic cavities.

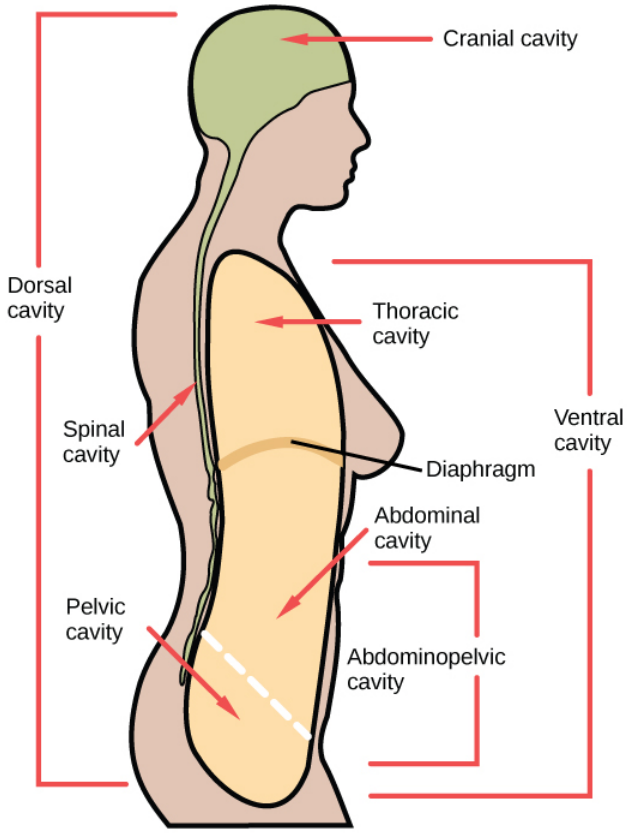


Figure 41.8.5: Vertebrate animals have two major body cavities. The dorsal cavity, indicated in green, contains the cranial and the spinal cavity. The ventral cavity, indicated in yellow, contains the thoracic cavity and the abdominopelvic cavity. The thoracic cavity is separated from the abdominopelvic cavity by the diaphragm. The thoracic cavity is separated into the abdominal cavity and the pelvic cavity by an imaginary line parallel to the pelvis bones. (credit: modification of work by NCI)

Career Connections: Physical Anthropologist

Physical anthropologists study the adaption, variability, and evolution of human beings, plus their living and fossil relatives. They can work in a variety of settings, although most will have an academic appointment at a university, usually in an anthropology department or a biology, genetics, or zoology department.

Non-academic positions are available in the automotive and aerospace industries where the focus is on human size, shape, and anatomy. Research by these professionals might range from studies of how the human body reacts to car crashes to exploring how to make seats more comfortable. Other non-academic positions can be obtained in museums of natural history, anthropology, archaeology, or science and technology. These positions involve educating students from grade school through graduate school. Physical anthropologists serve as education coordinators, collection managers, writers for museum publications, and as administrators. Zoos employ these professionals, especially if they have an expertise in primate biology; they work in collection management and captive breeding programs for endangered species. Forensic science utilizes physical anthropology expertise in identifying human and animal remains, assisting in determining the cause of death, and for expert testimony in trials.

Summary

Animal bodies come in a variety of sizes and shapes. Limits on animal size and shape include impacts to their movement. Diffusion affects their size and development. Bioenergetics describes how animals use and obtain energy in relation to their body size, activity level, and environment.

Glossary

apodeme
ingrowth of an animal’s exoskeleton that functions as an attachment site for muscles

asymmetrical
describes animals with no axis of symmetry in their body pattern

basal metabolic rate (BMR)
metabolic rate at rest in endothermic animals

dorsal cavity
body cavity on the posterior or back portion of an animal; includes the cranial and vertebral cavities

ectotherm
animal incapable of maintaining a relatively constant internal body temperature

endotherm
animal capable of maintaining a relatively constant internal body temperature

estivation
torpor in response to extremely high temperatures and low water availability

frontal (coronal) plane
plane cutting through an animal separating the individual into front and back portions

fusiform
animal body shape that is tubular and tapered at both ends

hibernation
torpor over a long period of time, such as a winter

midsagittal plane
plane cutting through an animal separating the individual into even right and left sides

sagittal plane
plane cutting through an animal separating the individual into right and left sides

standard metabolic rate (SMR)
metabolic rate at rest in ectothermic animals

torpor
decrease in activity and metabolism that allows an animal to survive adverse conditions

transverse (horizontal) plane
plane cutting through an animal separating the individual into upper and lower portions

ventral cavity
body cavity on the anterior or front portion of an animal that includes the thoracic cavities and the abdominopelvic cavities

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41.8.1: Homeostasis

Skills to Develop

- Define homeostasis
- Describe the factors affecting homeostasis
- Discuss positive and negative feedback mechanisms used in homeostasis
- Describe thermoregulation of endothermic and ectothermic animals

Animal organs and organ systems constantly adjust to internal and external changes through a process called homeostasis (“steady state”). These changes might be in the level of glucose or calcium in blood or in external temperatures. Homeostasis means to maintain dynamic equilibrium in the body. It is dynamic because it is constantly adjusting to the changes that the body’s systems encounter. It is equilibrium because body functions are kept within specific ranges. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium.

Homeostatic Process

The goal of homeostasis is the maintenance of equilibrium around a point or value called a set point. While there are normal fluctuations from the set point, the body’s systems will usually attempt to go back to this point. A change in the internal or external environment is called a stimulus and is detected by a receptor; the response of the system is to adjust the deviation parameter toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If the blood’s glucose rises after a meal, adjustments are made to lower the blood glucose level by getting the nutrient into tissues that need it or to store it for later use.

Control of Homeostasis

When a change occurs in an animal’s environment, an adjustment must be made. The receptor senses the change in the environment, then sends a signal to the control center (in most cases, the brain) which in turn generates a response that is signaled to an effector. The effector is a muscle (that contracts or relaxes) or a gland that secretes. Homeostatsis is maintained by negative feedback loops. Positive feedback loops actually push the organism further out of homeostasis, but may be necessary for life to occur. Homeostasis is controlled by the nervous and endocrine system of mammals.

Negative Feedback Mechanisms

Any homeostatic process that changes the direction of the stimulus is a negative feedback loop. It may either increase or decrease the stimulus, but the stimulus is not allowed to continue as it did before the receptor sensed it. In other words, if a level is too high, the body does something to bring it down, and conversely, if a level is too low, the body does something to make it go up. Hence the term negative feedback. An example is animal maintenance of blood glucose levels. When an animal has eaten, blood glucose levels rise. This is sensed by the nervous system. Specialized cells in the pancreas sense this, and the hormone insulin is released by the endocrine system. Insulin causes blood glucose levels to decrease, as would be expected in a negative feedback system, as illustrated in Figure **41.8.1.1**. However, if an animal has not eaten and blood glucose levels decrease, this is sensed in another group of cells in the pancreas, and the hormone glucagon is released causing glucose levels to increase. This is still a negative feedback loop, but not in the direction expected by the use of the term “negative.” Another example of an increase as a result of the feedback loop is the control of blood calcium. If calcium levels decrease, specialized cells in the parathyroid gland sense this and release parathyroid hormone (PTH), causing an increased absorption of calcium through the intestines and kidneys and, possibly, the breakdown of bone in order to liberate calcium. The effects of PTH are to raise blood levels of the element. Negative feedback loops are the predominant mechanism used in homeostasis.

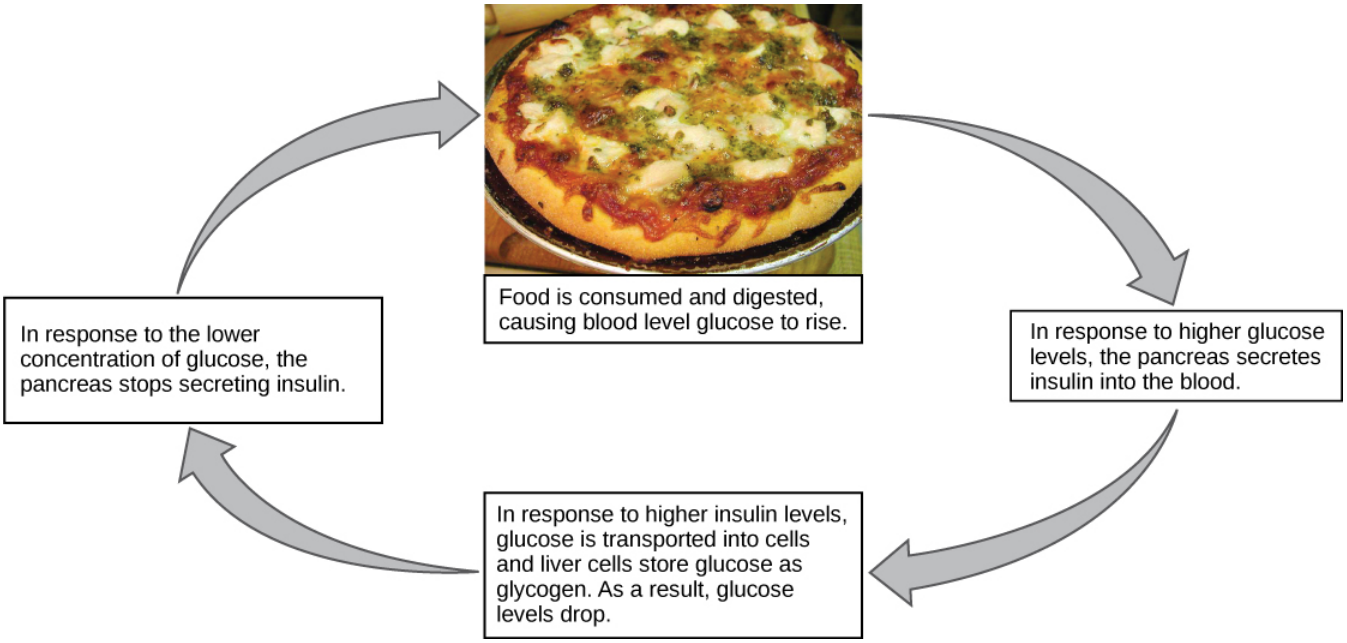


Figure **41.8.1.1**: Blood sugar levels are controlled by a negative feedback loop. (credit: modification of work by Jon Sullivan)

Positive Feedback Loop

A positive feedback loop maintains the direction of the stimulus, possibly accelerating it. Few examples of positive feedback loops exist in animal bodies, but one is found in the cascade of chemical reactions that result in blood clotting, or coagulation. As one clotting factor is activated, it activates the next factor in sequence until a fibrin clot is achieved. The direction is maintained, not changed, so this is positive feedback. Another example of positive feedback is uterine contractions during childbirth, as illustrated in Figure **41.8.1.2**. The hormone oxytocin, made by the endocrine system, stimulates the contraction of the uterus. This produces pain sensed by the nervous system. Instead of lowering the oxytocin and causing the pain to subside, more oxytocin is produced until the contractions are powerful enough to produce childbirth.

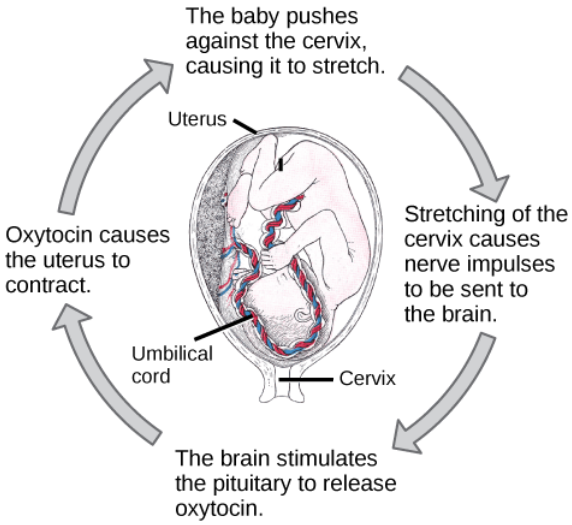


Figure **41.8.1.2**: The birth of a human infant is the result of positive feedback.

Exercise

State whether each of the following processes is regulated by a positive feedback loop or a negative feedback loop.

A. A person feels satiated after eating a large meal.
B. The blood has plenty of red blood cells. As a result, erythropoietin, a hormone that stimulates the production of new red blood cells, is no longer released from the kidney.

Answer

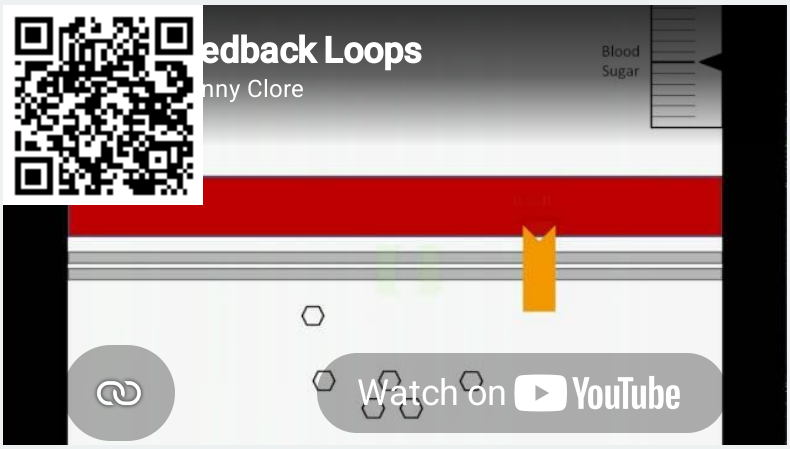
Both processes are the result of negative feedback loops. Negative feedback loops, which tend to keep a system at equilibrium, are more common than positive feedback loops.

Set Point

It is possible to adjust a system's set point. When this happens, the feedback loop works to maintain the new setting. An example of this is blood pressure: over time, the normal or set point for blood pressure can increase as a result of continued increases in blood pressure. The body no longer recognizes the elevation as abnormal and no attempt is made to return to the lower set point. The result is the maintenance of an elevated blood pressure that can have harmful effects on the body. Medication can lower blood pressure and lower the set point in the system to a more healthy level. This is called a process of alteration of the set point in a feedback loop.

Changes can be made in a group of body organ systems in order to maintain a set point in another system. This is called acclimatization. This occurs, for instance, when an animal migrates to a higher altitude than it is accustomed to. In order to adjust to the lower oxygen levels at the new altitude, the body increases the number of red blood cells circulating in the blood to ensure adequate oxygen delivery to the tissues. Another example of acclimatization is animals that have seasonal changes in their coats: a heavier coat in the winter ensures adequate heat retention, and a light coat in summer assists in keeping body temperature from rising to harmful levels.

Link to Learning



Feedback mechanisms can be understood in terms of driving a race car along a track: watch a short video lesson on positive and negative feedback loops.

Homeostasis: Thermoregulation

Body temperature affects body activities. Generally, as body temperature rises, enzyme activity rises as well. For every ten degree centigrade rise in temperature, enzyme activity doubles, up to a point. Body proteins, including enzymes, begin to denature and lose their function with high heat (around 50^{o}C for mammals). Enzyme activity will decrease by half for every ten degree centigrade drop in temperature, to the point of freezing, with a few exceptions. Some fish can withstand freezing solid and return to normal with thawing.

Link to Learning



Watch this Discovery Channel video on thermoregulation to see illustrations of this process in a variety of animals.

Endotherms and Ectotherms

Animals can be divided into two groups: some maintain a constant body temperature in the face of differing environmental temperatures, while others have a body temperature that is the same as their environment and thus varies with the environment. Animals that do not control their body temperature are ectotherms. This group has been called cold-blooded, but the term may not apply to an animal in the desert with a very warm body temperature. In contrast to ectotherms, which rely on external temperatures to set their body temperatures, poikilotherms are animals with constantly varying internal temperatures. An animal that maintains a constant body temperature in the face of environmental changes is called a homeotherm. Endotherms are animals that rely on internal sources for body temperature but which can exhibit extremes in temperature. These animals are able to maintain a level of activity at cooler temperature, which an ectotherm cannot due to differing enzyme levels of activity.

Heat can be exchanged between an animal and its environment through four mechanisms: radiation, evaporation, convection, and conduction (Figure **41.8.1.3**). Radiation is the emission of electromagnetic "heat" waves. Heat comes from the sun in this manner and radiates from dry skin the same way. Heat can be removed with liquid from a surface during evaporation. This occurs when a mammal sweats. Convection currents of air remove heat from the surface of dry skin as the air passes over it. Heat will be conducted from one surface to another during direct contact with the surfaces, such as an animal resting on a warm rock.



(a) Radiation (b) Evaporation



(c) Convection (d) Conduction

Figure **41.8.1.3**: Heat can be exchanged by four mechanisms: (a) radiation, (b) evaporation, (c) convection, or (d) conduction. (credit b: modification of work by “Kullez”/Flickr; credit c: modification of work by Chad Rosenthal; credit d: modification of work by “stacey.d”/Flickr)

Heat Conservation and Dissipation

Animals conserve or dissipate heat in a variety of ways. In certain climates, endothermic animals have some form of insulation, such as fur, fat, feathers, or some combination thereof. Animals with thick fur or feathers create an insulating layer of air between their skin and internal organs. Polar bears and seals live and swim in a subfreezing environment and yet maintain a constant, warm, body temperature. The arctic fox, for example, uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals have a residual effect from shivering and increased muscle activity: arrector pili muscles cause “goose bumps,” causing small hairs to stand up when the individual is cold; this has the intended effect of increasing body temperature. Mammals use layers of fat to achieve the same end. Loss of significant amounts of body fat will compromise an individual’s ability to conserve heat.

Endotherms use their circulatory systems to help maintain body temperature. Vasodilation brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, which helps to cool the body. Vasoconstriction reduces blood flow in peripheral blood vessels, forcing blood toward the core and the vital organs found there, and conserving heat. Some animals have adaptions to their circulatory system that enable them to transfer heat from arteries to veins, warming blood returning to the heart. This is called a countercurrent heat exchange; it prevents the cold venous blood from cooling the heart and other internal organs. This adaption can be shut down in some animals to prevent overheating the internal organs. The countercurrent adaption is found in many animals, including dolphins, sharks, bony fish, bees, and hummingbirds. In contrast, similar adaptations can help cool endotherms when needed, such as dolphin flukes and elephant ears.

Some ectothermic animals use changes in their behavior to help regulate body temperature. For example, a desert ectothermic animal may simply seek cooler areas during the hottest part of the day in the desert to keep from getting too warm. The same animals may climb onto rocks to capture heat during a cold desert night. Some animals seek water to aid evaporation in cooling them, as seen with reptiles. Other ectotherms use group activity such as the activity of bees to warm a hive to survive winter.

Many animals, especially mammals, use metabolic waste heat as a heat source. When muscles are contracted, most of the energy from the ATP used in muscle actions is wasted energy that translates into heat. Severe cold elicits a shivering reflex that generates heat for the body. Many species also have a type of adipose tissue called brown fat that specializes in generating heat.

Neural Control of Thermoregulation

The nervous system is important to thermoregulation, as illustrated in Figure **41.8.1.4**. The processes of homeostasis and temperature control are centered in the hypothalamus of the advanced animal brain.

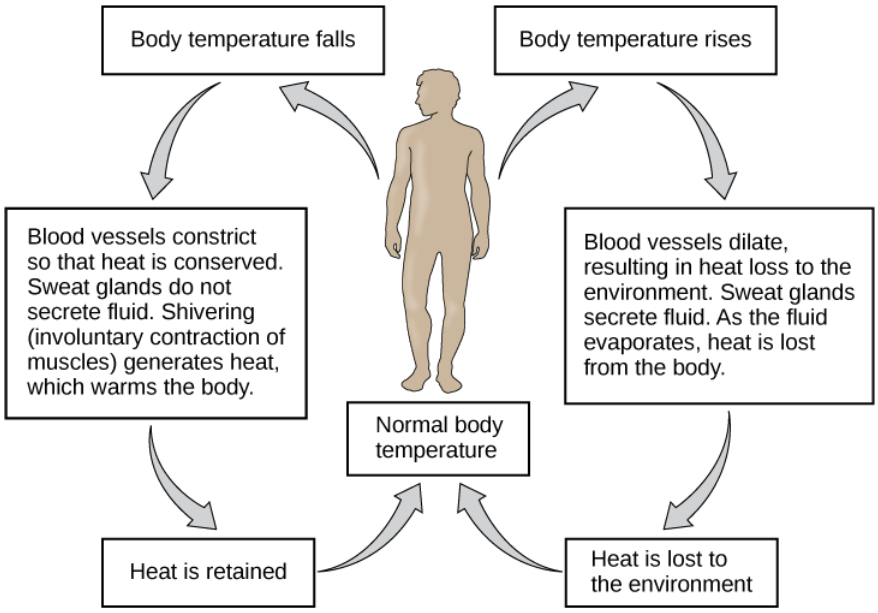


Figure **41.8.1.4**: The body is able to regulate temperature in response to signals from the nervous system.

Exercise

When bacteria are destroyed by leuckocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

Answer

Pyrogens increase body temperature by causing the blood vessels to constrict, inducing shivering, and stopping sweat glands from secreting fluid.

The hypothalamus maintains the set point for body temperature through reflexes that cause vasodilation and sweating when the body is too warm, or vasoconstriction and shivering when the body is too cold. It responds to chemicals from the body. When a bacterium is destroyed by phagocytic leukocytes, chemicals called endogenous pyrogens are released into the blood. These pyrogens circulate to the hypothalamus and reset the thermostat. This allows the body's temperature to increase in what is commonly called a fever. An increase in body temperature causes iron to be conserved, which reduces a nutrient needed by bacteria. An increase in body heat also increases the activity of the animal's enzymes and protective cells while inhibiting the enzymes and activity of the invading microorganisms. Finally, heat itself may also kill the pathogen. A fever that was once thought to be a complication of an infection is now understood to be a normal defense mechanism.

Summary

Homeostasis is a dynamic equilibrium that is maintained in body tissues and organs. It is dynamic because it is constantly adjusting to the changes that the systems encounter. It is in equilibrium because body functions are kept within a normal range, with some fluctuations around a set point for the processes.

Glossary

acclimatization
: alteration in a body system in response to environmental change

alteration
: change of the set point in a homeostatic system

homeostasis
: dynamic equilibrium maintaining appropriate body functions

negative feedback loop
: feedback to a control mechanism that increases or decreases a stimulus instead of maintaining it

positive feedback loop
: feedback to a control mechanism that continues the direction of a stimulus

set point
: midpoint or target point in homeostasis

thermoregulation
: regulation of body temperature

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CHAPTER OVERVIEW

42: The Nervous System

42.1: The Nervous System Organization

42.1.1: The Peripheral Nervous System

42.2: The Mechanism of Nerve Impulse Transmission

42.2.1: Sensory Processes

42.3: Synapses- Where Neurons Communicate With Other Cells

42.4: The Central Nervous System- Brain and Spinal Cord

42.5: The Peripheral Nervous System- Spinal and Cranial Nerves

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42.1: The Nervous System Organization

Skills to Develop

- List and describe the functions of the structural components of a neuron
- List and describe the four main types of neurons
- Compare the functions of different types of glial cells

Nervous systems throughout the animal kingdom vary in structure and complexity, as illustrated by the variety of animals shown in Figure 42.1.1. Some organisms, like sea sponges, lack a true nervous system. Others, like jellyfish, lack a true brain and instead have a system of separate but connected nerve cells (neurons) called a "nerve net." Echinoderms such as sea stars have nerve cells that are bundled into fibers called nerves. Flatworms of the phylum Platyhelminthes have both a central nervous system (CNS), made up of a small "brain" and two nerve cords, and a peripheral nervous system (PNS) containing a system of nerves that extend throughout the body. The insect nervous system is more complex but also fairly decentralized. It contains a brain, ventral nerve cord, and ganglia (clusters of connected neurons). These ganglia can control movements and behaviors without input from the brain. Octopi may have the most complicated of invertebrate nervous systems—they have neurons that are organized in specialized lobes and eyes that are structurally similar to vertebrate species.

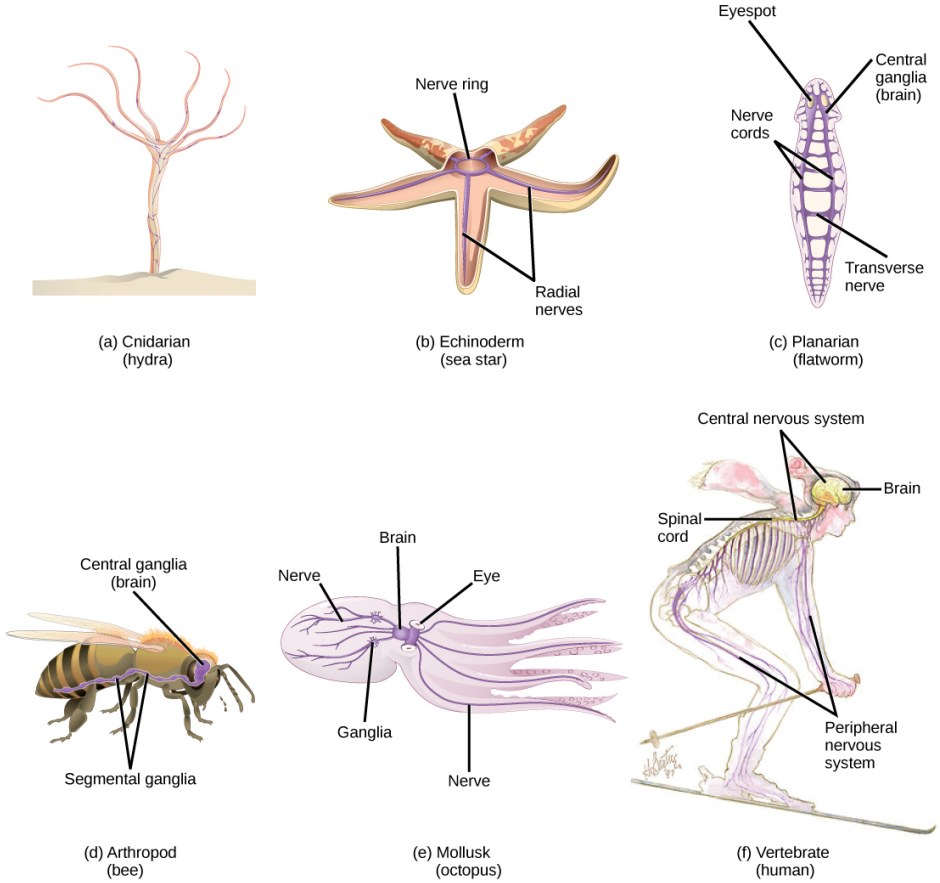


Figure 42.1.1: Nervous systems vary in structure and complexity. In (a) cnidarians, nerve cells form a decentralized nerve net. In (b) echinoderms, nerve cells are bundled into fibers called nerves. In animals exhibiting bilateral symmetry such as (c) planarians, neurons cluster into an anterior brain that processes information. In addition to a brain, (d) arthropods have clusters of nerve cell bodies, called peripheral ganglia, located along the ventral nerve cord. Mollusks such as squid and (e) octopi, which must hunt to survive, have complex brains containing millions of neurons. In (f) vertebrates, the brain and spinal cord comprise the central nervous system, while neurons extending into the rest of the body comprise the peripheral nervous system. (credit e: modification of work by Michael Vecchione, Clyde F.E. Roper, and Michael J. Sweeney, NOAA; credit f: modification of work by NIH).

Compared to invertebrates, vertebrate nervous systems are more complex, centralized, and specialized. While there is great diversity among different vertebrate nervous systems, they all share a basic structure: a CNS that contains a brain and spinal cord

and a PNS made up of peripheral sensory and motor nerves. One interesting difference between the nervous systems of invertebrates and vertebrates is that the nerve cords of many invertebrates are located ventrally whereas the vertebrate spinal cords are located dorsally. There is debate among evolutionary biologists as to whether these different nervous system plans evolved separately or whether the invertebrate body plan arrangement somehow "flipped" during the evolution of vertebrates.

Link to Learning



Watch this video of biologist Mark Kirschner discussing the "flipping" phenomenon of vertebrate evolution.

The nervous system is made up of neurons, specialized cells that can receive and transmit chemical or electrical signals, and glia, cells that provide support functions for the neurons by playing an information processing role that is complementary to neurons. A neuron can be compared to an electrical wire—it transmits a signal from one place to another. Glia can be compared to the workers at the electric company who make sure wires go to the right places, maintain the wires, and take down wires that are broken. Although glia have been compared to workers, recent evidence suggests that also usurp some of the signaling functions of neurons.

There is great diversity in the types of neurons and glia that are present in different parts of the nervous system. There are four major types of neurons, and they share several important cellular components.

Neurons

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors—from basic reflexes to more complicated behaviors like finding food and courting mates. The ability of neurons to communicate with each other as well as with other types of cells underlies all of these behaviors.

Most neurons share the same cellular components. But neurons are also highly specialized—different types of neurons have different sizes and shapes that relate to their functional roles.

Parts of a Neuron

Like other cells, each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components. Neurons also contain unique structures, illustrated in Figure **42.1.2** for receiving and sending the electrical signals that make neuronal communication possible. Dendrites are tree-like structures that extend away from the cell body to receive messages from other neurons at specialized junctions called synapses. Although some neurons do not have any dendrites, some types of neurons have multiple dendrites. Dendrites can have small protrusions called dendritic spines, which further increase surface area for possible synaptic connections.

Once a signal is received by the dendrite, it then travels passively to the cell body. The cell body contains a specialized structure, the axon hillock that integrates signals from multiple synapses and serves as a junction between the cell body and an axon. An axon is a tube-like structure that propagates the integrated signal to specialized endings called axon terminals. These terminals in turn synapse on other neurons, muscle, or target organs. Chemicals released at axon terminals allow signals to be communicated to

these other cells. Neurons usually have one or two axons, but some neurons, like amacrine cells in the retina, do not contain any axons. Some axons are covered with myelin, which acts as an insulator to minimize dissipation of the electrical signal as it travels down the axon, greatly increasing the speed on conduction. This insulation is important as the axon from a human motor neuron can be as long as a meter—from the base of the spine to the toes. The myelin sheath is not actually part of the neuron. Myelin is produced by glial cells. Along the axon there are periodic gaps in the myelin sheath. These gaps are called nodes of Ranvier and are sites where the signal is “recharged” as it travels along the axon.

It is important to note that a single neuron does not act alone—neuronal communication depends on the connections that neurons make with one another (as well as with other cells, like muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

Art Connection

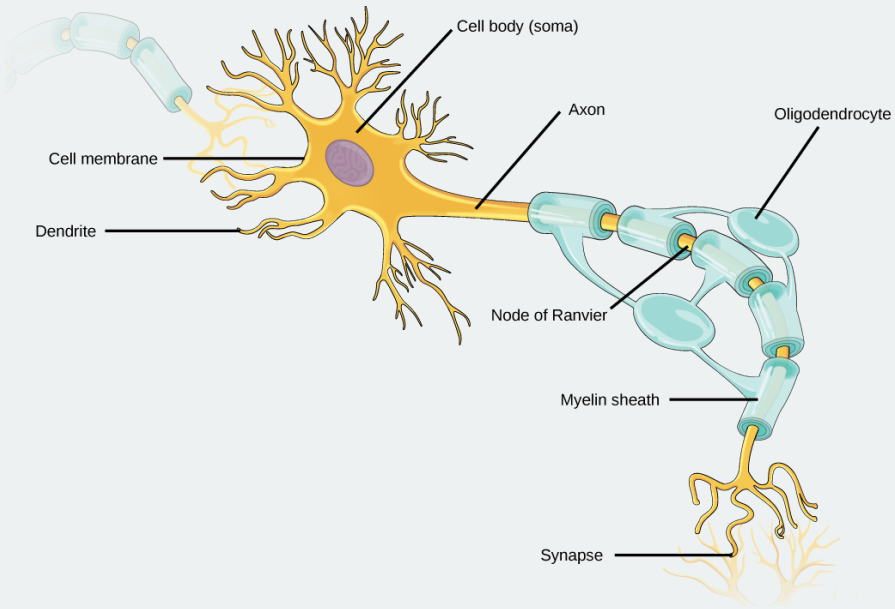


Figure 42.1.2: Neurons contain organelles common to many other cells, such as a nucleus and mitochondria. They also have more specialized structures, including dendrites and axons.

Which of the following statements is false?

A. The soma is the cell body of a nerve cell.
B. Myelin sheath provides an insulating layer to the dendrites.
C. Axons carry the signal from the soma to the target.
D. Dendrites carry the signal to the soma.

Types of Neurons

There are different types of neurons, and the functional role of a given neuron is intimately dependent on its structure. There is an amazing diversity of neuron shapes and sizes found in different parts of the nervous system (and across species), as illustrated by the neurons shown in Figure 42.1.3.

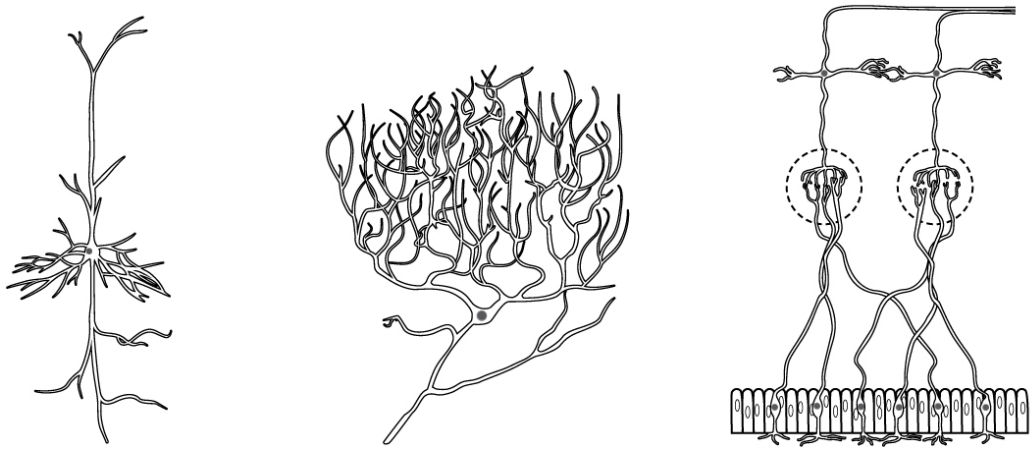


Figure 42.1.3: There is great diversity in the size and shape of neurons throughout the nervous system. Examples include (a) a pyramidal cell from the cerebral cortex, (b) a Purkinje cell from the cerebellar cortex, and (c) olfactory cells from the olfactory epithelium and olfactory bulb.

While there are many defined neuron cell subtypes, neurons are broadly divided into four basic types: unipolar, bipolar, multipolar, and pseudounipolar. Figure 42.1.4 illustrates these four basic neuron types. Unipolar neurons have only one structure that extends away from the soma. These neurons are not found in vertebrates but are found in insects where they stimulate muscles or glands. A bipolar neuron has one axon and one dendrite extending from the soma. An example of a bipolar neuron is a retinal bipolar cell, which receives signals from photoreceptor cells that are sensitive to light and transmits these signals to ganglion cells that carry the signal to the brain. Multipolar neurons are the most common type of neuron. Each multipolar neuron contains one axon and multiple dendrites. Multipolar neurons can be found in the central nervous system (brain and spinal cord). An example of a multipolar neuron is a Purkinje cell in the cerebellum, which has many branching dendrites but only one axon. Pseudounipolar cells share characteristics with both unipolar and bipolar cells. A pseudounipolar cell has a single process that extends from the soma, like a unipolar cell, but this process later branches into two distinct structures, like a bipolar cell. Most sensory neurons are pseudounipolar and have an axon that branches into two extensions: one connected to dendrites that receive sensory information and another that transmits this information to the spinal cord.

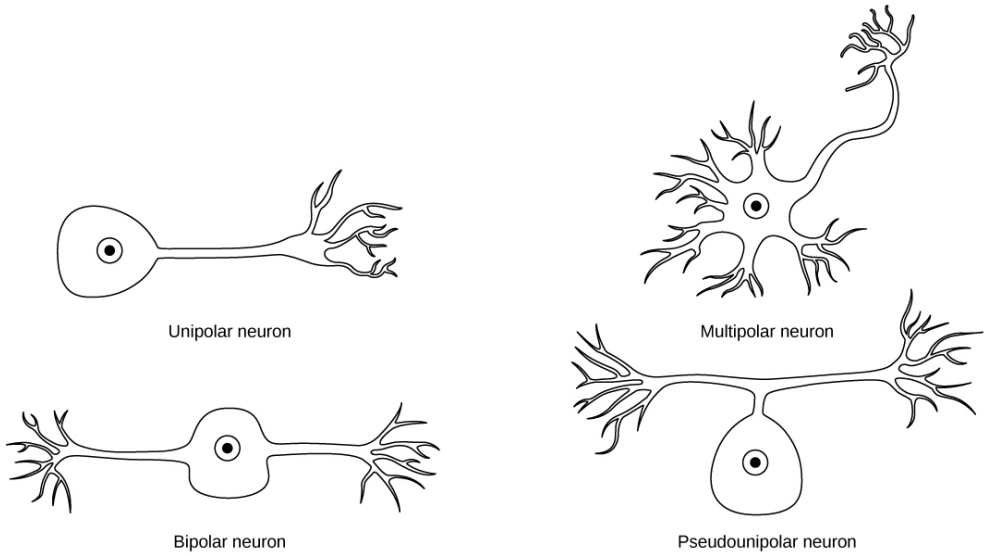


Figure 42.1.4: Neurons are broadly divided into four main types based on the number and placement of axons: (1) unipolar, (2) bipolar, (3) multipolar, and (4) pseudounipolar.

Everyday Connection: Neurogenesis

At one time, scientists believed that people were born with all the neurons they would ever have. Research performed during the last few decades indicates that neurogenesis, the birth of new neurons, continues into adulthood. Neurogenesis was first discovered in songbirds that produce new neurons while learning songs. For mammals, new neurons also play an important role in learning: about 1000 new neurons develop in the hippocampus (a brain structure involved in learning and memory) each day. While most of the new neurons will die, researchers found that an increase in the number of surviving new neurons in the hippocampus correlated with how well rats learned a new task. Interestingly, both exercise and some antidepressant medications also promote neurogenesis in the hippocampus. Stress has the opposite effect. While neurogenesis is quite limited compared to regeneration in other tissues, research in this area may lead to new treatments for disorders such as Alzheimer's, stroke, and epilepsy.

How do scientists identify new neurons? A researcher can inject a compound called bromodeoxyuridine (BrdU) into the brain of an animal. While all cells will be exposed to BrdU, BrdU will only be incorporated into the DNA of newly generated cells that are in S phase. A technique called immunohistochemistry can be used to attach a fluorescent label to the incorporated BrdU, and a researcher can use fluorescent microscopy to visualize the presence of BrdU, and thus new neurons, in brain tissue. Figure **42.1.5** is a micrograph which shows fluorescently labeled neurons in the hippocampus of a rat.

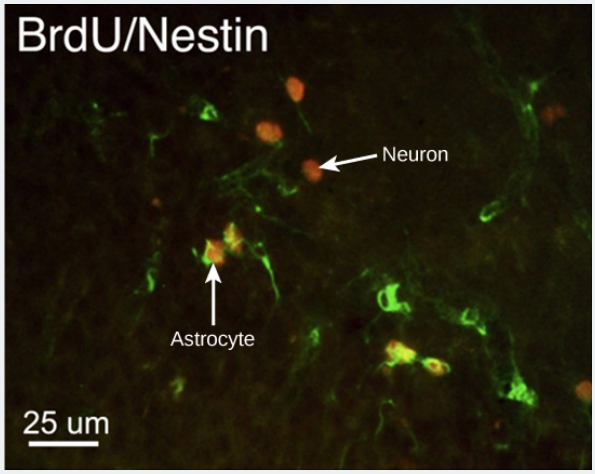


Figure **42.1.5**: This micrograph shows fluorescently labeled new neurons in a rat hippocampus. Cells that are actively dividing have bromodoxyuridine (BrdU) incorporated into their DNA and are labeled in red. Cells that express glial fibrillary acidic protein (GFAP) are labeled in green. Astrocytes, but not neurons, express GFAP. Thus, cells that are labeled both red and green are actively dividing astrocytes, whereas cells labeled red only are actively dividing neurons. (credit: modification of work by Dr. Maryam Faiz, et. al., University of Barcelona; scale-bar data from Matt Russell)

Link to Learning

This site contains more information about neurogenesis, including an interactive laboratory simulation and a video that explains how BrdU labels new cells.

Glia

While glia are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of ten. Neurons would be unable to function without the vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons, and provide myelin sheaths around axons. Scientists have recently discovered that they also play a role in responding to nerve activity and modulating communication between nerve cells. When glia do not function properly, the result can be disastrous—most brain tumors are caused by mutations in glia.

Types of Glia

There are several different types of glia with different functions, two of which are shown in Figure **42.1.6**. Astrocytes, shown in Figure **42.1.7** make contact with both capillaries and neurons in the CNS. They provide nutrients and other substances to neurons, regulate the concentrations of ions and chemicals in the extracellular fluid, and provide structural support for synapses. Astrocytes also form the blood-brain barrier—a structure that blocks entrance of toxic substances into the brain. Astrocytes, in particular, have been shown through calcium imaging experiments to become active in response to nerve activity, transmit calcium waves between astrocytes, and modulate the activity of surrounding synapses.

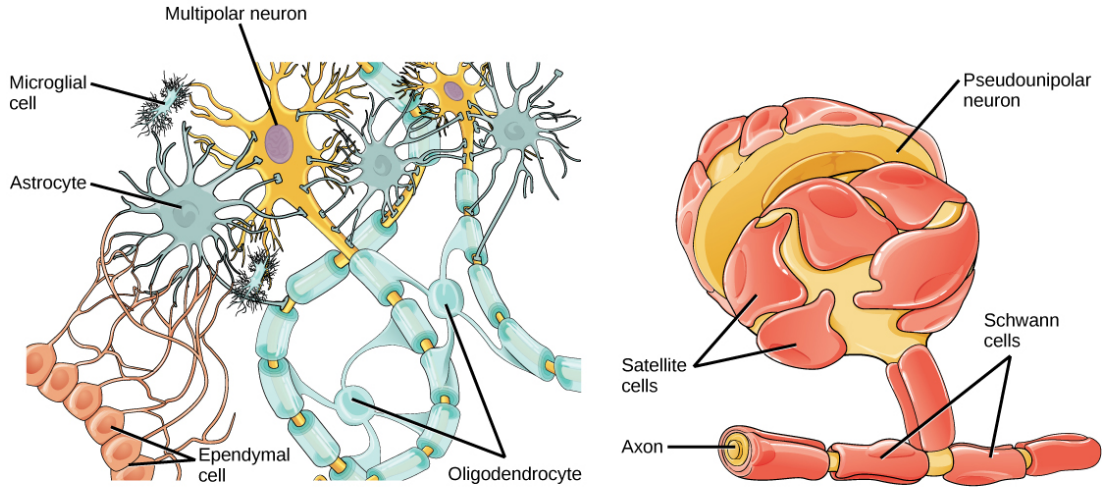
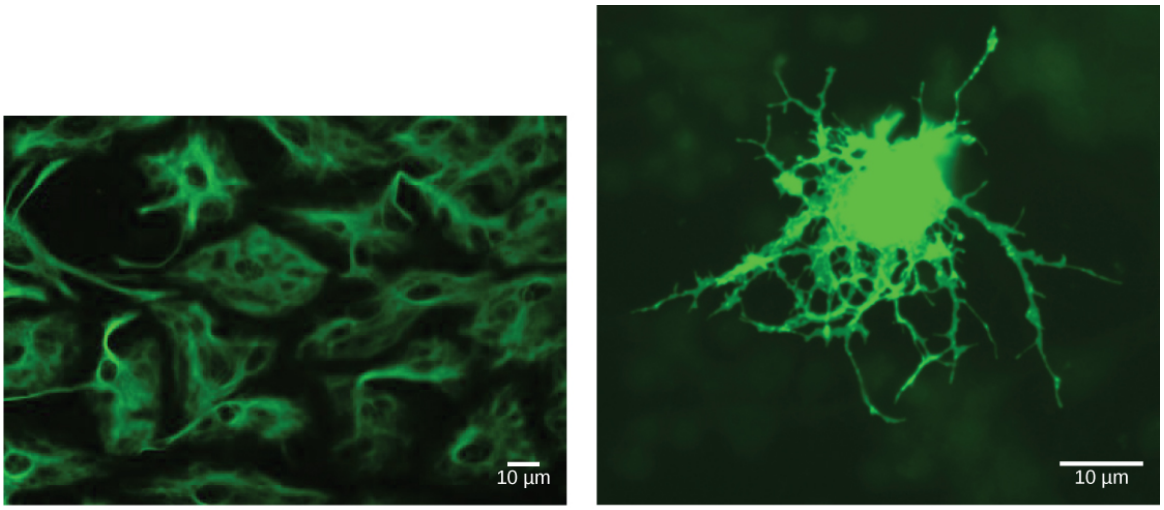


Figure **42.1.6**: Glial cells support neurons and maintain their environment. Glial cells of the (a) central nervous system include oligodendrocytes, astrocytes, ependymal cells, and microglial cells. Oligodendrocytes form the myelin sheath around axons. Astrocytes provide nutrients to neurons, maintain their extracellular environment, and provide structural support. Microglia scavenge pathogens and dead cells. Ependymal cells produce cerebrospinal fluid that cushions the neurons. Glial cells of the (b) peripheral nervous system include Schwann cells, which form the myelin sheath, and satellite cells, which provide nutrients and structural support to neurons.

Satellite glia provide nutrients and structural support for neurons in the PNS. Microglia scavenge and degrade dead cells and protect the brain from invading microorganisms. Oligodendrocytes, shown in Figure **42.1.7** form myelin sheaths around axons in the CNS. One axon can be myelinated by several oligodendrocytes, and one oligodendrocyte can provide myelin for multiple neurons. This is distinctive from the PNS where a single Schwann cell provides myelin for only one axon as the entire Schwann cell surrounds the axon. Radial glia serve as scaffolds for developing neurons as they migrate to their end destinations. Ependymal cells line fluid-filled ventricles of the brain and the central canal of the spinal cord. They are involved in the production of cerebrospinal fluid, which serves as a cushion for the brain, moves the fluid between the spinal cord and the brain, and is a component for the choroid plexus.



(a) Astrocyte (b) Oligodendrocyte

Figure 42.1.7: (a) Astrocytes and (b) oligodendrocytes are glial cells of the central nervous system. (credit a: modification of work by Uniformed Services University; credit b: modification of work by Jurjen Broeke; scale-bar data from Matt Russell)

Summary

The nervous system is made up of neurons and glia. Neurons are specialized cells that are capable of sending electrical as well as chemical signals. Most neurons contain dendrites, which receive these signals, and axons that send signals to other neurons or tissues. There are four main types of neurons: unipolar, bipolar, multipolar, and pseudounipolar neurons. Glia are non-neuronal cells in the nervous system that support neuronal development and signaling. There are several types of glia that serve different functions.

Art Connections

Figure 42.1.2: Which of the following statements is false?

A. The soma is the cell body of a nerve cell.
B. Myelin sheath provides an insulating layer to the dendrites.
C. Axons carry the signal from the soma to the target.
D. Dendrites carry the signal to the soma.

Answer

B

Glossary

astrocyte
glial cell in the central nervous system that provide nutrients, extracellular buffering, and structural support for neurons; also makes up the blood-brain barrier

axon
tube-like structure that propagates a signal from a neuron’s cell body to axon terminals

axon hillock
electrically sensitive structure on the cell body of a neuron that integrates signals from multiple neuronal connections

axon terminal
structure on the end of an axon that can form a synapse with another neuron

dendrite
structure that extends away from the cell body to receive messages from other neurons

ependymal
cell that lines fluid-filled ventricles of the brain and the central canal of the spinal cord; involved in production of cerebrospinal fluid

glia
(also, glial cells) cells that provide support functions for neurons

microglia
glia that scavenge and degrade dead cells and protect the brain from invading microorganisms

myelin
fatty substance produced by glia that insulates axons

neuron
specialized cell that can receive and transmit electrical and chemical signals

nodes of Ranvier
gaps in the myelin sheath where the signal is recharged

oligodendrocyte
glial cell that myelinates central nervous system neuron axons

radial glia
glia that serve as scaffolds for developing neurons as they migrate to their final destinations

satellite glia
glial cell that provides nutrients and structural support for neurons in the peripheral nervous system

Schwann cell
glial cell that creates myelin sheath around a peripheral nervous system neuron axon

synapse
junction between two neurons where neuronal signals are communicated

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42.1.1: The Peripheral Nervous System

Skills to Develop

- Describe the organization and functions of the sympathetic and parasympathetic nervous systems
- Describe the organization and function of the sensory-somatic nervous system

The peripheral nervous system (PNS) is the connection between the central nervous system and the rest of the body. The CNS is like the power plant of the nervous system. It creates the signals that control the functions of the body. The PNS is like the wires that go to individual houses. Without those “wires,” the signals produced by the CNS could not control the body (and the CNS would not be able to receive sensory information from the body either).

The PNS can be broken down into the autonomic nervous system, which controls bodily functions without conscious control, and the sensory-somatic nervous system, which transmits sensory information from the skin, muscles, and sensory organs to the CNS and sends motor commands from the CNS to the muscles.

Autonomic Nervous System

Art Connection

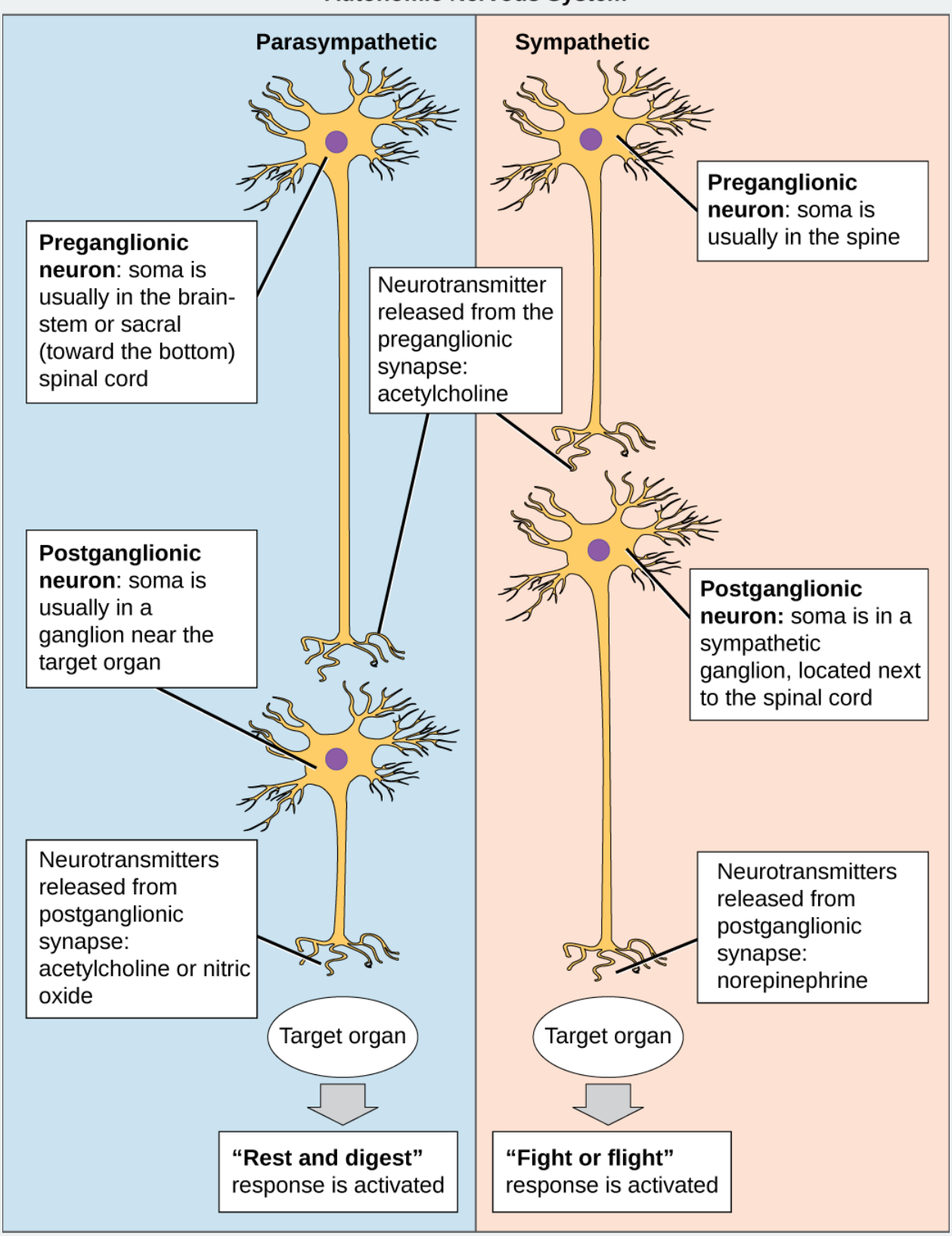


Figure 42.1.1.1: In the autonomic nervous system, a preganglionic neuron of the CNS synapses with a postganglionic neuron of the PNS. The postganglionic neuron, in turn, acts on a target organ. Autonomic responses are mediated by the sympathetic and the parasympathetic systems, which are antagonistic to one another. The sympathetic system activates the "fight or flight" response, while the parasympathetic system activates the "rest and digest" response.

https://bio.libretexts.org/@go/page/74334

Which of the following statements is false?

A. The parasympathetic pathway is responsible for resting the body, while the sympathetic pathway is responsible for preparing for an emergency.
B. Most preganglionic neurons in the sympathetic pathway originate in the spinal cord.
C. Slowing of the heartbeat is a parasympathetic response.
D. Parasympathetic neurons are responsible for releasing norepinephrine on the target organ, while sympathetic neurons are responsible for releasing acetylcholine.

The autonomic nervous system serves as the relay between the CNS and the internal organs. It controls the lungs, the heart, smooth muscle, and exocrine and endocrine glands. The autonomic nervous system controls these organs largely without conscious control; it can continuously monitor the conditions of these different systems and implement changes as needed. Signaling to the target tissue usually involves two synapses: a preganglionic neuron (originating in the CNS) synapses to a neuron in a ganglion that, in turn, synapses on the target organ, as illustrated in Figure **42.1.1.1**. There are two divisions of the autonomic nervous system that often have opposing effects: the sympathetic nervous system and the parasympathetic nervous system.

Sympathetic Nervous System

The sympathetic nervous system is responsible for the “fight or flight” response that occurs when an animal encounters a dangerous situation. One way to remember this is to think of the surprise a person feels when encountering a snake (“snake” and “sympathetic” both begin with “s”). Examples of functions controlled by the sympathetic nervous system include an accelerated heart rate and inhibited digestion. These functions help prepare an organism’s body for the physical strain required to escape a potentially dangerous situation or to fend off a predator.

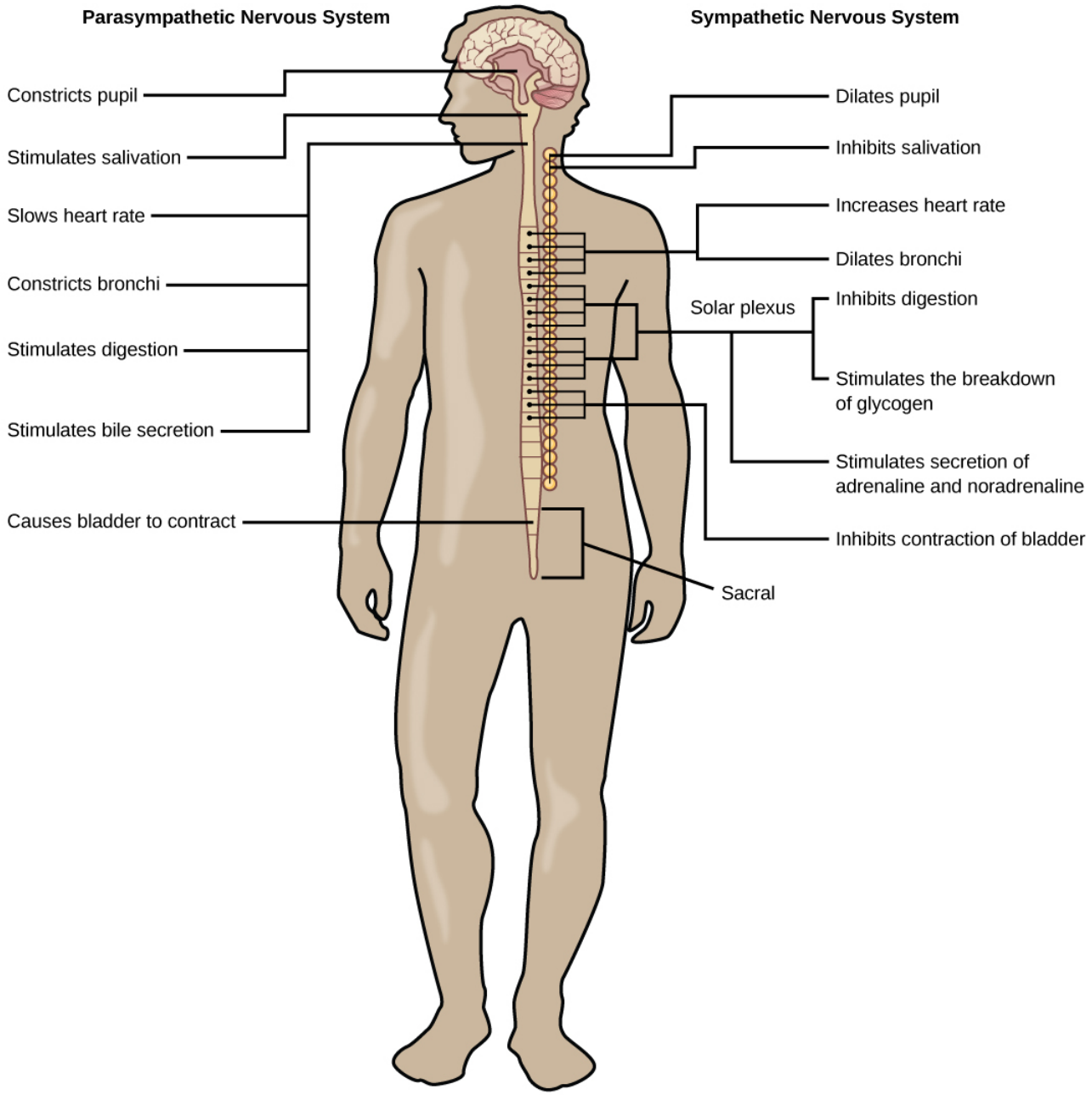


Figure 42.1.1.2: The sympathetic and parasympathetic nervous systems often have opposing effects on target organs.

Most preganglionic neurons in the sympathetic nervous system originate in the spinal cord, as illustrated in Figure 42.1.1.2. The axons of these neurons release acetylcholine on postganglionic neurons within sympathetic ganglia (the sympathetic ganglia form a chain that extends alongside the spinal cord). The acetylcholine activates the postganglionic neurons. Postganglionic neurons then release norepinephrine onto target organs. As anyone who has ever felt a rush before a big test, speech, or athletic event can attest, the effects of the sympathetic nervous system are quite pervasive. This is both because one preganglionic neuron synapses on multiple postganglionic neurons, amplifying the effect of the original synapse, and because the adrenal gland also releases norepinephrine (and the closely related hormone epinephrine) into the blood stream. The physiological effects of this norepinephrine release include dilating the trachea and bronchi (making it easier for the animal to breathe), increasing heart rate, and moving blood from the skin to the heart, muscles, and brain (so the animal can think and run). The strength and speed of the sympathetic response helps an organism avoid danger, and scientists have found evidence that it may also increase LTP—allowing the animal to remember the dangerous situation and avoid it in the future.

Parasympathetic Nervous System

While the sympathetic nervous system is activated in stressful situations, the parasympathetic nervous system allows an animal to "rest and digest." One way to remember this is to think that during a restful situation like a picnic, the parasympathetic nervous system is in control ("picnic" and "parasympathetic" both start with "p"). Parasympathetic preganglionic neurons have cell bodies located in the brainstem and in the sacral (toward the bottom) spinal cord, as shown in Figure **42.1.1.2**. The axons of the preganglionic neurons release acetylcholine on the postganglionic neurons, which are generally located very near the target organs. Most postganglionic neurons release acetylcholine onto target organs, although some release nitric oxide.

The parasympathetic nervous system resets organ function after the sympathetic nervous system is activated (the common adrenaline dump you feel after a 'fight-or-flight' event). Effects of acetylcholine release on target organs include slowing of heart rate, lowered blood pressure, and stimulation of digestion.

Sensory-Somatic Nervous System

The sensory-somatic nervous system is made up of cranial and spinal nerves and contains both sensory and motor neurons. Sensory neurons transmit sensory information from the skin, skeletal muscle, and sensory organs to the CNS. Motor neurons transmit messages about desired movement from the CNS to the muscles to make them contract. Without its sensory-somatic nervous system, an animal would be unable to process any information about its environment (what it sees, feels, hears, and so on) and could not control motor movements. Unlike the autonomic nervous system, which has two synapses between the CNS and the target organ, sensory and motor neurons have only one synapse—one ending of the neuron is at the organ and the other directly contacts a CNS neuron. Acetylcholine is the main neurotransmitter released at these synapses.

Humans have 12 cranial nerves, nerves that emerge from or enter the skull (cranium), as opposed to the spinal nerves, which emerge from the vertebral column. Each cranial nerve is accorded a name, which are detailed in Figure **42.1.1.3**. Some cranial nerves transmit only sensory information. For example, the olfactory nerve transmits information about smells from the nose to the brainstem. Other cranial nerves transmit almost solely motor information. For example, the oculomotor nerve controls the opening and closing of the eyelid and some eye movements. Other cranial nerves contain a mix of sensory and motor fibers. For example, the glossopharyngeal nerve has a role in both taste (sensory) and swallowing (motor).

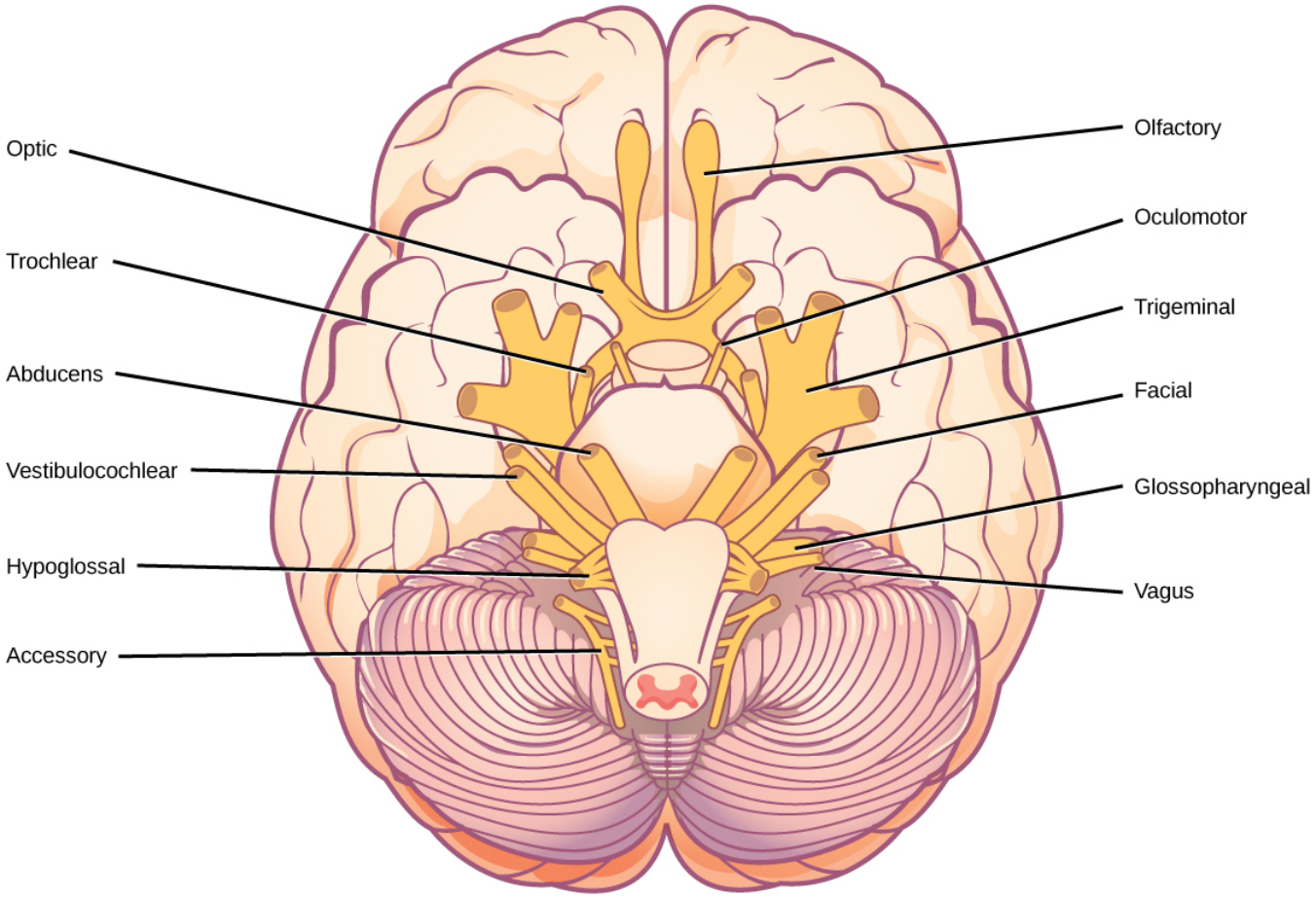


Figure **42.1.1.3**: The human brain contains 12 cranial nerves that receive sensory input and control motor output for the head and neck.

Spinal nerves transmit sensory and motor information between the spinal cord and the rest of the body. Each of the 31 spinal nerves (in humans) contains both sensory and motor axons. The sensory neuron cell bodies are grouped in structures called dorsal root ganglia and are shown in Figure **42.1.1.4**. Each sensory neuron has one projection—with a sensory receptor ending in skin, muscle, or sensory organs—and another that synapses with a neuron in the dorsal spinal cord. Motor neurons have cell bodies in the ventral gray matter of the spinal cord that project to muscle through the ventral root. These neurons are usually stimulated by interneurons within the spinal cord but are sometimes directly stimulated by sensory neurons.

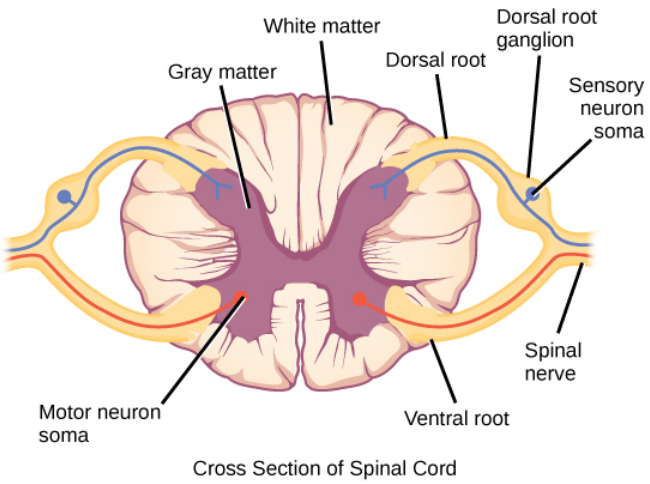


Figure **42.1.1.4**: Spinal nerves contain both sensory and motor axons. The somas of sensory neurons are located in dorsal root ganglia. The somas of motor neurons are found in the ventral portion of the gray matter of the spinal cord.

Summary

The peripheral nervous system contains both the autonomic and sensory-somatic nervous systems. The autonomic nervous system provides unconscious control over visceral functions and has two divisions: the sympathetic and parasympathetic nervous systems. The sympathetic nervous system is activated in stressful situations to prepare the animal for a “fight or flight” response. The parasympathetic nervous system is active during restful periods. The sensory-somatic nervous system is made of cranial and spinal nerves that transmit sensory information from skin and muscle to the CNS and motor commands from the CNS to the muscles.

Art Connections

Figure **42.1.1.1**: Which of the following statements is false?

A. The parasympathetic pathway is responsible for relaxing the body, while the sympathetic pathway is responsible for preparing for an emergency.
B. Most preganglionic neurons in the sympathetic pathway originate in the spinal cord.
C. Slowing of the heartbeat is a parasympathetic response.
D. Parasympathetic neurons are responsible for releasing norepinephrine on the target organ, while sympathetic neurons are responsible for releasing acetylcholine.

Answer

D

Glossary

acetylcholine
neurotransmitter released by neurons in the central nervous system and peripheral nervous system

autonomic nervous system
part of the peripheral nervous system that controls bodily functions

cranial nerve
sensory and/or motor nerve that emanates from the brain

norepinephrine
neurotransmitter and hormone released by activation of the sympathetic nervous system

parasympathetic nervous system

division of autonomic nervous system that regulates visceral functions during rest and digestion

sensory-somatic nervous system

system of sensory and motor nerves

spinal nerve

nerve projecting between skin or muscle and spinal cord

sympathetic nervous system

division of autonomic nervous system activated during stressful “fight or flight” situations

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42.2: The Mechanism of Nerve Impulse Transmission

Skills to Develop

- Describe the basis of the resting membrane potential
- Explain the stages of an action potential and how action potentials are propagated
- Explain the similarities and differences between chemical and electrical synapses
- Describe long-term potentiation and long-term depression

All functions performed by the nervous system—from a simple motor reflex to more advanced functions like making a memory or a decision—require neurons to communicate with one another. While humans use words and body language to communicate, neurons use electrical and chemical signals. Just like a person in a committee, one neuron usually receives and synthesizes messages from multiple other neurons before "making the decision" to send the message on to other neurons.

Nerve Impulse Transmission within a Neuron

For the nervous system to function, neurons must be able to send and receive signals. These signals are possible because each neuron has a charged cellular membrane (a voltage difference between the inside and the outside), and the charge of this membrane can change in response to neurotransmitter molecules released from other neurons and environmental stimuli. To understand how neurons communicate, one must first understand the basis of the baseline or 'resting' membrane charge.

Neuronal Charged Membranes

The lipid bilayer membrane that surrounds a neuron is impermeable to charged molecules or ions. To enter or exit the neuron, ions must pass through special proteins called ion channels that span the membrane. Ion channels have different configurations: open, closed, and inactive, as illustrated in Figure **42.2.1**. Some ion channels need to be activated in order to open and allow ions to pass into or out of the cell. These ion channels are sensitive to the environment and can change their shape accordingly. Ion channels that change their structure in response to voltage changes are called voltage-gated ion channels. Voltage-gated ion channels regulate the relative concentrations of different ions inside and outside the cell. The difference in total charge between the inside and outside of the cell is called the membrane potential.

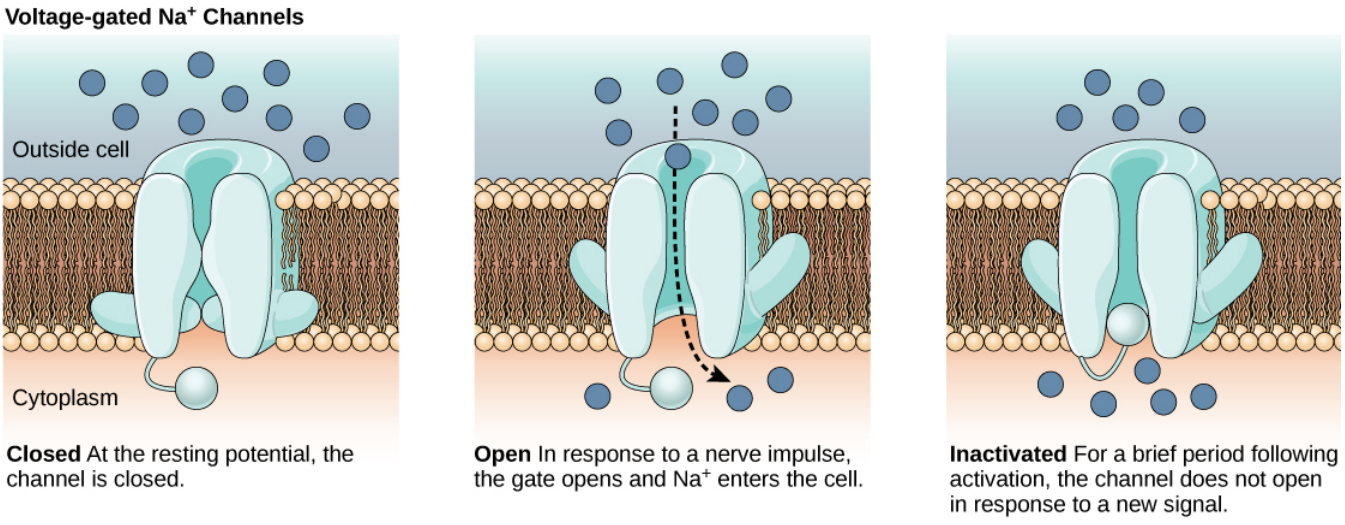


Figure **42.2.1**: Voltage-gated ion channels open in response to changes in membrane voltage. After activation, they become inactivated for a brief period and will no longer open in response to a signal.

Link to Learning



This video discusses the basis of the resting membrane potential.

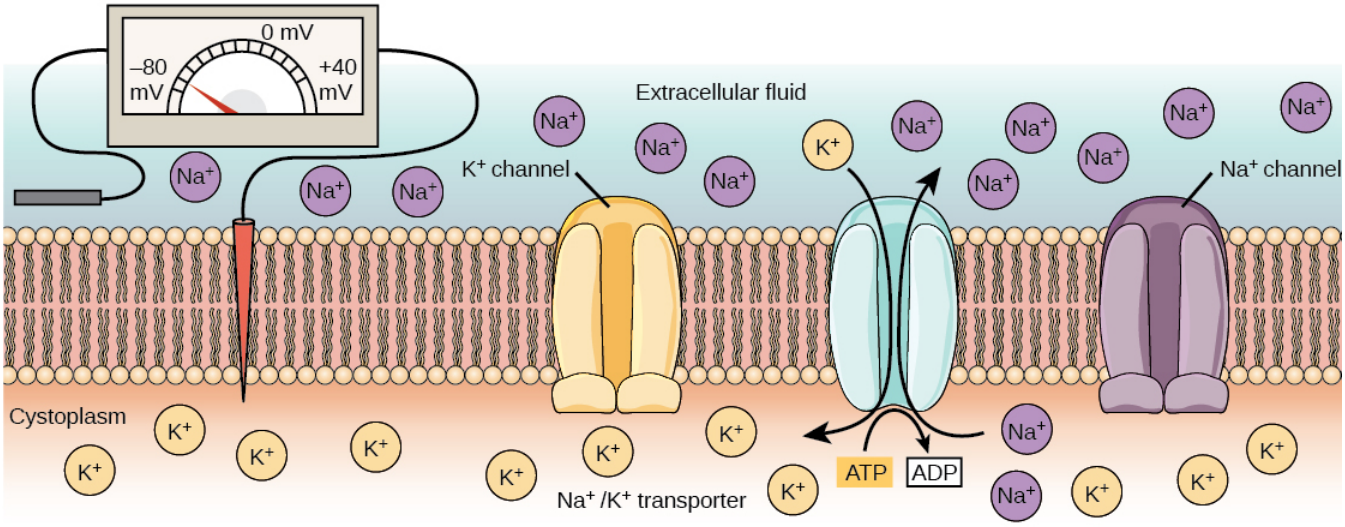
Resting Membrane Potential

A neuron at rest is negatively charged: the inside of a cell is approximately 70 millivolts more negative than the outside (−70 mV, note that this number varies by neuron type and by species). This voltage is called the resting membrane potential; it is caused by differences in the concentrations of ions inside and outside the cell. If the membrane were equally permeable to all ions, each type of ion would flow across the membrane and the system would reach equilibrium. Because ions cannot simply cross the membrane at will, there are different concentrations of several ions inside and outside the cell, as shown in the table below. The difference in the number of positively charged potassium ions (K^+) inside and outside the cell dominates the resting membrane potential (Figure 42.2.2). When the membrane is at rest, K^+ ions accumulate inside the cell due to a net movement with the concentration gradient. The negative resting membrane potential is created and maintained by increasing the concentration of cations outside the cell (in the extracellular fluid) relative to inside the cell (in the cytoplasm). The negative charge within the cell is created by the cell membrane being more permeable to potassium ion movement than sodium ion movement. In neurons, potassium ions are maintained at high concentrations within the cell while sodium ions are maintained at high concentrations outside of the cell. The cell possesses potassium and sodium leakage channels that allow the two cations to diffuse down their concentration gradient. However, the neurons have far more potassium leakage channels than sodium leakage channels. Therefore, potassium diffuses out of the cell at a much faster rate than sodium leaks in. Because more cations are leaving the cell than are entering, this causes the interior of the cell to be negatively charged relative to the outside of the cell. The actions of the sodium potassium pump help to maintain the resting potential, once established. Recall that sodium potassium pumps brings two K^+ ions into the cell while removing three Na^+ ions per ATP consumed. As more cations are expelled from the cell than taken in, the inside of the cell remains negatively charged relative to the extracellular fluid. It should be noted that calcium ions (Cl^-) tend to accumulate outside of the cell because they are repelled by negatively-charged proteins within the cytoplasm.

Table 42.2.1: Ion Concentration Inside and Outside Neurons. The resting membrane potential is a result of different concentrations inside and outside the cell.

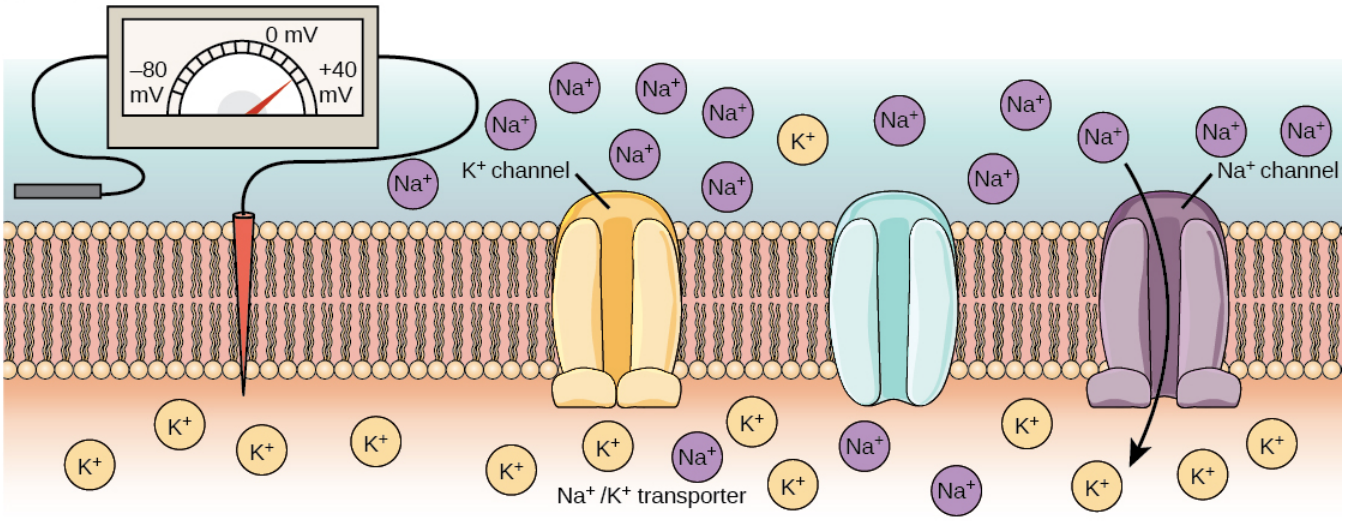
Ion	Extracellular concentration (mM)	Intracellular concentration (mM)	Ratio outside/inside
Na^+	145	12	12
K^+	4	155	0.026
Cl^-	120	4	30
Organic anions (A−)	—	100	

(a) Resting potential



At the resting potential, all voltage-gated Na^+ channels and most voltage-gated K^+ channels are closed. The Na^+/K^+ transporter pumps K^+ ions into the cell and Na^+ ions out.

(b) Depolarization



In response to a depolarization, some Na^+ channels open, allowing Na^+ ions to enter the cell. The membrane starts to depolarize (the charge across the membrane lessens). If the threshold of excitation is reached, all the Na^+ channels open.

(c) Hyperpolarization

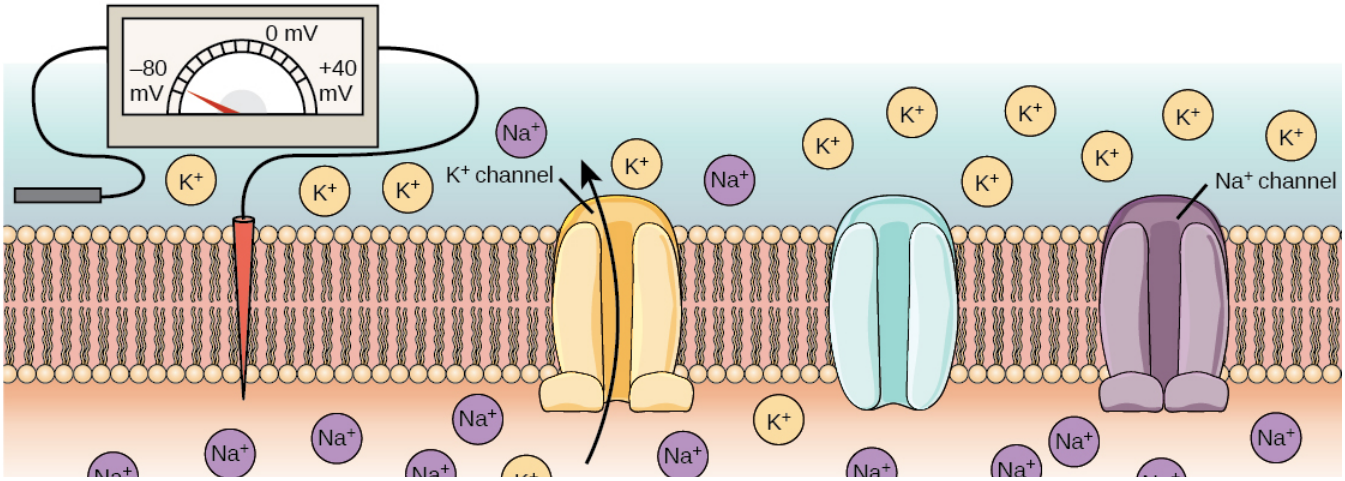


Figure 42.2.2: The (a) resting membrane potential is a result of different concentrations of Na^+ and K^+ ions inside and outside the cell. A nerve impulse causes Na^+ to enter the cell, resulting in (b) depolarization. At the peak action potential, K^+ channels open and the cell becomes (c) hyperpolarized.

At the peak action potential, Na^+ channels close while K^+ channels open. K^+ leaves the cell, and the membrane eventually becomes hyperpolarized.

Action Potential

A neuron can receive input from other neurons and, if this input is strong enough, send the signal to downstream neurons. Transmission of a signal between neurons is generally carried by a chemical called a neurotransmitter. Transmission of a signal within a neuron (from dendrite to axon terminal) is carried by a brief reversal of the resting membrane potential called an action potential. When neurotransmitter molecules bind to receptors located on a neuron's dendrites, ion channels open. At excitatory synapses, this opening allows positive ions to enter the neuron and results in depolarization of the membrane—a decrease in the difference in voltage between the inside and outside of the neuron. A stimulus from a sensory cell or another neuron depolarizes the target neuron to its threshold potential (-55 mV). Na^+ channels in the axon hillock open, allowing positive ions to enter the cell (Figure 42.2.3 and Figure 42.2.4). Once the sodium channels open, the neuron completely depolarizes to a membrane potential of about +40 mV. Action potentials are considered an "all-or nothing" event, in that, once the threshold potential is reached, the neuron always completely depolarizes. Once depolarization is complete, the cell must now "reset" its membrane voltage back to the resting potential. To accomplish this, the Na^+ channels close and cannot be opened. This begins the neuron's refractory period, in which it cannot produce another action potential because its sodium channels will not open. At the same time, voltage-gated K^+ channels open, allowing K^+ to leave the cell. As K^+ ions leave the cell, the membrane potential once again becomes negative. The diffusion of K^+ out of the cell actually hyperpolarizes the cell, in that the membrane potential becomes more negative than the cell's normal resting potential. At this point, the sodium channels will return to their resting state, meaning they are ready to open again if the membrane potential again exceeds the threshold potential. Eventually the extra K^+ ions diffuse out of the cell through the potassium leakage channels, bringing the cell from its hyperpolarized state, back to its resting membrane potential.

Art Connection

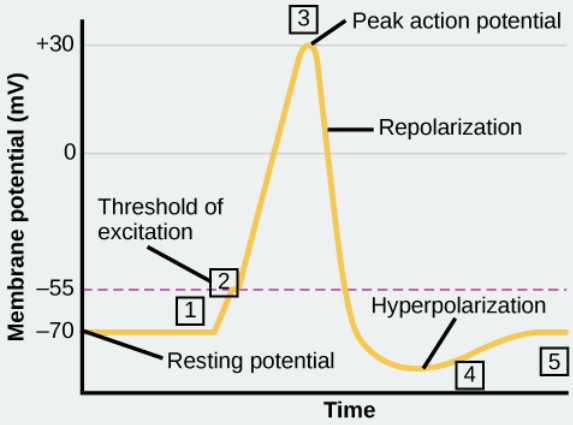


Figure 42.2.3: The formation of an action potential can be divided into five steps: (1) A stimulus from a sensory cell or another neuron causes the target cell to depolarize toward the threshold potential. (2) If the threshold of excitation is reached, all Na^+ channels open and the membrane depolarizes. (3) At the peak action potential, K^+ channels open and K^+ begins to leave the cell. At the same time, Na^+ channels close. (4) The membrane becomes hyperpolarized as K^+ ions continue to leave the cell. The hyperpolarized membrane is in a refractory period and cannot fire. (5) The K^+ channels close and the Na^+/K^+ transporter restores the resting potential.

Potassium channel blockers, such as amiodarone and procainamide, which are used to treat abnormal electrical activity in the heart, called cardiac dysrhythmia, impede the movement of K^+ through voltage-gated K^+ channels. Which part of the action potential would you expect potassium channels to affect?

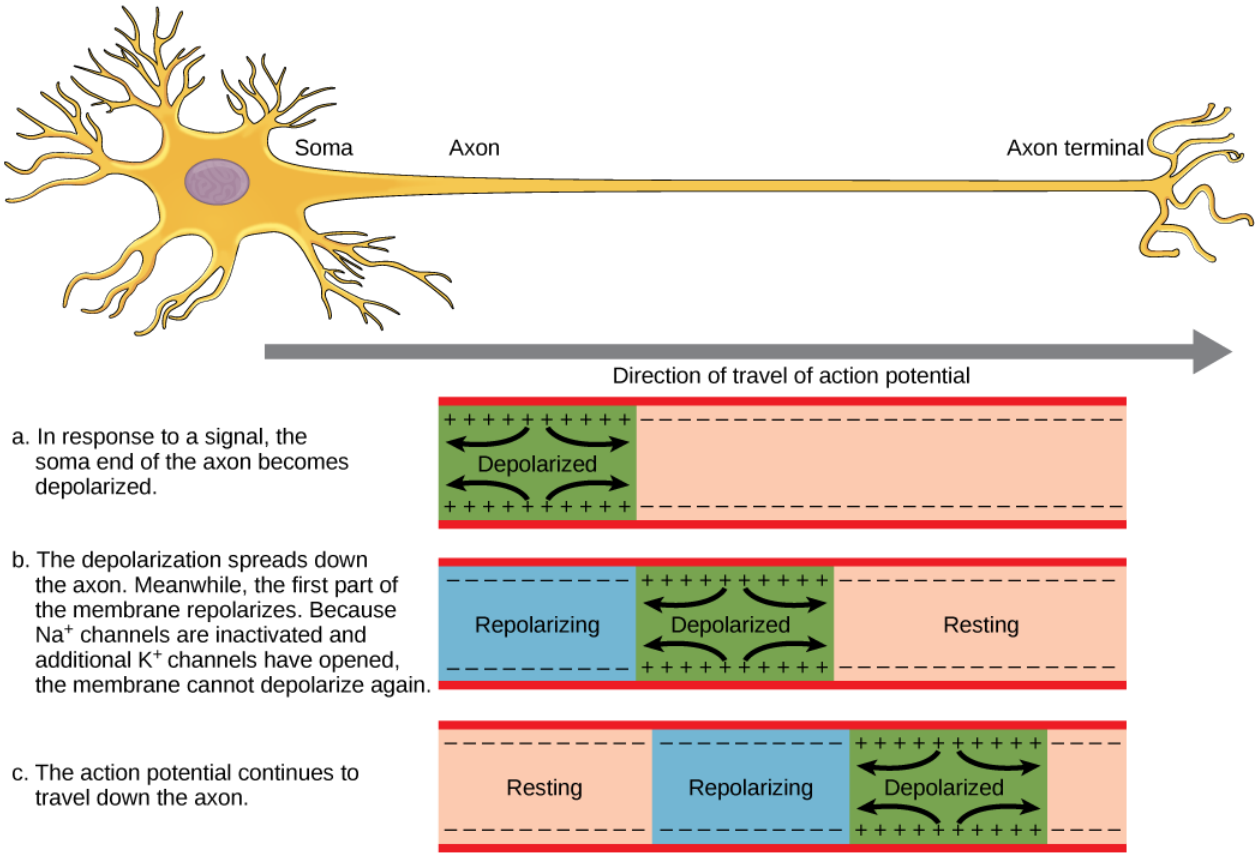
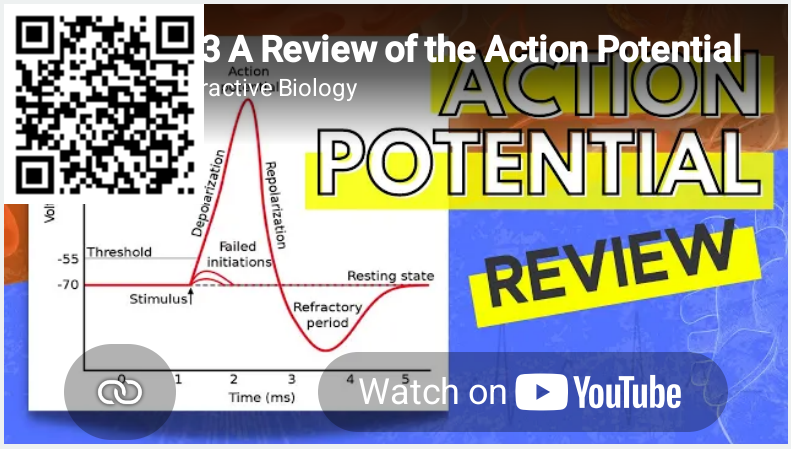


Figure **42.2.4**: The action potential is conducted down the axon as the axon membrane depolarizes, then repolarizes.

Link to Learning



This video presents an overview of action potential.

Myelin and the Propagation of the Action Potential

For an action potential to communicate information to another neuron, it must travel along the axon and reach the axon terminals where it can initiate neurotransmitter release. The speed of conduction of an action potential along an axon is influenced by both the diameter of the axon and the axon's resistance to current leak. Myelin acts as an insulator that prevents current from leaving the axon; this increases the speed of action potential conduction. In demyelinating diseases like multiple sclerosis, action potential conduction slows because current leaks from previously insulated axon areas. The nodes of Ranvier, illustrated in Figure **42.2.5** are gaps in the myelin sheath along the axon. These unmyelinated spaces are about one micrometer long and contain voltage gated Na^+

and K^+ channels. Flow of ions through these channels, particularly the Na^+ channels, regenerates the action potential over and over again along the axon. This 'jumping' of the action potential from one node to the next is called saltatory conduction. If nodes of Ranvier were not present along an axon, the action potential would propagate very slowly since Na^+ and K^+ channels would have to continuously regenerate action potentials at every point along the axon instead of at specific points. Nodes of Ranvier also save energy for the neuron since the channels only need to be present at the nodes and not along the entire axon.

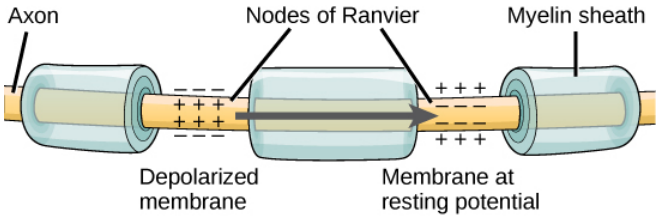


Figure **42.2.5**: Nodes of Ranvier are gaps in myelin coverage along axons. Nodes contain voltage-gated K^+ and Na^+ channels. Action potentials travel down the axon by jumping from one node to the next.

Synaptic Transmission

The synapse or "gap" is the place where information is transmitted from one neuron to another. Synapses usually form between axon terminals and dendritic spines, but this is not universally true. There are also axon-to-axon, dendrite-to-dendrite, and axon-to-cell body synapses. The neuron transmitting the signal is called the presynaptic neuron, and the neuron receiving the signal is called the postsynaptic neuron. Note that these designations are relative to a particular synapse—most neurons are both presynaptic and postsynaptic. There are two types of synapses: chemical and electrical.

Chemical Synapse

When an action potential reaches the axon terminal it depolarizes the membrane and opens voltage-gated Na^+ channels. Na^+ ions enter the cell, further depolarizing the presynaptic membrane. This depolarization causes voltage-gated Ca^{2+} channels to open. Calcium ions entering the cell initiate a signaling cascade that causes small membrane-bound vesicles, called synaptic vesicles, containing neurotransmitter molecules to fuse with the presynaptic membrane. Synaptic vesicles are shown in Figure **42.2.6**, which is an image from a scanning electron microscope.

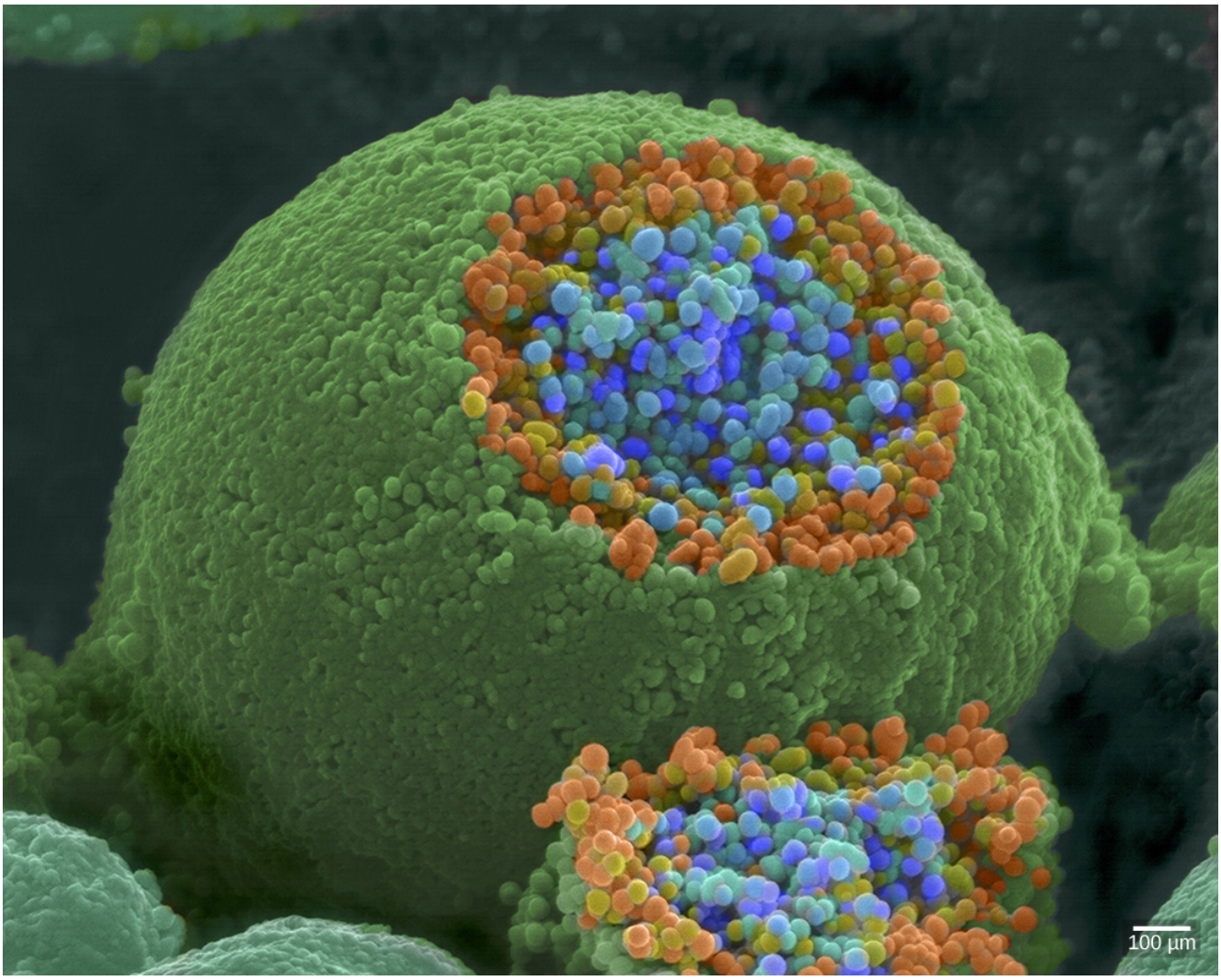
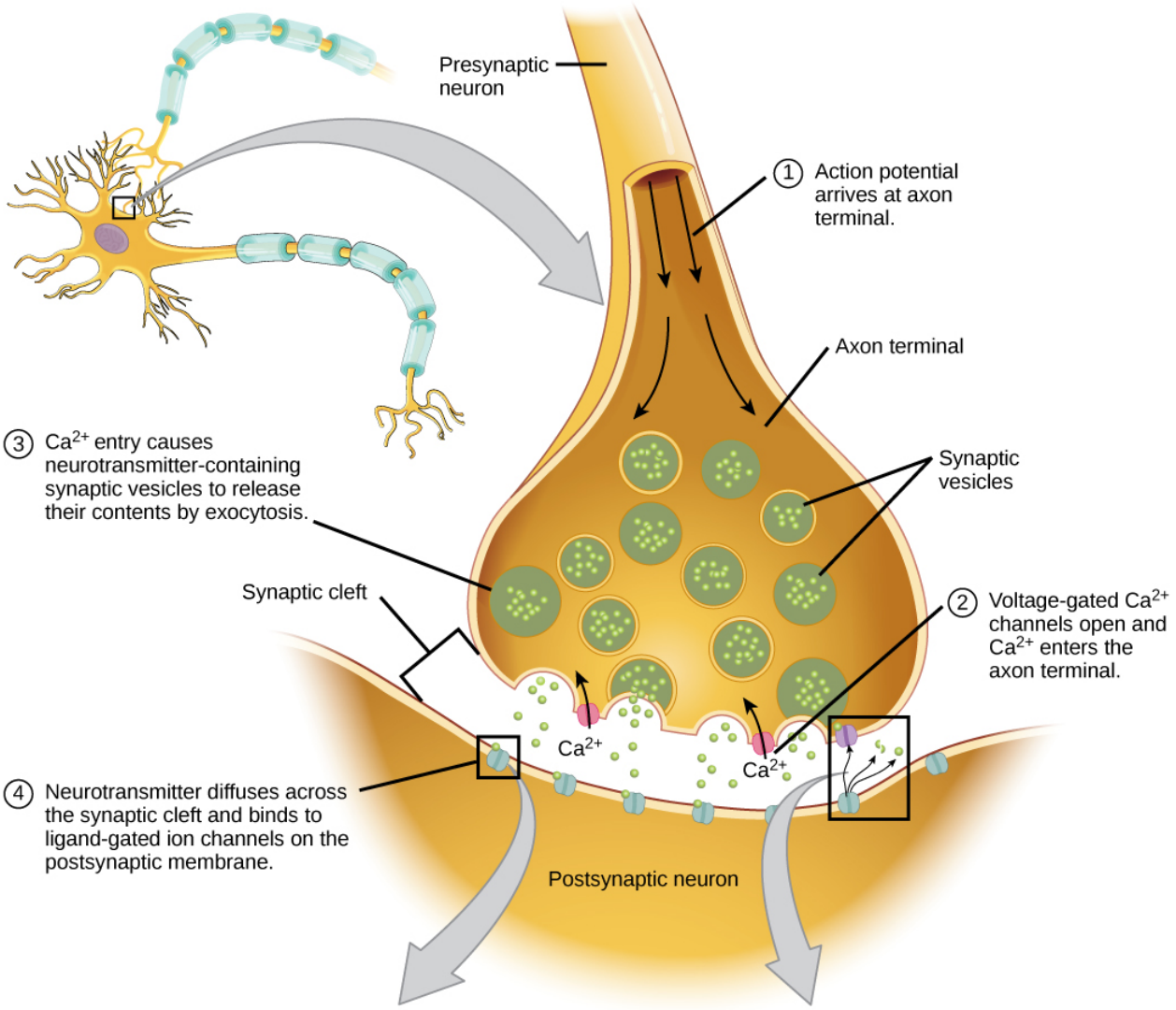
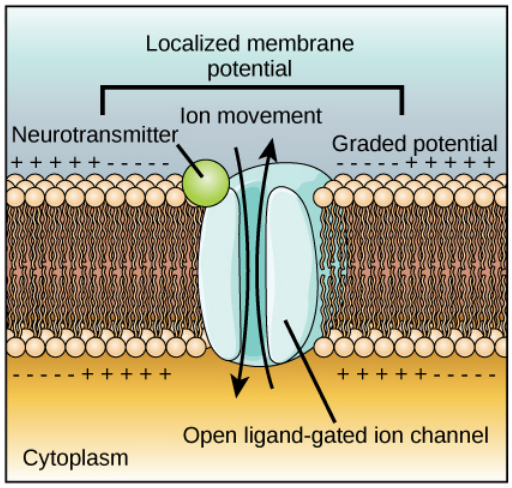


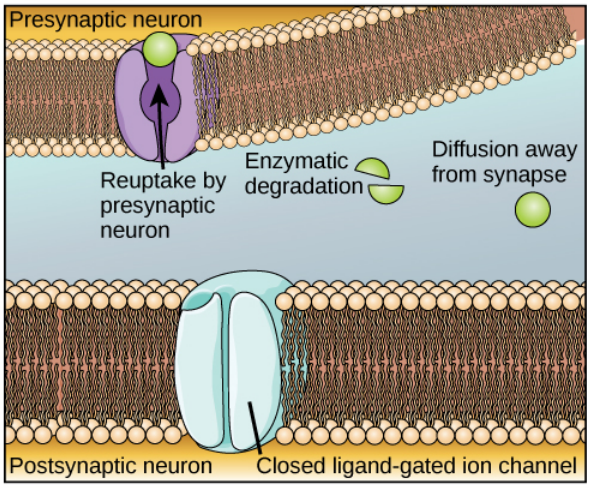
Figure 42.2.6: This pseudocolored image taken with a scanning electron microscope shows an axon terminal that was broken open to reveal synaptic vesicles (blue and orange) inside the neuron. (credit: modification of work by Tina Carvalho, NIH-NIGMS; scale-bar data from Matt Russell)

Fusion of a vesicle with the presynaptic membrane causes neurotransmitter to be released into the synaptic cleft, the extracellular space between the presynaptic and postsynaptic membranes, as illustrated in Figure 42.2.7. The neurotransmitter diffuses across the synaptic cleft and binds to receptor proteins on the postsynaptic membrane.





5 Binding of neurotransmitter opens ligand-gated ion channels, resulting in graded potentials.



6 Reuptake by the presynapic neuron, enzymatic degradation, and diffusion reduce neurotransmitter levels, terminating the signal.

Figure 42.2.7: Communication at chemical synapses requires release of neurotransmitters. When the presynaptic membrane is depolarized, voltage-gated Ca^{2+} channels open and allow Ca^{2+} to enter the cell. The calcium entry causes synaptic vesicles to fuse with the membrane and release neurotransmitter molecules into the synaptic cleft. The neurotransmitter diffuses across the synaptic cleft and binds to ligand-gated ion channels in the postsynaptic membrane, resulting in a localized depolarization or hyperpolarization of the postsynaptic neuron.

The binding of a specific neurotransmitter causes particular ion channels, in this case ligand-gated channels, on the postsynaptic membrane to open. Neurotransmitters can either have excitatory or inhibitory effects on the postsynaptic membrane, as detailed in the table below. For example, when acetylcholine is released at the synapse between a nerve and muscle (called the neuromuscular junction) by a presynaptic neuron, it causes postsynaptic Na^+ channels to open. Na^+ enters the postsynaptic cell and causes the postsynaptic membrane to depolarize. This depolarization is called an excitatory postsynaptic potential (EPSP) and makes the postsynaptic neuron more likely to fire an action potential. Release of neurotransmitter at inhibitory synapses causes inhibitory postsynaptic potentials (IPSPs), a hyperpolarization of the presynaptic membrane. For example, when the neurotransmitter GABA (gamma-aminobutyric acid) is released from a presynaptic neuron, it binds to and opens Cl^- channels. Cl^- ions enter the cell and hyperpolarizes the membrane, making the neuron less likely to fire an action potential.

Once neurotransmission has occurred, the neurotransmitter must be removed from the synaptic cleft so the postsynaptic membrane can “reset” and be ready to receive another signal. This can be accomplished in three ways: the neurotransmitter can diffuse away from the synaptic cleft, it can be degraded by enzymes in the synaptic cleft, or it can be recycled (sometimes called reuptake) by the presynaptic neuron. Several drugs act at this step of neurotransmission. For example, some drugs that are given to Alzheimer’s patients work by inhibiting acetylcholinesterase, the enzyme that degrades acetylcholine. This inhibition of the enzyme essentially increases neurotransmission at synapses that release acetylcholine. Once released, the acetylcholine stays in the cleft and can continually bind and unbind to postsynaptic receptors.

Table 42.2.2: Neurotransmitter Function and Location

Neurotransmitter	Example	Location
Acetylcholine	—	CNS and/or PNS
Biogenic amine	Dopamine, serotonin, norepinephrine	CNS and/or PNS
Amino acid	Glycine, glutamate, aspartate, gamma aminobutyric acid	CNS
Neuropeptide	Substance P, endorphins	CNS and/or PNS

Electrical Synapse

While electrical synapses are fewer in number than chemical synapses, they are found in all nervous systems and play important and unique roles. The mode of neurotransmission in electrical synapses is quite different from that in chemical synapses. In an electrical synapse, the presynaptic and postsynaptic membranes are very close together and are actually physically connected by channel proteins forming gap junctions. Gap junctions allow current to pass directly from one cell to the next. In addition to the ions that carry this current, other molecules, such as ATP, can diffuse through the large gap junction pores.

There are key differences between chemical and electrical synapses. Because chemical synapses depend on the release of neurotransmitter molecules from synaptic vesicles to pass on their signal, there is an approximately one millisecond delay between when the axon potential reaches the presynaptic terminal and when the neurotransmitter leads to opening of postsynaptic ion channels. Additionally, this signaling is unidirectional. Signaling in electrical synapses, in contrast, is virtually instantaneous (which is important for synapses involved in key reflexes), and some electrical synapses are bidirectional. Electrical synapses are also more reliable as they are less likely to be blocked, and they are important for synchronizing the electrical activity of a group of neurons. For example, electrical synapses in the thalamus are thought to regulate slow-wave sleep, and disruption of these synapses can cause seizures.

Signal Summation

Sometimes a single EPSP is strong enough to induce an action potential in the postsynaptic neuron, but often multiple presynaptic inputs must create EPSPs around the same time for the postsynaptic neuron to be sufficiently depolarized to fire an action potential.

This process is called summation and occurs at the axon hillock, as illustrated in Figure 42.2.8. Additionally, one neuron often has inputs from many presynaptic neurons—some excitatory and some inhibitory—so IPSPs can cancel out EPSPs and vice versa. It is the net change in postsynaptic membrane voltage that determines whether the postsynaptic cell has reached its threshold of excitation needed to fire an action potential. Together, synaptic summation and the threshold for excitation act as a filter so that random "noise" in the system is not transmitted as important information.

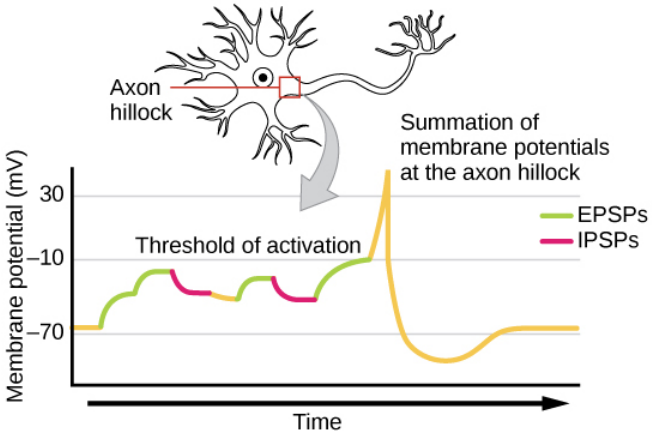


Figure 42.2.8: A single neuron can receive both excitatory and inhibitory inputs from multiple neurons, resulting in local membrane depolarization (EPSP input) and hyperpolarization (IPSP input). All these inputs are added together at the axon hillock. If the EPSPs are strong enough to overcome the IPSPs and reach the threshold of excitation, the neuron will fire.

Everyday Connection: Brain-computer interface

Amyotrophic lateral sclerosis (ALS, also called Lou Gehrig's Disease) is a neurological disease characterized by the degeneration of the motor neurons that control voluntary movements. The disease begins with muscle weakening and lack of coordination and eventually destroys the neurons that control speech, breathing, and swallowing; in the end, the disease can lead to paralysis. At that point, patients require assistance from machines to be able to breathe and to communicate. Several special technologies have been developed to allow "locked-in" patients to communicate with the rest of the world. One technology, for example, allows patients to type out sentences by twitching their cheek. These sentences can then be read aloud by a computer.

A relatively new line of research for helping paralyzed patients, including those with ALS, to communicate and retain a degree of self-sufficiency is called brain-computer interface (BCI) technology and is illustrated in Figure 42.2.9. This technology sounds like something out of science fiction: it allows paralyzed patients to control a computer using only their thoughts. There are several forms of BCI. Some forms use EEG recordings from electrodes taped onto the skull. These recordings contain information from large populations of neurons that can be decoded by a computer. Other forms of BCI require the implantation of an array of electrodes smaller than a postage stamp in the arm and hand area of the motor cortex. This form of BCI, while more invasive, is very powerful as each electrode can record actual action potentials from one or more neurons. These signals are then sent to a computer, which has been trained to decode the signal and feed it to a tool—such as a cursor on a computer screen. This means that a patient with ALS can use e-mail, read the Internet, and communicate with others by thinking of moving his or her hand or arm (even though the paralyzed patient cannot make that bodily movement). Recent advances have allowed a paralyzed locked-in patient who suffered a stroke 15 years ago to control a robotic arm and even to feed herself coffee using BCI technology.

Despite the amazing advancements in BCI technology, it also has limitations. The technology can require many hours of training and long periods of intense concentration for the patient; it can also require brain surgery to implant the devices.

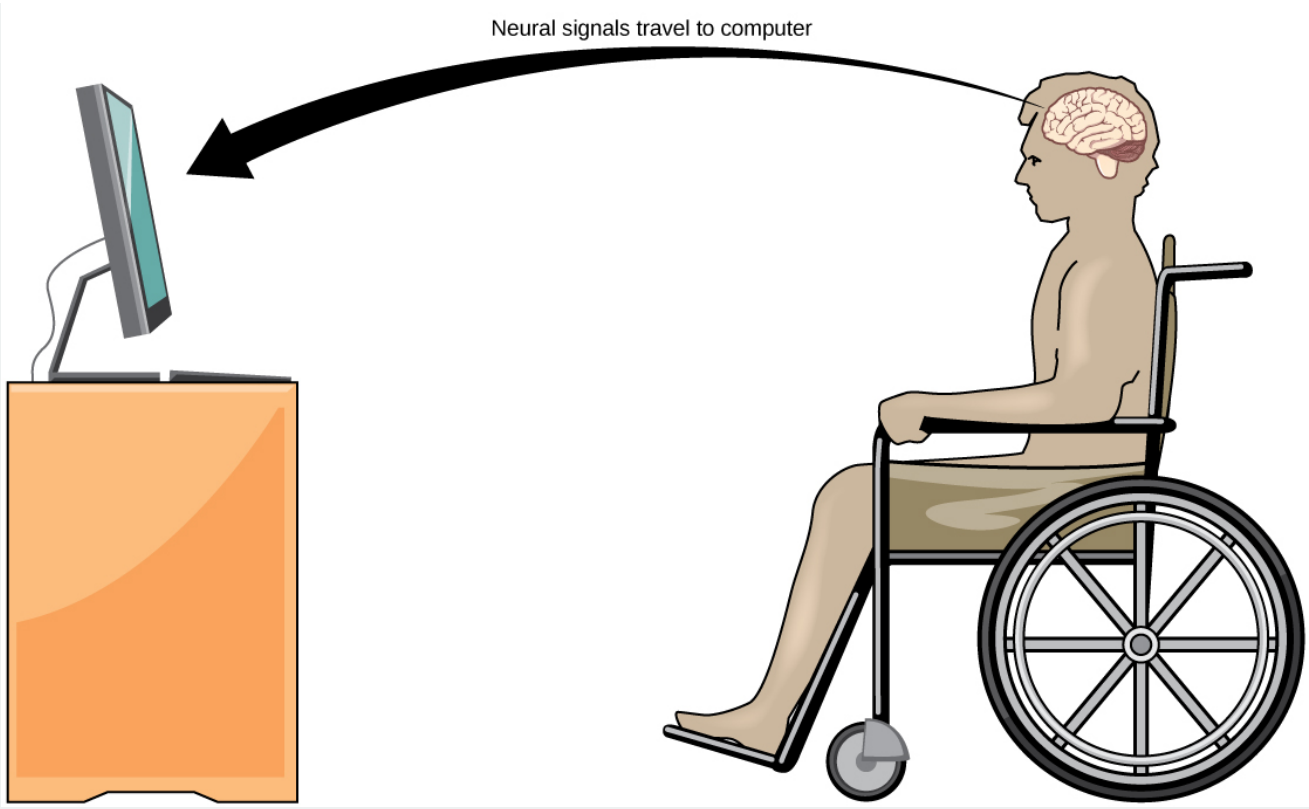
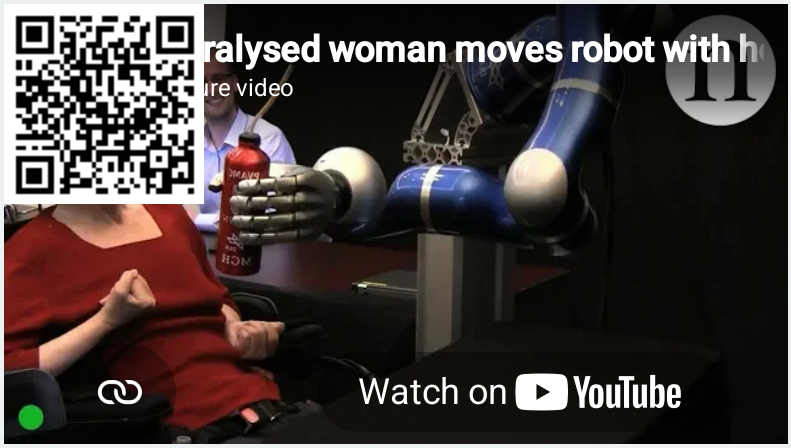


Figure **42.2.9**: With brain-computer interface technology, neural signals from a paralyzed patient are collected, decoded, and then fed to a tool, such as a computer, a wheelchair, or a robotic arm.

Link to Learning



Watch this video in which a paralyzed woman use a brain-controlled robotic arm to bring a drink to her mouth, among other images of brain-computer interface technology in action.

Synaptic Plasticity

Synapses are not static structures. They can be weakened or strengthened. They can be broken, and new synapses can be made. Synaptic plasticity allows for these changes, which are all needed for a functioning nervous system. In fact, synaptic plasticity is the basis of learning and memory. Two processes in particular, long-term potentiation (LTP) and long-term depression (LTD) are

important forms of synaptic plasticity that occur in synapses in the hippocampus, a brain region that is involved in storing memories.

Long-term Potentiation (LTP)

Long-term potentiation (LTP) is a persistent strengthening of a synaptic connection. LTP is based on the Hebbian principle: cells that fire together wire together. There are various mechanisms, none fully understood, behind the synaptic strengthening seen with LTP. One known mechanism involves a type of postsynaptic glutamate receptor, called NMDA (N-Methyl-D-aspartate) receptors, shown in Figure **42.2.10**. These receptors are normally blocked by magnesium ions; however, when the postsynaptic neuron is depolarized by multiple presynaptic inputs in quick succession (either from one neuron or multiple neurons), the magnesium ions are forced out allowing Ca ions to pass into the postsynaptic cell. Next, Ca^{2+} ions entering the cell initiate a signaling cascade that causes a different type of glutamate receptor, called AMPA (α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid) receptors, to be inserted into the postsynaptic membrane, since activated AMPA receptors allow positive ions to enter the cell. So, the next time glutamate is released from the presynaptic membrane, it will have a larger excitatory effect (EPSP) on the postsynaptic cell because the binding of glutamate to these AMPA receptors will allow more positive ions into the cell. The insertion of additional AMPA receptors strengthens the synapse and means that the postsynaptic neuron is more likely to fire in response to presynaptic neurotransmitter release. Some drugs of abuse co-opt the LTP pathway, and this synaptic strengthening can lead to addiction.

Long-term Depression (LTD)

Long-term depression (LTD) is essentially the reverse of LTP: it is a long-term weakening of a synaptic connection. One mechanism known to cause LTD also involves AMPA receptors. In this situation, calcium that enters through NMDA receptors initiates a different signaling cascade, which results in the removal of AMPA receptors from the postsynaptic membrane, as illustrated in Figure **42.2.10**. The decrease in AMPA receptors in the membrane makes the postsynaptic neuron less responsive to glutamate released from the presynaptic neuron. While it may seem counterintuitive, LTD may be just as important for learning and memory as LTP. The weakening and pruning of unused synapses allows for unimportant connections to be lost and makes the synapses that have undergone LTP that much stronger by comparison.

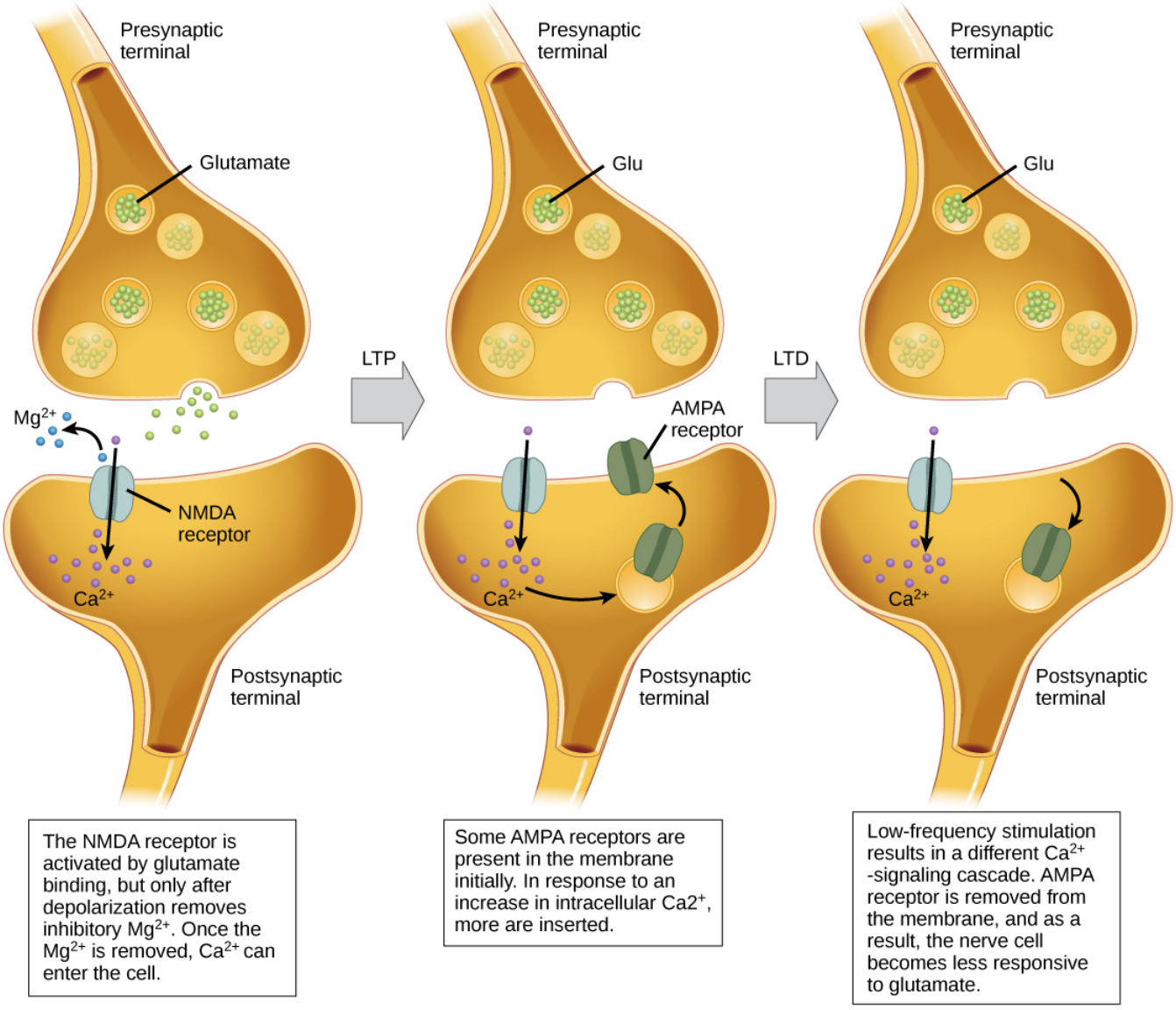


Figure 42.2.10: Calcium entry through postsynaptic NMDA receptors can initiate two different forms of synaptic plasticity: long-term potentiation (LTP) and long-term depression (LTD). LTP arises when a single synapse is repeatedly stimulated. This stimulation causes a calcium- and CaMKII-dependent cellular cascade, which results in the insertion of more AMPA receptors into the postsynaptic membrane. The next time glutamate is released from the presynaptic cell, it will bind to both NMDA and the newly inserted AMPA receptors, thus depolarizing the membrane more efficiently. LTD occurs when few glutamate molecules bind to NMDA receptors at a synapse (due to a low firing rate of the presynaptic neuron). The calcium that does flow through NMDA receptors initiates a different calcineurin and protein phosphatase 1-dependent cascade, which results in the endocytosis of AMPA receptors. This makes the postsynaptic neuron less responsive to glutamate released from the presynaptic neuron.

Summary

Neurons have charged membranes because there are different concentrations of ions inside and outside of the cell. Voltage-gated ion channels control the movement of ions into and out of a neuron. When a neuronal membrane is depolarized to at least the threshold of excitation, an action potential is fired. The action potential is then propagated along a myelinated axon to the axon terminals. In a chemical synapse, the action potential causes release of neurotransmitter molecules into the synaptic cleft. Through binding to postsynaptic receptors, the neurotransmitter can cause excitatory or inhibitory postsynaptic potentials by depolarizing or hyperpolarizing, respectively, the postsynaptic membrane. In electrical synapses, the action potential is directly communicated to the postsynaptic cell through gap junctions—large channel proteins that connect the pre-and postsynaptic membranes. Synapses are not static structures and can be strengthened and weakened. Two mechanisms of synaptic plasticity are long-term potentiation and long-term depression.

Art Connections

Figure 42.2.3: Potassium channel blockers, such as amiodarone and procainamide, which are used to treat abnormal electrical activity in the heart, called cardiac dysrhythmia, impede the movement of K^+ through voltage-gated K^+ channels. Which part of the action potential would you expect potassium channels to affect?

Answer

Potassium channel blockers slow the repolarization phase, but have no effect on depolarization.

Glossary

action potential
self-propagating momentary change in the electrical potential of a neuron (or muscle) membrane

depolarization
change in the membrane potential to a less negative value

excitatory postsynaptic potential (EPSP)
depolarization of a postsynaptic membrane caused by neurotransmitter molecules released from a presynaptic cell

hyperpolarization
change in the membrane potential to a more negative value

inhibitory postsynaptic potential (IPSP)
hyperpolarization of a postsynaptic membrane caused by neurotransmitter molecules released from a presynaptic cell

long-term depression (LTD)
prolonged decrease in synaptic coupling between a pre- and postsynaptic cell

long-term potentiation (LTP)
prolonged increase in synaptic coupling between a pre-and postsynaptic cell

membrane potential
difference in electrical potential between the inside and outside of a cell

refractory period
period after an action potential when it is more difficult or impossible for an action potential to be fired; caused by inactivation of sodium channels and activation of additional potassium channels of the membrane

saltatory conduction
“jumping” of an action potential along an axon from one node of Ranvier to the next

summation
process of multiple presynaptic inputs creating EPSPs around the same time for the postsynaptic neuron to be sufficiently depolarized to fire an action potential

synaptic cleft
space between the presynaptic and postsynaptic membranes

synaptic vesicle
spherical structure that contains a neurotransmitter

threshold of excitation

level of depolarization needed for an action potential to fire

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42.2.1: Sensory Processes

Skills to Develop

- Identify the general and special senses in humans
- Describe three important steps in sensory perception
- Explain the concept of just-noticeable difference in sensory perception

Senses provide information about the body and its environment. Humans have five special senses: olfaction (smell), gustation (taste), equilibrium (balance and body position), vision, and hearing. Additionally, we possess general senses, also called somatosensation, which respond to stimuli like temperature, pain, pressure, and vibration. Vestibular sensation, which is an organism's sense of spatial orientation and balance, proprioception (position of bones, joints, and muscles), and the sense of limb position that is used to track kinesthesia (limb movement) are part of somatosensation. Although the sensory systems associated with these senses are very different, all share a common function: to convert a stimulus (such as light, or sound, or the position of the body) into an electrical signal in the nervous system. This process is called sensory transduction.

There are two broad types of cellular systems that perform sensory transduction. In one, a neuron works with a sensory receptor, a cell, or cell process that is specialized to engage with and detect a specific stimulus. Stimulation of the sensory receptor activates the associated afferent neuron, which carries information about the stimulus to the central nervous system. In the second type of sensory transduction, a sensory nerve ending responds to a stimulus in the internal or external environment: this neuron constitutes the sensory receptor. Free nerve endings can be stimulated by several different stimuli, thus showing little receptor specificity. For example, pain receptors in your gums and teeth may be stimulated by temperature changes, chemical stimulation, or pressure.

Reception

The first step in sensation is reception, which is the activation of sensory receptors by stimuli such as mechanical stimuli (being bent or squished, for example), chemicals, or temperature. The receptor can then respond to the stimuli. The region in space in which a given sensory receptor can respond to a stimulus, be it far away or in contact with the body, is that receptor's receptive field. Think for a moment about the differences in receptive fields for the different senses. For the sense of touch, a stimulus must come into contact with body. For the sense of hearing, a stimulus can be a moderate distance away (some baleen whale sounds can propagate for many kilometers). For vision, a stimulus can be very far away; for example, the visual system perceives light from stars at enormous distances.

Transduction

The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system. This takes place at the sensory receptor, and the change in electrical potential that is produced is called the receptor potential. How is sensory input, such as pressure on the skin, changed to a receptor potential? In this example, a type of receptor called a mechanoreceptor (as shown in Figure **42.2.1.1**) possesses specialized membranes that respond to pressure. Disturbance of these dendrites by compressing them or bending them opens gated ion channels in the plasma membrane of the sensory neuron, changing its electrical potential. Recall that in the nervous system, a positive change of a neuron's electrical potential (also called the membrane potential), depolarizes the neuron. Receptor potentials are graded potentials: the magnitude of these graded (receptor) potentials varies with the strength of the stimulus. If the magnitude of depolarization is sufficient (that is, if membrane potential reaches a threshold), the neuron will fire an action potential. In most cases, the correct stimulus impinging on a sensory receptor will drive membrane potential in a positive direction, although for some receptors, such as those in the visual system, this is not always the case.

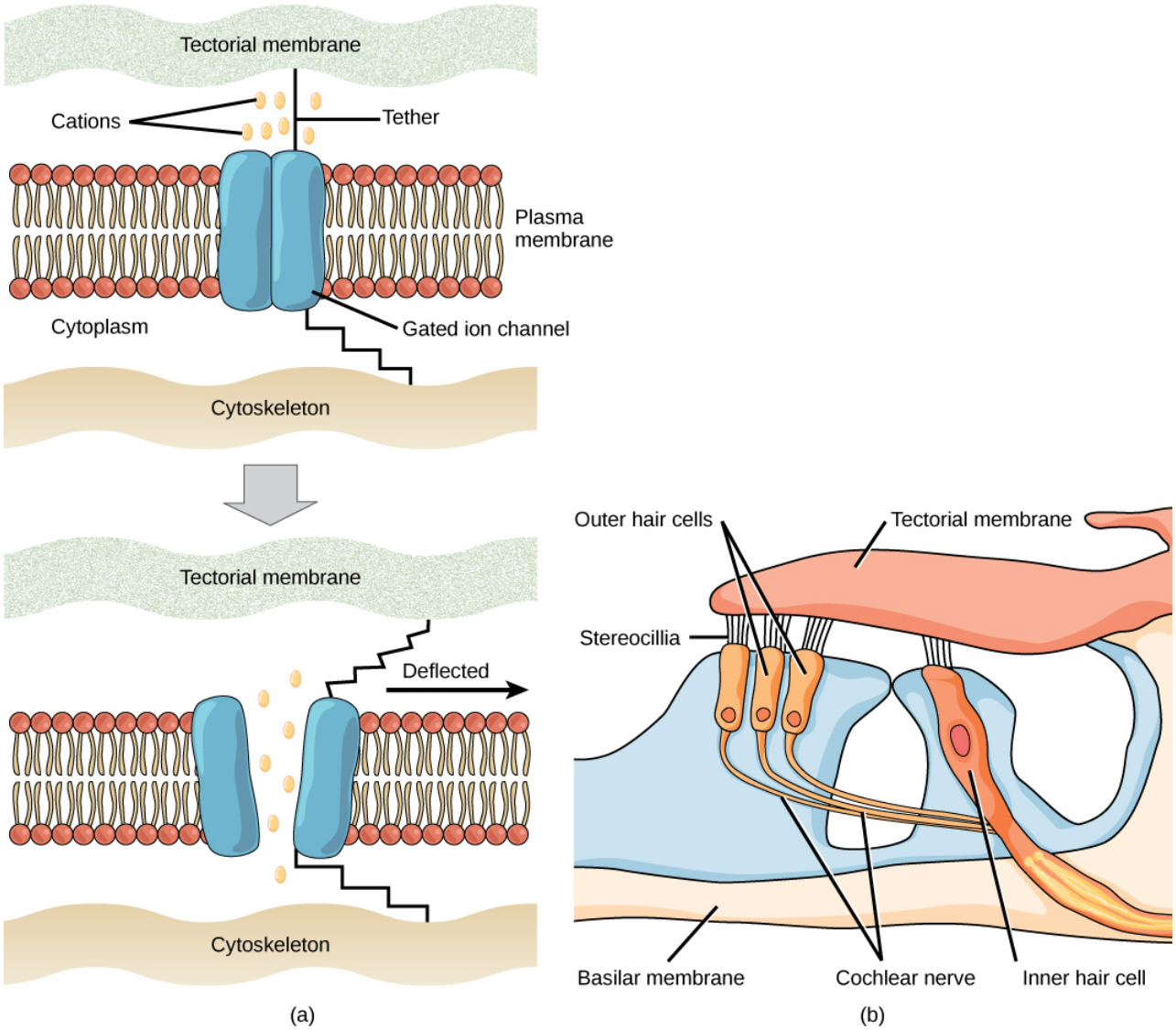


Figure 42.2.1.1: (a) Mechanosensitive ion channels are gated ion channels that respond to mechanical deformation of the plasma membrane. A mechanosensitive channel is connected to the plasma membrane and the cytoskeleton by hair-like tethers. When pressure causes the extracellular matrix to move, the channel opens, allowing ions to enter or exit the cell. (b) Stereocilia in the human ear are connected to mechanosensitive ion channels. When a sound causes the stereocilia to move, mechanosensitive ion channels transduce the signal to the cochlear nerve.

Sensory receptors for different senses are very different from each other, and they are specialized according to the type of stimulus they sense: they have receptor specificity. For example, touch receptors, light receptors, and sound receptors are each activated by different stimuli. Touch receptors are not sensitive to light or sound; they are sensitive only to touch or pressure. However, stimuli may be combined at higher levels in the brain, as happens with olfaction, contributing to our sense of taste.

Encoding and Transmission of Sensory Information

Four aspects of sensory information are encoded by sensory systems: the type of stimulus, the location of the stimulus in the receptive field, the duration of the stimulus, and the relative intensity of the stimulus. Thus, action potentials transmitted over a sensory receptor's afferent axons encode one type of stimulus, and this segregation of the senses is preserved in other sensory circuits. For example, auditory receptors transmit signals over their own dedicated system, and electrical activity in the axons of the auditory receptors will be interpreted by the brain as an auditory stimulus—a sound.

The intensity of a stimulus is often encoded in the rate of action potentials produced by the sensory receptor. Thus, an intense stimulus will produce a more rapid train of action potentials, and reducing the stimulus will likewise slow the rate of production of

action potentials. A second way in which intensity is encoded is by the number of receptors activated. An intense stimulus might initiate action potentials in a large number of adjacent receptors, while a less intense stimulus might stimulate fewer receptors. Integration of sensory information begins as soon as the information is received in the CNS, and the brain will further process incoming signals.

Perception

Perception is an individual's interpretation of a sensation. Although perception relies on the activation of sensory receptors, perception happens not at the level of the sensory receptor, but at higher levels in the nervous system, in the brain. The brain distinguishes sensory stimuli through a sensory pathway: action potentials from sensory receptors travel along neurons that are dedicated to a particular stimulus. These neurons are dedicated to that particular stimulus and synapse with particular neurons in the brain or spinal cord.

All sensory signals, except those from the olfactory system, are transmitted though the central nervous system and are routed to the thalamus and to the appropriate region of the cortex. Recall that the thalamus is a structure in the forebrain that serves as a clearinghouse and relay station for sensory (as well as motor) signals. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex (Figure **42.2.1.2**) dedicated to processing that particular sense.

How are neural signals interpreted? Interpretation of sensory signals between individuals of the same species is largely similar, owing to the inherited similarity of their nervous systems; however, there are some individual differences. A good example of this is individual tolerances to a painful stimulus, such as dental pain, which certainly differ.

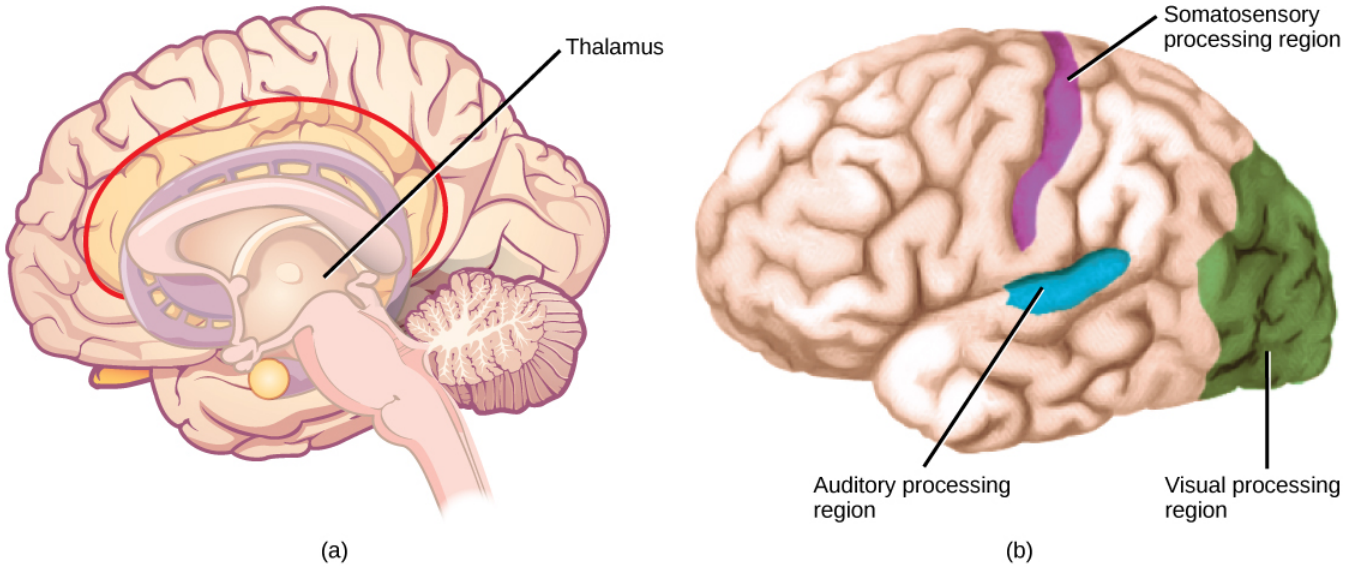


Figure **42.2.1.2:** In humans, with the exception of olfaction, all sensory signals are routed from the (a) thalamus to (b) final processing regions in the cortex of the brain. (credit b: modification of work by Polina Tishina)

Scientific Method Connection: Just-Noticeable Difference

It is easy to differentiate between a one-pound bag of rice and a two-pound bag of rice. There is a one-pound difference, and one bag is twice as heavy as the other. However, would it be as easy to differentiate between a 20- and a 21-pound bag?

Question: What is the smallest detectible weight difference between a one-pound bag of rice and a larger bag? What is the smallest detectible difference between a 20-pound bag and a larger bag? In both cases, at what weights are the differences detected? This smallest detectible difference in stimuli is known as the just-noticeable difference (JND).

Background: Research background literature on JND and on Weber's Law, a description of a proposed mathematical relationship between the overall magnitude of the stimulus and the JND. You will be testing JND of different weights of rice in bags. Choose a convenient increment that is to be stepped through while testing. For example, you could choose 10 percent increments between one and two pounds (1.1, 1.2, 1.3, 1.4, and so on) or 20 percent increments (1.2, 1.4, 1.6, and 1.8).

Hypothesis: Develop a hypothesis about JND in terms of percentage of the whole weight being tested (such as "the JND between the two small bags and between the two large bags is proportionally the same," or ". . . is not proportionally the same.") So, for the first hypothesis, if the JND between the one-pound bag and a larger bag is 0.2 pounds (that is, 20 percent; 1.0 pound feels the same as 1.1 pounds, but 1.0 pound feels less than 1.2 pounds), then the JND between the 20-pound bag and a larger bag will also be 20 percent. (So, 20 pounds feels the same as 22 pounds or 23 pounds, but 20 pounds feels less than 24 pounds.)

Test the hypothesis: Enlist 24 participants, and split them into two groups of 12. To set up the demonstration, assuming a 10 percent increment was selected, have the first group be the one-pound group. As a counter-balancing measure against a systematic error, however, six of the first group will compare one pound to two pounds, and step down in weight (1.0 to 2.0, 1.0 to 1.9, and so on.), while the other six will step up (1.0 to 1.1, 1.0 to 1.2, and so on). Apply the same principle to the 20-pound group (20 to 40, 20 to 38, and so on, and 20 to 22, 20 to 24, and so on). Given the large difference between 20 and 40 pounds, you may wish to use 30 pounds as your larger weight. In any case, use two weights that are easily detectable as different.

Record the observations: Record the data in a table similar to the table below. For the one-pound and 20-pound groups (base weights) record a plus sign (+) for each participant that detects a difference between the base weight and the step weight. Record a minus sign (-) for each participant that finds no difference. If one-tenth steps were not used, then replace the steps in the "Step Weight" columns with the step you are using.

Table 42.2.1.1: Results of JND Testing (+ = difference; – = no difference)

Step Weight	One pound	20 pounds	Step Weight
1.1			22
1.2			24
1.3			26
1.4			28
1.5			30
1.6			32
1.7			34
1.8			36
1.9			38
2.0			40

Analyze the data/report the results: What step weight did all participants find to be equal with one-pound base weight? What about the 20-pound group?

Draw a conclusion: Did the data support the hypothesis? Are the final weights proportionally the same? If not, why not? Do the findings adhere to Weber's Law? Weber's Law states that the concept that a just-noticeable difference in a stimulus is proportional to the magnitude of the original stimulus.

Summary

A sensory activation occurs when a physical or chemical stimulus is processed into a neural signal (sensory transduction) by a sensory receptor. Perception is an individual interpretation of a sensation and is a brain function. Humans have special senses: olfaction, gustation, equilibrium, and hearing, plus the general senses of somatosensation.

Sensory receptors are either specialized cells associated with sensory neurons or the specialized ends of sensory neurons that are a part of the peripheral nervous system, and they are used to receive information about the environment (internal or external). Each sensory receptor is modified for the type of stimulus it detects. For example, neither gustatory receptors nor auditory receptors are sensitive to light. Each sensory receptor is responsive to stimuli within a specific region in space, which is known as that receptor's receptive field. The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system.

All sensory signals, except those from the olfactory system, enter the central nervous system and are routed to the thalamus. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex dedicated to processing that particular sense.

Glossary

kinesthesia
sense of body movement

mechanoreceptor
sensory receptor modified to respond to mechanical disturbance such as being bent, touch, pressure, motion, and sound

perception
individual interpretation of a sensation; a brain function

proprioception
sense of limb position; used to track kinesthesia

reception
receipt of a signal (such as light or sound) by sensory receptors

receptive field
region in space in which a stimulus can activate a given sensory receptor

receptor potential
membrane potential in a sensory receptor in response to detection of a stimulus

sensory receptor
specialized neuron or other cells associated with a neuron that is modified to receive specific sensory input

sensory transduction
conversion of a sensory stimulus into electrical energy in the nervous system by a change in the membrane potential

vestibular sense
sense of spatial orientation and balance

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42.3: Synapses- Where Neurons Communicate With Other Cells

Skills to Develop

- Identify the spinal cord, cerebral lobes, and other brain areas on a diagram of the brain
- Describe the basic functions of the spinal cord, cerebral lobes, and other brain areas

The central nervous system (CNS) is made up of the brain, a part of which is shown in Figure **42.3.1** and spinal cord and is covered with three layers of protective coverings called meninges (from the Greek word for membrane). The outermost layer is the dura mater (Latin for “hard mother”). As the Latin suggests, the primary function for this thick layer is to protect the brain and spinal cord. The dura mater also contains vein-like structures that carry blood from the brain back to the heart. The middle layer is the web-like arachnoid mater. The last layer is the pia mater (Latin for “soft mother”), which directly contacts and covers the brain and spinal cord like plastic wrap. The space between the arachnoid and pia maters is filled with cerebrospinal fluid (CSF). CSF is produced by a tissue called choroid plexus in fluid-filled compartments in the CNS called ventricles. The brain floats in CSF, which acts as a cushion and shock absorber and makes the brain neutrally buoyant. CSF also functions to circulate chemical substances throughout the brain and into the spinal cord.

The entire brain contains only about 8.5 tablespoons of CSF, but CSF is constantly produced in the ventricles. This creates a problem when a ventricle is blocked—the CSF builds up and creates swelling and the brain is pushed against the skull. This swelling condition is called hydrocephalus (“water head”) and can cause seizures, cognitive problems, and even death if a shunt is not inserted to remove the fluid and pressure.

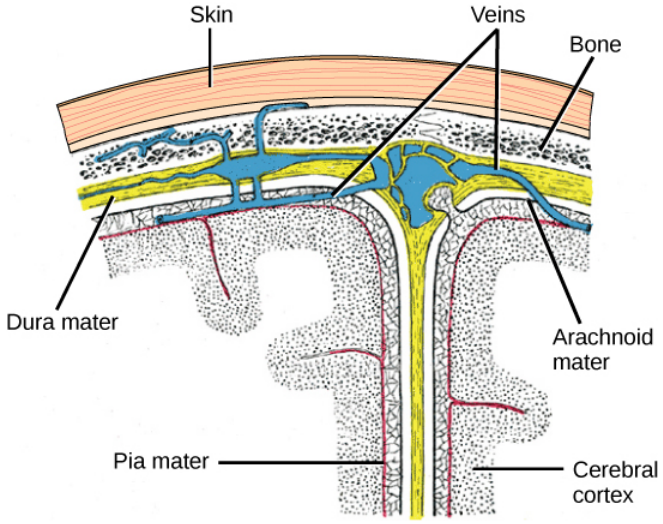


Figure **42.3.1**: The cerebral cortex is covered by three layers of meninges: the dura, arachnoid, and pia maters. (credit: modification of work by Gray’s Anatomy)

Brain

The brain is the part of the central nervous system that is contained in the cranial cavity of the skull. It includes the cerebral cortex, limbic system, basal ganglia, thalamus, hypothalamus, and cerebellum. There are three different ways that a brain can be sectioned in order to view internal structures: a sagittal section cuts the brain left to right, as shown in Figure **42.3.2b**, a coronal section cuts the brain front to back, as shown in Figure **42.3.2a**, and a horizontal section cuts the brain top to bottom.

Cerebral Cortex

The outermost part of the brain is a thick piece of nervous system tissue called the cerebral cortex, which is folded into hills called gyri (singular: gyrus) and valleys called sulci (singular: sulcus). The cortex is made up of two hemispheres—right and left—which are separated by a large sulcus. A thick fiber bundle called the corpus callosum (Latin: “tough body”) connects the two hemispheres and allows information to be passed from one side to the other. Although there are some brain functions that are localized more to one hemisphere than the other, the functions of the two hemispheres are largely redundant. In fact, sometimes (very rarely) an

entire hemisphere is removed to treat severe epilepsy. While patients do suffer some deficits following the surgery, they can have surprisingly few problems, especially when the surgery is performed on children who have very immature nervous systems.

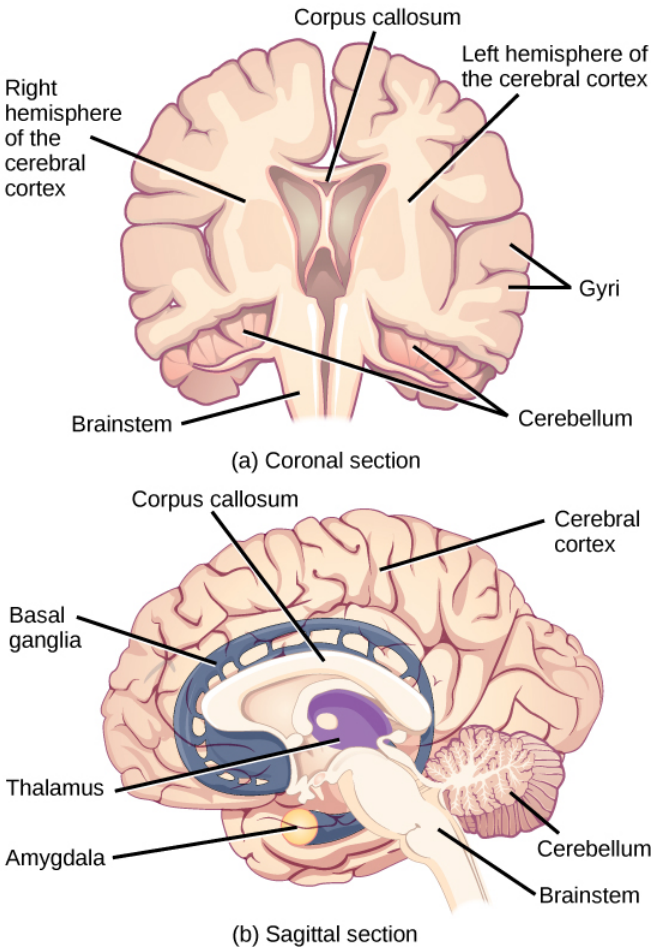


Figure **42.3.2**: These illustrations show the (a) coronal and (b) sagittal sections of the human brain.

In other surgeries to treat severe epilepsy, the corpus callosum is cut instead of removing an entire hemisphere. This causes a condition called split-brain, which gives insights into unique functions of the two hemispheres. For example, when an object is presented to patients' left visual field, they may be unable to verbally name the object (and may claim to not have seen an object at all). This is because the visual input from the left visual field crosses and enters the right hemisphere and cannot then signal to the speech center, which generally is found in the left side of the brain. Remarkably, if a split-brain patient is asked to pick up a specific object out of a group of objects with the left hand, the patient will be able to do so but will still be unable to vocally identify it.

Link to Learning

See this website to learn more about split-brain patients and to play a game where you can model the split-brain experiments yourself.

Each cortical hemisphere contains regions called lobes that are involved in different functions. Scientists use various techniques to determine what brain areas are involved in different functions: they examine patients who have had injuries or diseases that affect specific areas and see how those areas are related to functional deficits. They also conduct animal studies where they stimulate brain areas and see if there are any behavioral changes. They use a technique called transmagnetic stimulation (TMS) to temporarily deactivate specific parts of the cortex using strong magnets placed outside the head; and they use functional magnetic resonance imaging (fMRI) to look at changes in oxygenated blood flow in particular brain regions that correlate with specific behavioral tasks. These techniques, and others, have given great insight into the functions of different brain regions but have also showed that any given brain area can be involved in more than one behavior or process, and any given behavior or process generally involves neurons in multiple brain areas. That being said, each hemisphere of the mammalian cerebral cortex can be broken down into four functionally and spatially defined lobes: frontal, parietal, temporal, and occipital. Figure **42.3.3** illustrates these four lobes of the human cerebral cortex.

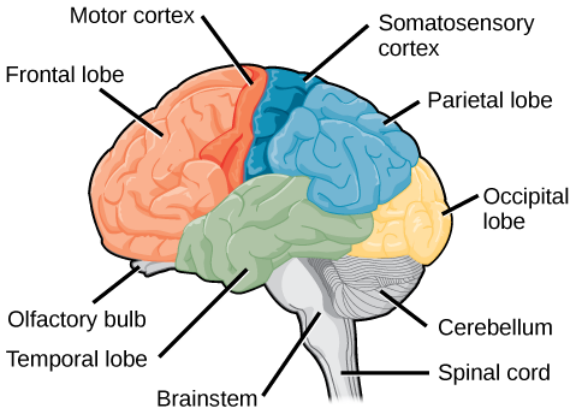


Figure **42.3.3**: The human cerebral cortex includes the frontal, parietal, temporal, and occipital lobes.

The frontal lobe is located at the front of the brain, over the eyes. This lobe contains the olfactory bulb, which processes smells. The frontal lobe also contains the motor cortex, which is important for planning and implementing movement. Areas within the motor cortex map to different muscle groups, and there is some organization to this map, as shown in Figure **42.3.4**. For example, the neurons that control movement of the fingers are next to the neurons that control movement of the hand. Neurons in the frontal lobe also control cognitive functions like maintaining attention, speech, and decision-making. Studies of humans who have damaged their frontal lobes show that parts of this area are involved in personality, socialization, and assessing risk.

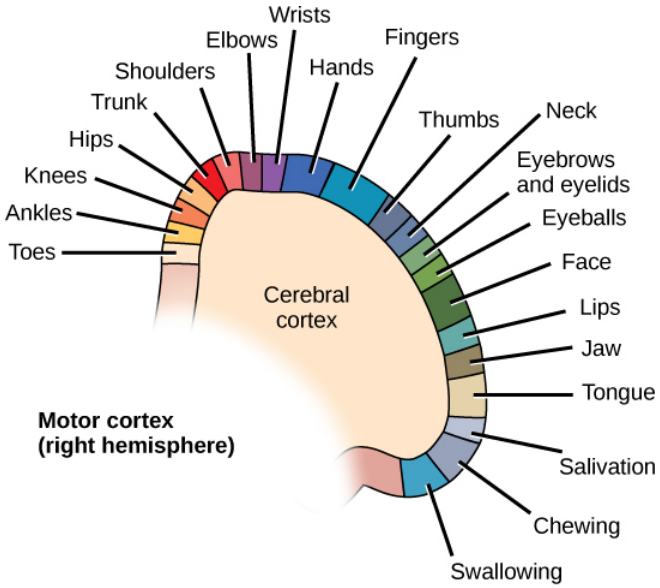


Figure 42.3.4: Different parts of the motor cortex control different muscle groups. Muscle groups that are neighbors in the body are generally controlled by neighboring regions of the motor cortex as well. For example, the neurons that control finger movement are near the neurons that control hand movement.

The parietal lobe is located at the top of the brain. Neurons in the parietal lobe are involved in speech and also reading. Two of the parietal lobe's main functions are processing somatosensation—touch sensations like pressure, pain, heat, cold—and processing proprioception—the sense of how parts of the body are oriented in space. The parietal lobe contains a somatosensory map of the body similar to the motor cortex.

The occipital lobe is located at the back of the brain. It is primarily involved in vision—seeing, recognizing, and identifying the visual world.

The temporal lobe is located at the base of the brain by your ears and is primarily involved in processing and interpreting sounds. It also contains the hippocampus (Greek for "seahorse")—a structure that processes memory formation. The hippocampus is illustrated in Figure 42.3.6. The role of the hippocampus in memory was partially determined by studying one famous epileptic patient, HM, who had both sides of his hippocampus removed in an attempt to cure his epilepsy. His seizures went away, but he could no longer form new memories (although he could remember some facts from before his surgery and could learn new motor tasks).

Evolution Connection: Cerebral Cortex

Compared to other vertebrates, mammals have exceptionally large brains for their body size. An entire alligator's brain, for example, would fill about one and a half teaspoons. This increase in brain to body size ratio is especially pronounced in apes, whales, and dolphins. While this increase in overall brain size doubtlessly played a role in the evolution of complex behaviors unique to mammals, it does not tell the whole story. Scientists have found a relationship between the relatively high surface area of the cortex and the intelligence and complex social behaviors exhibited by some mammals. This increased surface area is due, in part, to increased folding of the cortical sheet (more sulci and gyri). For example, a rat cortex is very smooth with very few sulci and gyri. Cat and sheep cortices have more sulci and gyri. Chimps, humans, and dolphins have even more.

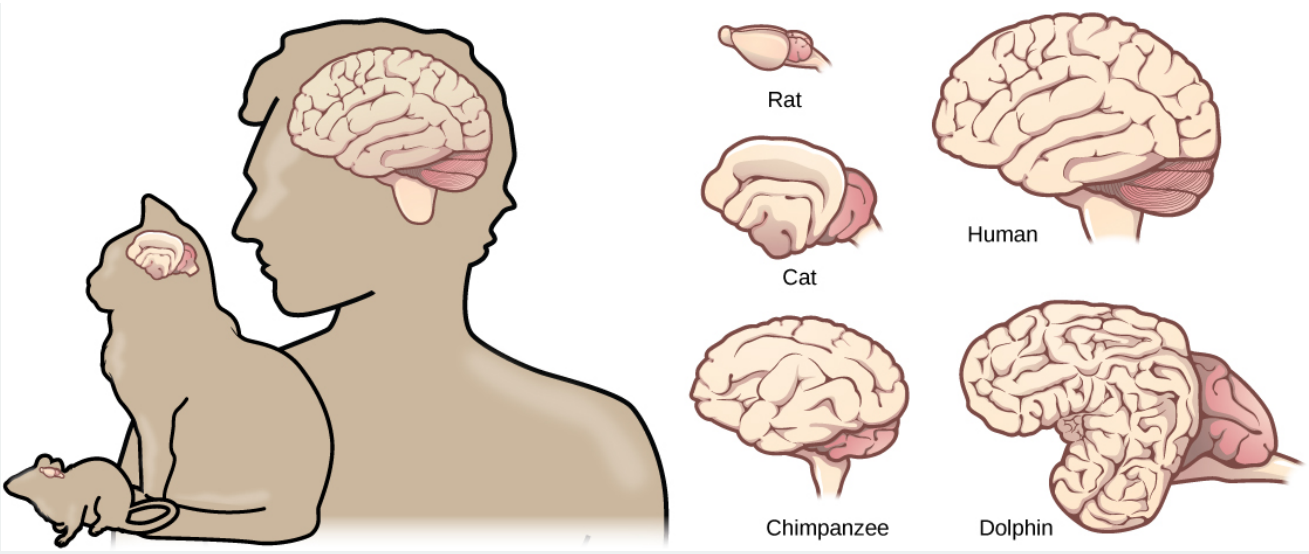


Figure **42.3.5**: Mammals have larger brain-to-body ratios than other vertebrates. Within mammals, increased cortical folding and surface area is correlated with complex behavior.

Basal Ganglia

Interconnected brain areas called the basal ganglia (or basal nuclei) play important roles in movement control and posture. Damage to the basal ganglia, as in Parkinson's disease, leads to motor impairments like a shuffling gait when walking. The basal ganglia also regulate motivation. For example, when a wasp sting led to bilateral basal ganglia damage in a 25-year-old businessman, he began to spend all his days in bed and showed no interest in anything or anybody. But when he was externally stimulated—as when someone asked to play a card game with him—he was able to function normally. Interestingly, he and other similar patients do not report feeling bored or frustrated by their state.

Thalamus

The thalamus (Greek for "inner chamber"), illustrated in Figure **42.3.6**, acts as a gateway to and from the cortex. It receives sensory and motor inputs from the body and also receives feedback from the cortex. This feedback mechanism can modulate conscious awareness of sensory and motor inputs depending on the attention and arousal state of the animal. The thalamus helps regulate consciousness, arousal, and sleep states. A rare genetic disorder called fatal familial insomnia causes the degeneration of thalamic neurons and glia. This disorder prevents affected patients from being able to sleep, among other symptoms, and is eventually fatal.

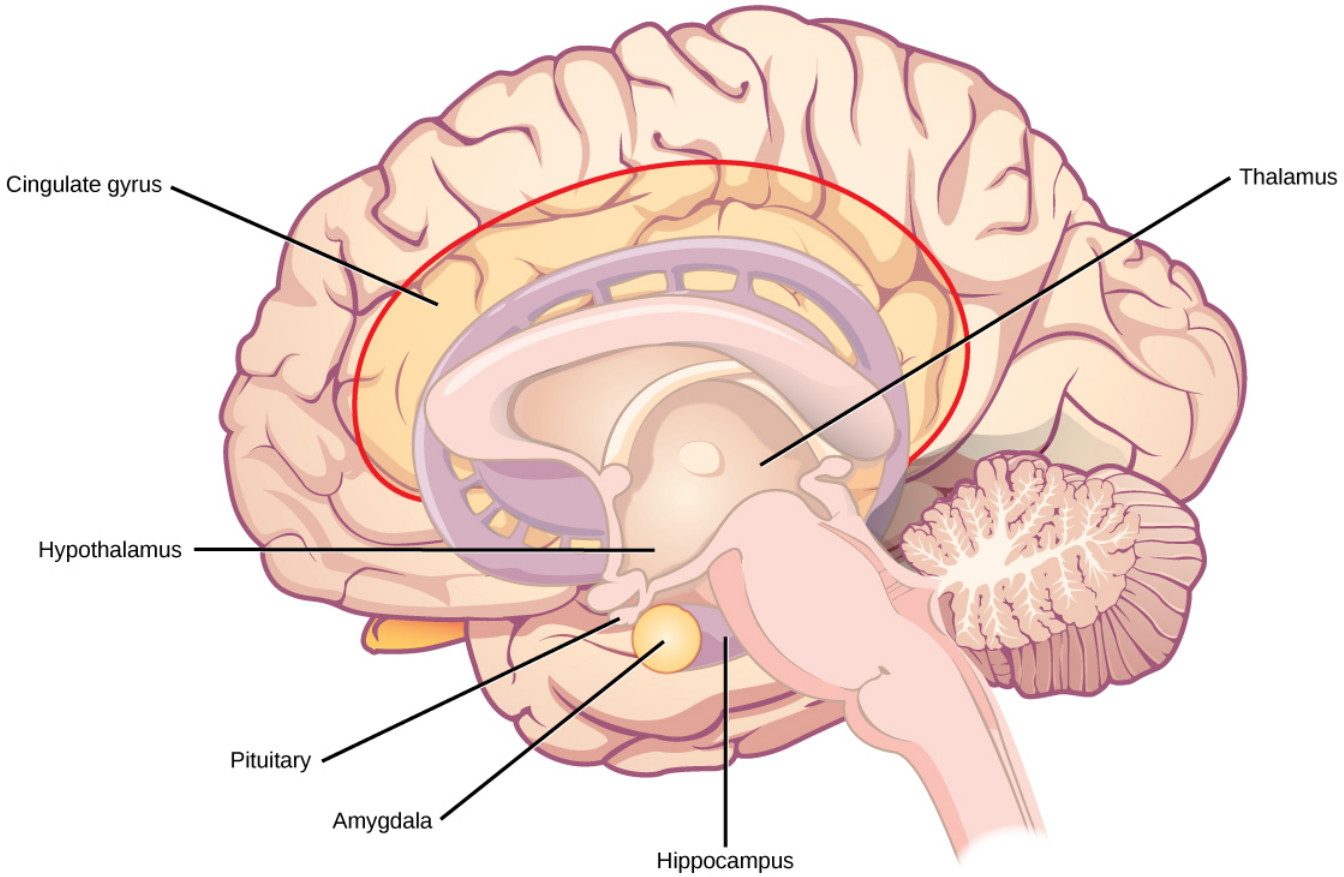


Figure 42.3.6: The limbic system regulates emotion and other behaviors. It includes parts of the cerebral cortex located near the center of the brain, including the cingulate gyrus and the hippocampus as well as the thalamus, hypothalamus and amygdala.

Hypothalamus

Below the thalamus is the hypothalamus, shown in Figure 42.3.6. The hypothalamus controls the endocrine system by sending signals to the pituitary gland, a pea-sized endocrine gland that releases several different hormones that affect other glands as well as other cells. This relationship means that the hypothalamus regulates important behaviors that are controlled by these hormones. The hypothalamus is the body's thermostat—it makes sure key functions like food and water intake, energy expenditure, and body temperature are kept at appropriate levels. Neurons within the hypothalamus also regulate circadian rhythms, sometimes called sleep cycles.

Limbic System

The limbic system is a connected set of structures that regulates emotion, as well as behaviors related to fear and motivation. It plays a role in memory formation and includes parts of the thalamus and hypothalamus as well as the hippocampus. One important structure within the limbic system is a temporal lobe structure called the amygdala (Greek for "almond"), illustrated in Figure 42.3.6. The two amygdala are important both for the sensation of fear and for recognizing fearful faces. The cingulate gyrus helps regulate emotions and pain.

Cerebellum

The cerebellum (Latin for "little brain"), shown in Figure 42.3.3, sits at the base of the brain on top of the brainstem. The cerebellum controls balance and aids in coordinating movement and learning new motor tasks.

Brainstem

The brainstem, illustrated in Figure 42.3.3, connects the rest of the brain with the spinal cord. It consists of the midbrain, medulla oblongata, and the pons. Motor and sensory neurons extend through the brainstem allowing for the relay of signals between the brain and spinal cord. Ascending neural pathways cross in this section of the brain allowing the left hemisphere of the cerebrum to

control the right side of the body and vice versa. The brainstem coordinates motor control signals sent from the brain to the body. The brainstem controls several important functions of the body including alertness, arousal, breathing, blood pressure, digestion, heart rate, swallowing, walking, and sensory and motor information integration.

Spinal Cord

Connecting to the brainstem and extending down the body through the spinal column is the spinal cord, shown in Figure **42.3.3**. The spinal cord is a thick bundle of nerve tissue that carries information about the body to the brain and from the brain to the body. The spinal cord is contained within the bones of the vertebrate column but is able to communicate signals to and from the body through its connections with spinal nerves (part of the peripheral nervous system). A cross-section of the spinal cord looks like a white oval containing a gray butterfly-shape, as illustrated in Figure **42.3.7**. Myelinated axons make up the "white matter" and neuron and glial cell bodies make up the "gray matter." Gray matter is also composed of interneurons, which connect two neurons each located in different parts of the body. Axons and cell bodies in the dorsal (facing the back of the animal) spinal cord convey mostly sensory information from the body to the brain. Axons and cell bodies in the ventral (facing the front of the animal) spinal cord primarily transmit signals controlling movement from the brain to the body.

The spinal cord also controls motor reflexes. These reflexes are quick, unconscious movements—like automatically removing a hand from a hot object. Reflexes are so fast because they involve local synaptic connections. For example, the knee reflex that a doctor tests during a routine physical is controlled by a single synapse between a sensory neuron and a motor neuron. While a reflex may only require the involvement of one or two synapses, synapses with interneurons in the spinal column transmit information to the brain to convey what happened (the knee jerked, or the hand was hot).

In the United States, there around 10,000 spinal cord injuries each year. Because the spinal cord is the information superhighway connecting the brain with the body, damage to the spinal cord can lead to paralysis. The extent of the paralysis depends on the location of the injury along the spinal cord and whether the spinal cord was completely severed. For example, if the spinal cord is damaged at the level of the neck, it can cause paralysis from the neck down, whereas damage to the spinal column further down may limit paralysis to the legs. Spinal cord injuries are notoriously difficult to treat because spinal nerves do not regenerate, although ongoing research suggests that stem cell transplants may be able to act as a bridge to reconnect severed nerves. Researchers are also looking at ways to prevent the inflammation that worsens nerve damage after injury. One such treatment is to pump the body with cold saline to induce hypothermia. This cooling can prevent swelling and other processes that are thought to worsen spinal cord injuries.

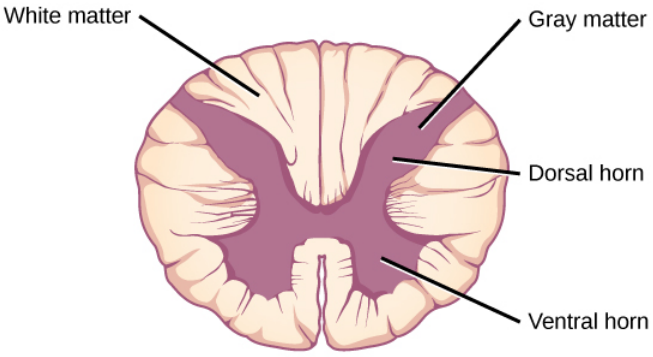


Figure **42.3.7**: A cross-section of the spinal cord shows gray matter (containing cell bodies and interneurons) and white matter (containing axons).

Summary

The vertebrate central nervous system contains the brain and the spinal cord, which are covered and protected by three meninges. The brain contains structurally and functionally defined regions. In mammals, these include the cortex (which can be broken down into four primary functional lobes: frontal, temporal, occipital, and parietal), basal ganglia, thalamus, hypothalamus, limbic system, cerebellum, and brainstem—although structures in some of these designations overlap. While functions may be primarily localized to one structure in the brain, most complex functions, like language and sleep, involve neurons in multiple brain regions. The spinal cord is the information superhighway that connects the brain with the rest of the body through its connections with peripheral nerves. It transmits sensory and motor input and also controls motor reflexes.

Glossary

amygdala
structure within the limbic system that processes fear

arachnoid mater
spiderweb-like middle layer of the meninges that cover the central nervous system

basal ganglia
interconnected collections of cells in the brain that are involved in movement and motivation; also known as basal nuclei

basal nuclei
see basal ganglia

brainstem
portion of the brain that connects with the spinal cord; controls basic nervous system functions like breathing, heart rate, and swallowing

cerebellum
brain structure involved in posture, motor coordination, and learning new motor actions

cerebral cortex
outermost sheet of brain tissue; involved in many higher-order functions

choroid plexus
spongy tissue within ventricles that produces cerebrospinal fluid

cingulate gyrus
helps regulate emotions and pain; thought to directly drive the body's conscious response to unpleasant experiences

corpus callosum
thick fiber bundle that connects the cerebral hemispheres

cerebrospinal fluid (CSF)
clear liquid that surrounds the brain and spinal cord and fills the ventricles and central canal; acts as a shock absorber and circulates material throughout the brain and spinal cord.

dura mater
tough outermost layer that covers the central nervous system

frontal lobe
part of the cerebral cortex that contains the motor cortex and areas involved in planning, attention, and language

gyrus
(plural: gyri) ridged protrusions in the cortex

hippocampus
brain structure in the temporal lobe involved in processing memories

hypothalamus
brain structure that controls hormone release and body homeostasis

limbic system

connected brain areas that process emotion and motivation

meninge
membrane that covers and protects the central nervous system

occipital lobe
part of the cerebral cortex that contains visual cortex and processes visual stimuli

parietal lobe
part of the cerebral cortex involved in processing touch and the sense of the body in space

pia mater
thin membrane layer directly covering the brain and spinal cord

proprioception
sense about how parts of the body are oriented in space

somatosensation
sense of touch

spinal cord
thick fiber bundle that connects the brain with peripheral nerves; transmits sensory and motor information; contains neurons that control motor reflexes

sulcus
(plural: sulci) indents or “valleys” in the cortex

temporal lobe
part of the cerebral cortex that processes auditory input; parts of the temporal lobe are involved in speech, memory, and emotion processing

thalamus
brain area that relays sensory information to the cortex

ventricle
cavity within brain that contains cerebrospinal fluid

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42.4: The Central Nervous System- Brain and Spinal Cord

Skills to Develop

- Identify the spinal cord, cerebral lobes, and other brain areas on a diagram of the brain
- Describe the basic functions of the spinal cord, cerebral lobes, and other brain areas

The central nervous system (CNS) is made up of the brain, a part of which is shown in Figure **42.4.1** and spinal cord and is covered with three layers of protective coverings called meninges (from the Greek word for membrane). The outermost layer is the dura mater (Latin for “hard mother”). As the Latin suggests, the primary function for this thick layer is to protect the brain and spinal cord. The dura mater also contains vein-like structures that carry blood from the brain back to the heart. The middle layer is the web-like arachnoid mater. The last layer is the pia mater (Latin for “soft mother”), which directly contacts and covers the brain and spinal cord like plastic wrap. The space between the arachnoid and pia maters is filled with cerebrospinal fluid (CSF). CSF is produced by a tissue called choroid plexus in fluid-filled compartments in the CNS called ventricles. The brain floats in CSF, which acts as a cushion and shock absorber and makes the brain neutrally buoyant. CSF also functions to circulate chemical substances throughout the brain and into the spinal cord.

The entire brain contains only about 8.5 tablespoons of CSF, but CSF is constantly produced in the ventricles. This creates a problem when a ventricle is blocked—the CSF builds up and creates swelling and the brain is pushed against the skull. This swelling condition is called hydrocephalus (“water head”) and can cause seizures, cognitive problems, and even death if a shunt is not inserted to remove the fluid and pressure.

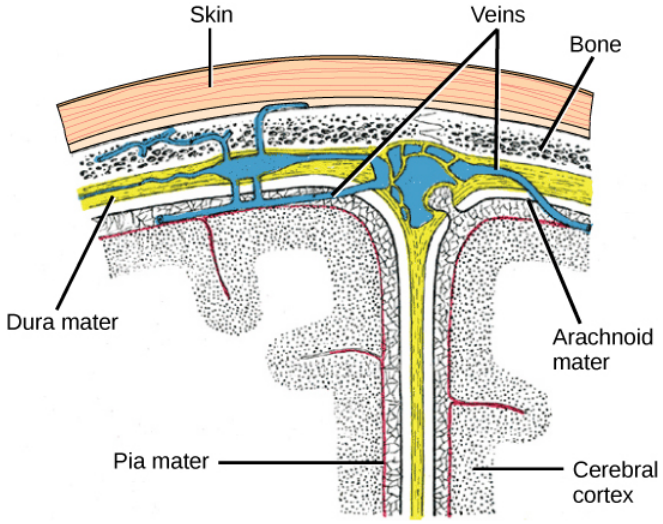


Figure **42.4.1**: The cerebral cortex is covered by three layers of meninges: the dura, arachnoid, and pia maters. (credit: modification of work by Gray’s Anatomy)

Brain

The brain is the part of the central nervous system that is contained in the cranial cavity of the skull. It includes the cerebral cortex, limbic system, basal ganglia, thalamus, hypothalamus, and cerebellum. There are three different ways that a brain can be sectioned in order to view internal structures: a sagittal section cuts the brain left to right, as shown in Figure **42.4.2b**, a coronal section cuts the brain front to back, as shown in Figure **42.4.2a**, and a horizontal section cuts the brain top to bottom.

Cerebral Cortex

The outermost part of the brain is a thick piece of nervous system tissue called the cerebral cortex, which is folded into hills called gyri (singular: gyrus) and valleys called sulci (singular: sulcus). The cortex is made up of two hemispheres—right and left—which are separated by a large sulcus. A thick fiber bundle called the corpus callosum (Latin: “tough body”) connects the two hemispheres and allows information to be passed from one side to the other. Although there are some brain functions that are localized more to one hemisphere than the other, the functions of the two hemispheres are largely redundant. In fact, sometimes (very rarely) an

entire hemisphere is removed to treat severe epilepsy. While patients do suffer some deficits following the surgery, they can have surprisingly few problems, especially when the surgery is performed on children who have very immature nervous systems.

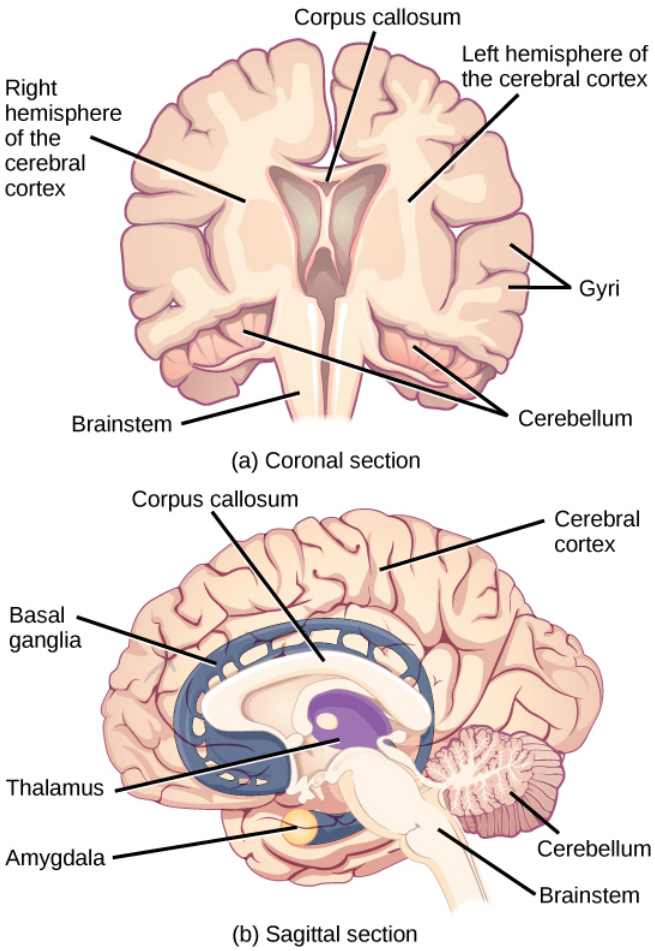


Figure **42.4.2**: These illustrations show the (a) coronal and (b) sagittal sections of the human brain.

In other surgeries to treat severe epilepsy, the corpus callosum is cut instead of removing an entire hemisphere. This causes a condition called split-brain, which gives insights into unique functions of the two hemispheres. For example, when an object is presented to patients' left visual field, they may be unable to verbally name the object (and may claim to not have seen an object at all). This is because the visual input from the left visual field crosses and enters the right hemisphere and cannot then signal to the speech center, which generally is found in the left side of the brain. Remarkably, if a split-brain patient is asked to pick up a specific object out of a group of objects with the left hand, the patient will be able to do so but will still be unable to vocally identify it.

Link to Learning

See this website to learn more about split-brain patients and to play a game where you can model the split-brain experiments yourself.

Each cortical hemisphere contains regions called lobes that are involved in different functions. Scientists use various techniques to determine what brain areas are involved in different functions: they examine patients who have had injuries or diseases that affect specific areas and see how those areas are related to functional deficits. They also conduct animal studies where they stimulate brain areas and see if there are any behavioral changes. They use a technique called transmagnetic stimulation (TMS) to temporarily deactivate specific parts of the cortex using strong magnets placed outside the head; and they use functional magnetic resonance imaging (fMRI) to look at changes in oxygenated blood flow in particular brain regions that correlate with specific behavioral tasks. These techniques, and others, have given great insight into the functions of different brain regions but have also showed that any given brain area can be involved in more than one behavior or process, and any given behavior or process generally involves neurons in multiple brain areas. That being said, each hemisphere of the mammalian cerebral cortex can be broken down into four functionally and spatially defined lobes: frontal, parietal, temporal, and occipital. Figure **42.4.3** illustrates these four lobes of the human cerebral cortex.

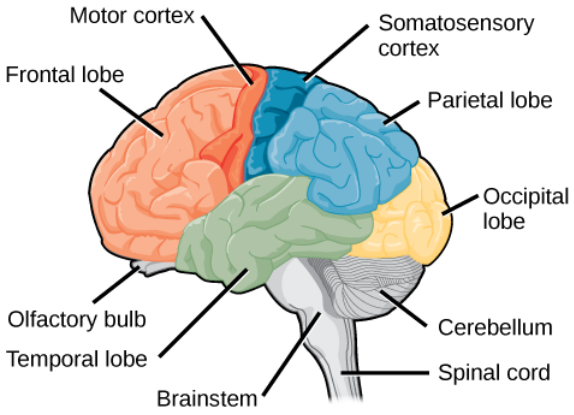


Figure **42.4.3**: The human cerebral cortex includes the frontal, parietal, temporal, and occipital lobes.

The frontal lobe is located at the front of the brain, over the eyes. This lobe contains the olfactory bulb, which processes smells. The frontal lobe also contains the motor cortex, which is important for planning and implementing movement. Areas within the motor cortex map to different muscle groups, and there is some organization to this map, as shown in Figure **42.4.4**. For example, the neurons that control movement of the fingers are next to the neurons that control movement of the hand. Neurons in the frontal lobe also control cognitive functions like maintaining attention, speech, and decision-making. Studies of humans who have damaged their frontal lobes show that parts of this area are involved in personality, socialization, and assessing risk.

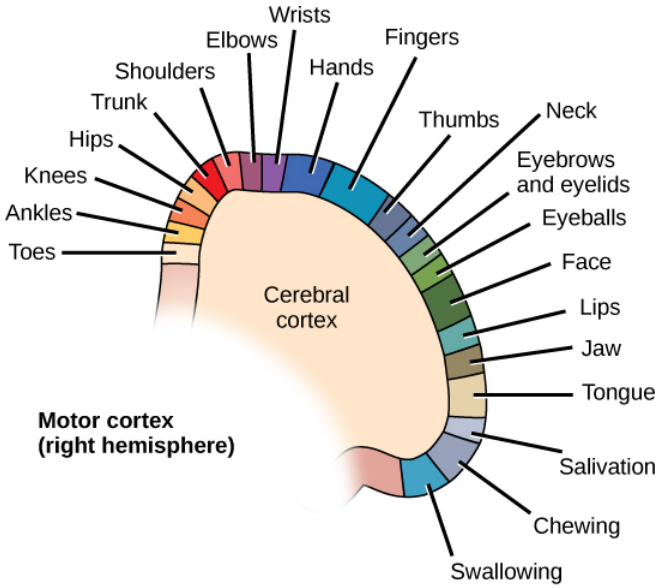


Figure 42.4.4: Different parts of the motor cortex control different muscle groups. Muscle groups that are neighbors in the body are generally controlled by neighboring regions of the motor cortex as well. For example, the neurons that control finger movement are near the neurons that control hand movement.

The parietal lobe is located at the top of the brain. Neurons in the parietal lobe are involved in speech and also reading. Two of the parietal lobe's main functions are processing somatosensation—touch sensations like pressure, pain, heat, cold—and processing proprioception—the sense of how parts of the body are oriented in space. The parietal lobe contains a somatosensory map of the body similar to the motor cortex.

The occipital lobe is located at the back of the brain. It is primarily involved in vision—seeing, recognizing, and identifying the visual world.

The temporal lobe is located at the base of the brain by your ears and is primarily involved in processing and interpreting sounds. It also contains the hippocampus (Greek for "seahorse")—a structure that processes memory formation. The hippocampus is illustrated in Figure 42.4.6. The role of the hippocampus in memory was partially determined by studying one famous epileptic patient, HM, who had both sides of his hippocampus removed in an attempt to cure his epilepsy. His seizures went away, but he could no longer form new memories (although he could remember some facts from before his surgery and could learn new motor tasks).

Evolution Connection: Cerebral Cortex

Compared to other vertebrates, mammals have exceptionally large brains for their body size. An entire alligator's brain, for example, would fill about one and a half teaspoons. This increase in brain to body size ratio is especially pronounced in apes, whales, and dolphins. While this increase in overall brain size doubtlessly played a role in the evolution of complex behaviors unique to mammals, it does not tell the whole story. Scientists have found a relationship between the relatively high surface area of the cortex and the intelligence and complex social behaviors exhibited by some mammals. This increased surface area is due, in part, to increased folding of the cortical sheet (more sulci and gyri). For example, a rat cortex is very smooth with very few sulci and gyri. Cat and sheep cortices have more sulci and gyri. Chimps, humans, and dolphins have even more.

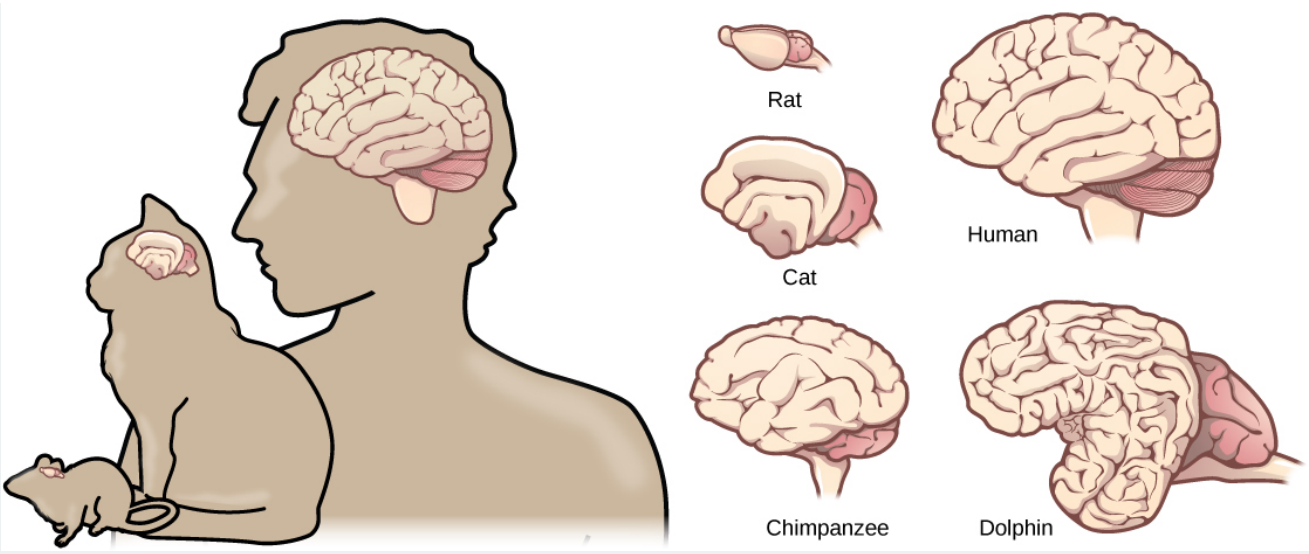


Figure 42.4.5: Mammals have larger brain-to-body ratios than other vertebrates. Within mammals, increased cortical folding and surface area is correlated with complex behavior.

Basal Ganglia

Interconnected brain areas called the basal ganglia (or basal nuclei) play important roles in movement control and posture. Damage to the basal ganglia, as in Parkinson's disease, leads to motor impairments like a shuffling gait when walking. The basal ganglia also regulate motivation. For example, when a wasp sting led to bilateral basal ganglia damage in a 25-year-old businessman, he began to spend all his days in bed and showed no interest in anything or anybody. But when he was externally stimulated—as when someone asked to play a card game with him—he was able to function normally. Interestingly, he and other similar patients do not report feeling bored or frustrated by their state.

Thalamus

The thalamus (Greek for "inner chamber"), illustrated in Figure 42.4.6, acts as a gateway to and from the cortex. It receives sensory and motor inputs from the body and also receives feedback from the cortex. This feedback mechanism can modulate conscious awareness of sensory and motor inputs depending on the attention and arousal state of the animal. The thalamus helps regulate consciousness, arousal, and sleep states. A rare genetic disorder called fatal familial insomnia causes the degeneration of thalamic neurons and glia. This disorder prevents affected patients from being able to sleep, among other symptoms, and is eventually fatal.

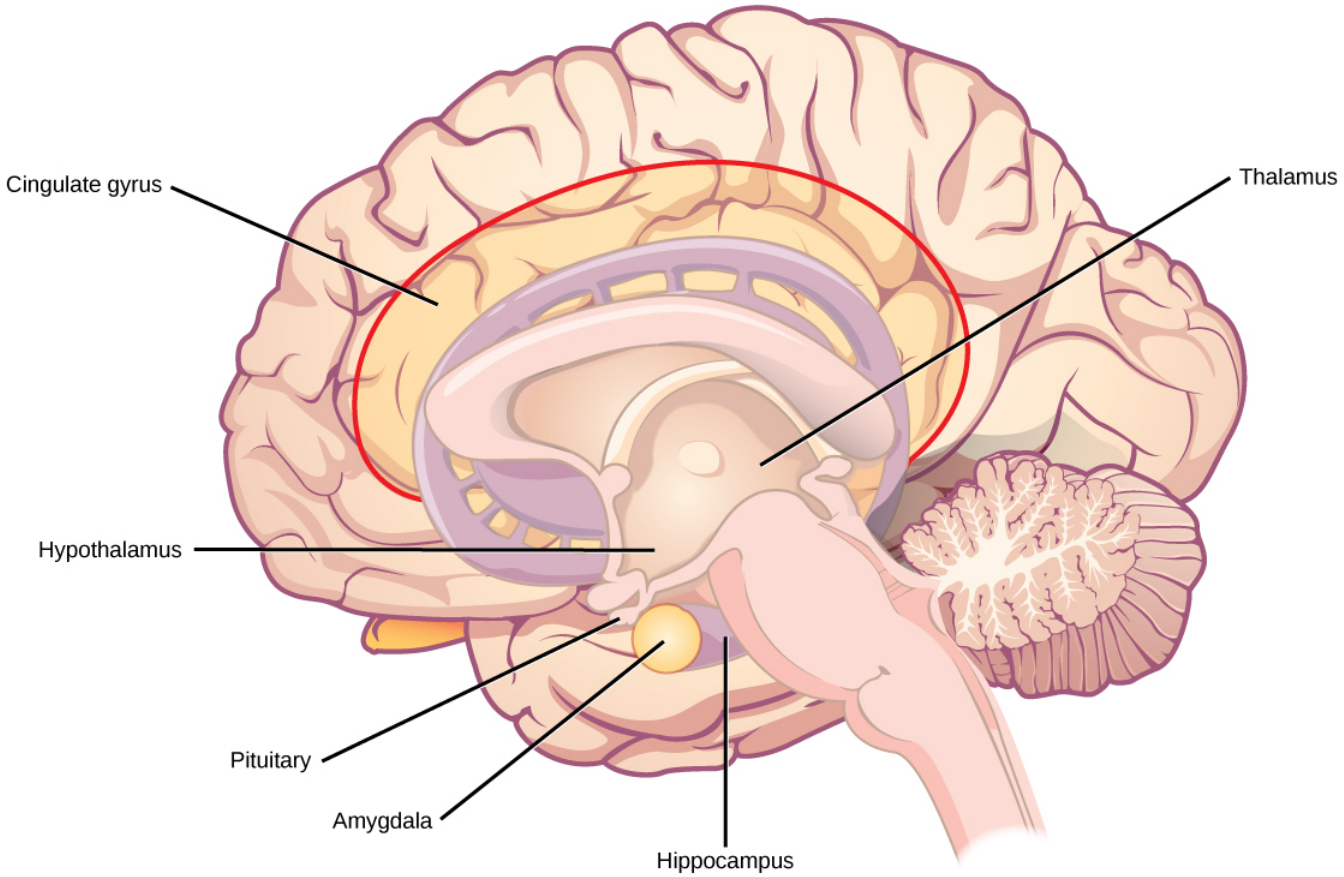


Figure 42.4.6: The limbic system regulates emotion and other behaviors. It includes parts of the cerebral cortex located near the center of the brain, including the cingulate gyrus and the hippocampus as well as the thalamus, hypothalamus and amygdala.

Hypothalamus

Below the thalamus is the hypothalamus, shown in Figure 42.4.6. The hypothalamus controls the endocrine system by sending signals to the pituitary gland, a pea-sized endocrine gland that releases several different hormones that affect other glands as well as other cells. This relationship means that the hypothalamus regulates important behaviors that are controlled by these hormones. The hypothalamus is the body's thermostat—it makes sure key functions like food and water intake, energy expenditure, and body temperature are kept at appropriate levels. Neurons within the hypothalamus also regulate circadian rhythms, sometimes called sleep cycles.

Limbic System

The limbic system is a connected set of structures that regulates emotion, as well as behaviors related to fear and motivation. It plays a role in memory formation and includes parts of the thalamus and hypothalamus as well as the hippocampus. One important structure within the limbic system is a temporal lobe structure called the amygdala (Greek for "almond"), illustrated in Figure 42.4.6. The two amygdala are important both for the sensation of fear and for recognizing fearful faces. The cingulate gyrus helps regulate emotions and pain.

Cerebellum

The cerebellum (Latin for "little brain"), shown in Figure 42.4.3, sits at the base of the brain on top of the brainstem. The cerebellum controls balance and aids in coordinating movement and learning new motor tasks.

Brainstem

The brainstem, illustrated in Figure 42.4.3, connects the rest of the brain with the spinal cord. It consists of the midbrain, medulla oblongata, and the pons. Motor and sensory neurons extend through the brainstem allowing for the relay of signals between the brain and spinal cord. Ascending neural pathways cross in this section of the brain allowing the left hemisphere of the cerebrum to

control the right side of the body and vice versa. The brainstem coordinates motor control signals sent from the brain to the body. The brainstem controls several important functions of the body including alertness, arousal, breathing, blood pressure, digestion, heart rate, swallowing, walking, and sensory and motor information integration.

Spinal Cord

Connecting to the brainstem and extending down the body through the spinal column is the spinal cord, shown in Figure **42.4.3**. The spinal cord is a thick bundle of nerve tissue that carries information about the body to the brain and from the brain to the body. The spinal cord is contained within the bones of the vertebrate column but is able to communicate signals to and from the body through its connections with spinal nerves (part of the peripheral nervous system). A cross-section of the spinal cord looks like a white oval containing a gray butterfly-shape, as illustrated in Figure **42.4.7**. Myelinated axons make up the "white matter" and neuron and glial cell bodies make up the "gray matter." Gray matter is also composed of interneurons, which connect two neurons each located in different parts of the body. Axons and cell bodies in the dorsal (facing the back of the animal) spinal cord convey mostly sensory information from the body to the brain. Axons and cell bodies in the ventral (facing the front of the animal) spinal cord primarily transmit signals controlling movement from the brain to the body.

The spinal cord also controls motor reflexes. These reflexes are quick, unconscious movements—like automatically removing a hand from a hot object. Reflexes are so fast because they involve local synaptic connections. For example, the knee reflex that a doctor tests during a routine physical is controlled by a single synapse between a sensory neuron and a motor neuron. While a reflex may only require the involvement of one or two synapses, synapses with interneurons in the spinal column transmit information to the brain to convey what happened (the knee jerked, or the hand was hot).

In the United States, there around 10,000 spinal cord injuries each year. Because the spinal cord is the information superhighway connecting the brain with the body, damage to the spinal cord can lead to paralysis. The extent of the paralysis depends on the location of the injury along the spinal cord and whether the spinal cord was completely severed. For example, if the spinal cord is damaged at the level of the neck, it can cause paralysis from the neck down, whereas damage to the spinal column further down may limit paralysis to the legs. Spinal cord injuries are notoriously difficult to treat because spinal nerves do not regenerate, although ongoing research suggests that stem cell transplants may be able to act as a bridge to reconnect severed nerves. Researchers are also looking at ways to prevent the inflammation that worsens nerve damage after injury. One such treatment is to pump the body with cold saline to induce hypothermia. This cooling can prevent swelling and other processes that are thought to worsen spinal cord injuries.

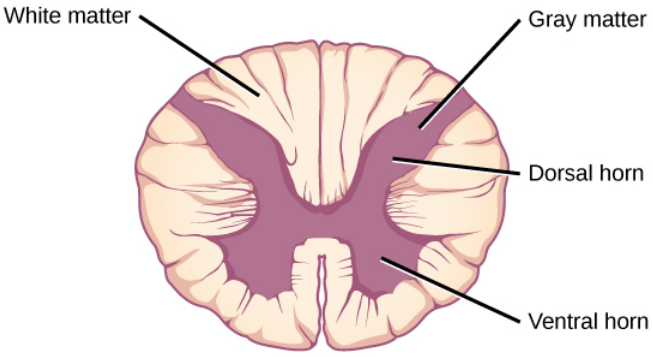


Figure **42.4.7**: A cross-section of the spinal cord shows gray matter (containing cell bodies and interneurons) and white matter (containing axons).

Summary

The vertebrate central nervous system contains the brain and the spinal cord, which are covered and protected by three meninges. The brain contains structurally and functionally defined regions. In mammals, these include the cortex (which can be broken down into four primary functional lobes: frontal, temporal, occipital, and parietal), basal ganglia, thalamus, hypothalamus, limbic system, cerebellum, and brainstem—although structures in some of these designations overlap. While functions may be primarily localized to one structure in the brain, most complex functions, like language and sleep, involve neurons in multiple brain regions. The spinal cord is the information superhighway that connects the brain with the rest of the body through its connections with peripheral nerves. It transmits sensory and motor input and also controls motor reflexes.

Glossary

amygdala
structure within the limbic system that processes fear

arachnoid mater
spiderweb-like middle layer of the meninges that cover the central nervous system

basal ganglia
interconnected collections of cells in the brain that are involved in movement and motivation; also known as basal nuclei

basal nuclei
see basal ganglia

brainstem
portion of the brain that connects with the spinal cord; controls basic nervous system functions like breathing, heart rate, and swallowing

cerebellum
brain structure involved in posture, motor coordination, and learning new motor actions

cerebral cortex
outermost sheet of brain tissue; involved in many higher-order functions

choroid plexus
spongy tissue within ventricles that produces cerebrospinal fluid

cingulate gyrus
helps regulate emotions and pain; thought to directly drive the body's conscious response to unpleasant experiences

corpus callosum
thick fiber bundle that connects the cerebral hemispheres

cerebrospinal fluid (CSF)
clear liquid that surrounds the brain and spinal cord and fills the ventricles and central canal; acts as a shock absorber and circulates material throughout the brain and spinal cord.

dura mater
tough outermost layer that covers the central nervous system

frontal lobe
part of the cerebral cortex that contains the motor cortex and areas involved in planning, attention, and language

gyrus
(plural: gyri) ridged protrusions in the cortex

hippocampus
brain structure in the temporal lobe involved in processing memories

hypothalamus
brain structure that controls hormone release and body homeostasis

limbic system

connected brain areas that process emotion and motivation

meninge
membrane that covers and protects the central nervous system

occipital lobe
part of the cerebral cortex that contains visual cortex and processes visual stimuli

parietal lobe
part of the cerebral cortex involved in processing touch and the sense of the body in space

pia mater
thin membrane layer directly covering the brain and spinal cord

proprioception
sense about how parts of the body are oriented in space

somatosensation
sense of touch

spinal cord
thick fiber bundle that connects the brain with peripheral nerves; transmits sensory and motor information; contains neurons that control motor reflexes

sulcus
(plural: sulci) indents or “valleys” in the cortex

temporal lobe
part of the cerebral cortex that processes auditory input; parts of the temporal lobe are involved in speech, memory, and emotion processing

thalamus
brain area that relays sensory information to the cortex

ventricle
cavity within brain that contains cerebrospinal fluid

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42.5: The Peripheral Nervous System- Spinal and Cranial Nerves

Skills to Develop

- Describe the organization and functions of the sympathetic and parasympathetic nervous systems
- Describe the organization and function of the sensory-somatic nervous system

The peripheral nervous system (PNS) is the connection between the central nervous system and the rest of the body. The CNS is like the power plant of the nervous system. It creates the signals that control the functions of the body. The PNS is like the wires that go to individual houses. Without those “wires,” the signals produced by the CNS could not control the body (and the CNS would not be able to receive sensory information from the body either).

The PNS can be broken down into the autonomic nervous system, which controls bodily functions without conscious control, and the sensory-somatic nervous system, which transmits sensory information from the skin, muscles, and sensory organs to the CNS and sends motor commands from the CNS to the muscles.

Autonomic Nervous System

Art Connection

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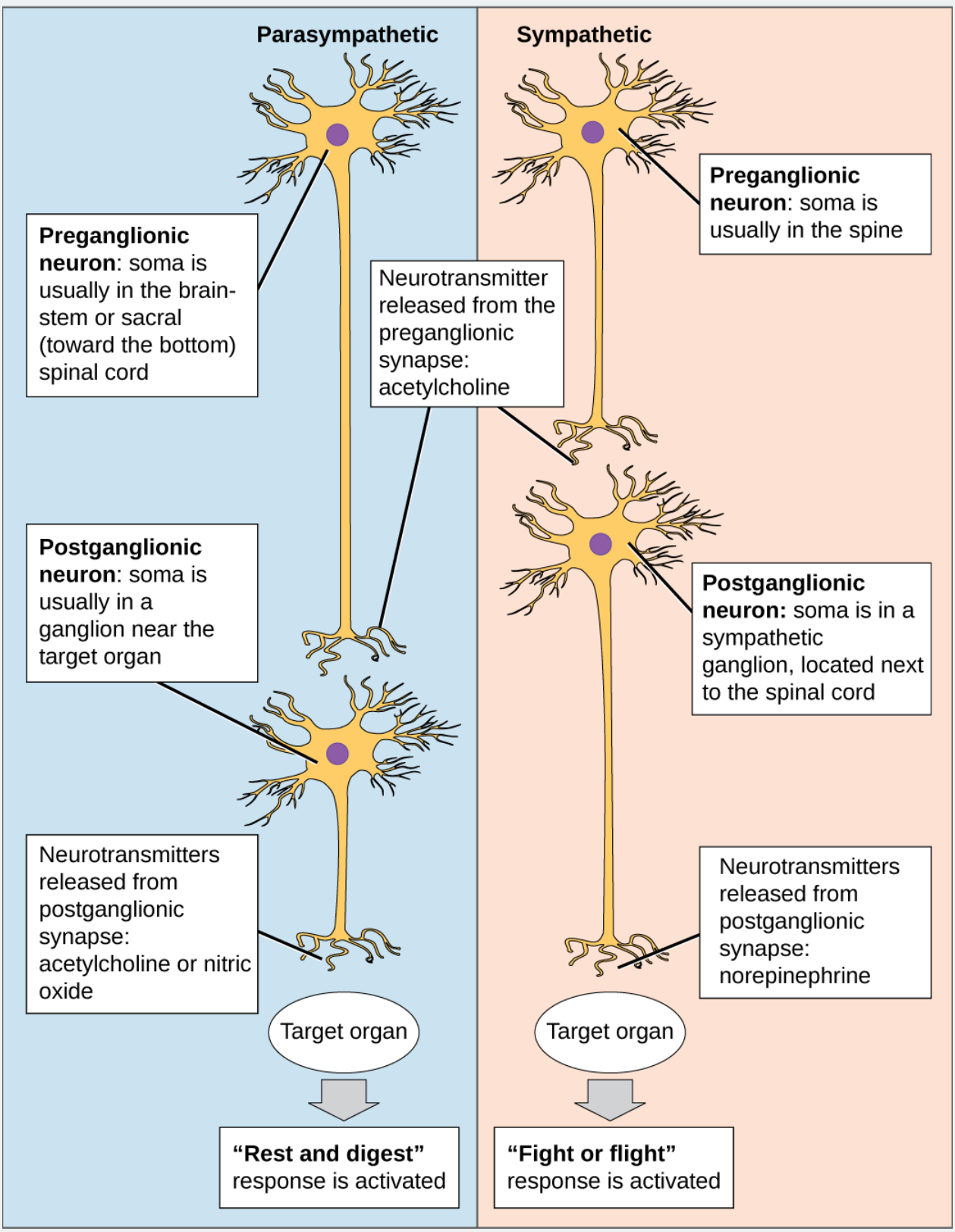


Figure 42.5.1: In the autonomic nervous system, a preganglionic neuron of the CNS synapses with a postganglionic neuron of the PNS. The postganglionic neuron, in turn, acts on a target organ. Autonomic responses are mediated by the sympathetic and the parasympathetic systems, which are antagonistic to one another. The sympathetic system activates the "fight or flight" response, while the parasympathetic system activates the "rest and digest" response.

Which of the following statements is false?

A. The parasympathetic pathway is responsible for resting the body, while the sympathetic pathway is responsible for preparing for an emergency.
B. Most preganglionic neurons in the sympathetic pathway originate in the spinal cord.
C. Slowing of the heartbeat is a parasympathetic response.
D. Parasympathetic neurons are responsible for releasing norepinephrine on the target organ, while sympathetic neurons are responsible for releasing acetylcholine.

The autonomic nervous system serves as the relay between the CNS and the internal organs. It controls the lungs, the heart, smooth muscle, and exocrine and endocrine glands. The autonomic nervous system controls these organs largely without conscious control; it can continuously monitor the conditions of these different systems and implement changes as needed. Signaling to the target tissue usually involves two synapses: a preganglionic neuron (originating in the CNS) synapses to a neuron in a ganglion that, in turn, synapses on the target organ, as illustrated in Figure **42.5.1**. There are two divisions of the autonomic nervous system that often have opposing effects: the sympathetic nervous system and the parasympathetic nervous system.

Sympathetic Nervous System

The sympathetic nervous system is responsible for the “fight or flight” response that occurs when an animal encounters a dangerous situation. One way to remember this is to think of the surprise a person feels when encountering a snake (“snake” and “sympathetic” both begin with “s”). Examples of functions controlled by the sympathetic nervous system include an accelerated heart rate and inhibited digestion. These functions help prepare an organism’s body for the physical strain required to escape a potentially dangerous situation or to fend off a predator.

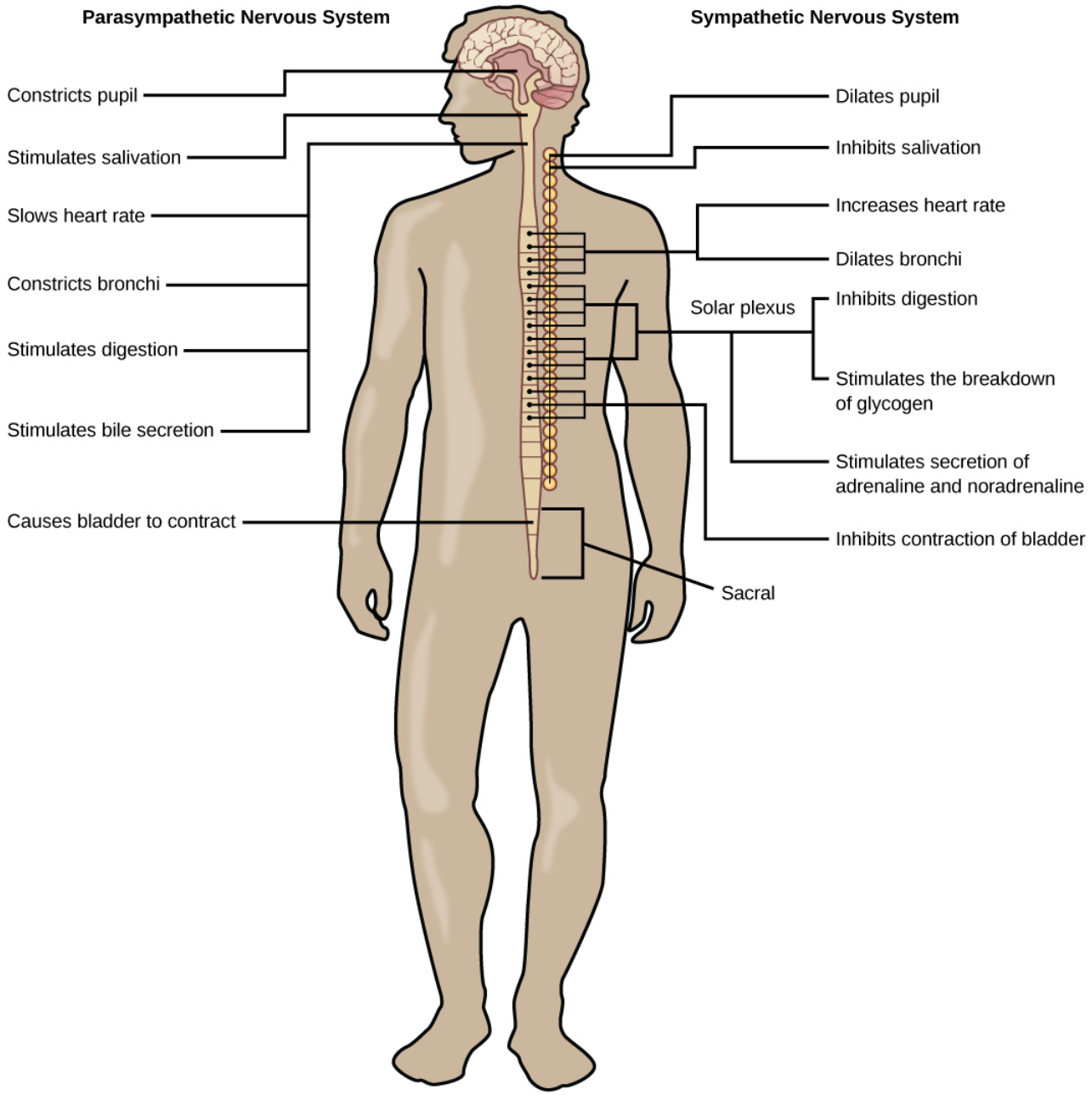


Figure **42.5.2**: The sympathetic and parasympathetic nervous systems often have opposing effects on target organs.

Most preganglionic neurons in the sympathetic nervous system originate in the spinal cord, as illustrated in Figure **42.5.2**. The axons of these neurons release acetylcholine on postganglionic neurons within sympathetic ganglia (the sympathetic ganglia form a chain that extends alongside the spinal cord). The acetylcholine activates the postganglionic neurons. Postganglionic neurons then release norepinephrine onto target organs. As anyone who has ever felt a rush before a big test, speech, or athletic event can attest, the effects of the sympathetic nervous system are quite pervasive. This is both because one preganglionic neuron synapses on multiple postganglionic neurons, amplifying the effect of the original synapse, and because the adrenal gland also releases norepinephrine (and the closely related hormone epinephrine) into the blood stream. The physiological effects of this norepinephrine release include dilating the trachea and bronchi (making it easier for the animal to breathe), increasing heart rate, and moving blood from the skin to the heart, muscles, and brain (so the animal can think and run). The strength and speed of the sympathetic response helps an organism avoid danger, and scientists have found evidence that it may also increase LTP—allowing the animal to remember the dangerous situation and avoid it in the future.

Parasympathetic Nervous System

While the sympathetic nervous system is activated in stressful situations, the parasympathetic nervous system allows an animal to "rest and digest." One way to remember this is to think that during a restful situation like a picnic, the parasympathetic nervous system is in control ("picnic" and "parasympathetic" both start with "p"). Parasympathetic preganglionic neurons have cell bodies located in the brainstem and in the sacral (toward the bottom) spinal cord, as shown in Figure **42.5.2**. The axons of the preganglionic neurons release acetylcholine on the postganglionic neurons, which are generally located very near the target organs. Most postganglionic neurons release acetylcholine onto target organs, although some release nitric oxide.

The parasympathetic nervous system resets organ function after the sympathetic nervous system is activated (the common adrenaline dump you feel after a 'fight-or-flight' event). Effects of acetylcholine release on target organs include slowing of heart rate, lowered blood pressure, and stimulation of digestion.

Sensory-Somatic Nervous System

The sensory-somatic nervous system is made up of cranial and spinal nerves and contains both sensory and motor neurons. Sensory neurons transmit sensory information from the skin, skeletal muscle, and sensory organs to the CNS. Motor neurons transmit messages about desired movement from the CNS to the muscles to make them contract. Without its sensory-somatic nervous system, an animal would be unable to process any information about its environment (what it sees, feels, hears, and so on) and could not control motor movements. Unlike the autonomic nervous system, which has two synapses between the CNS and the target organ, sensory and motor neurons have only one synapse—one ending of the neuron is at the organ and the other directly contacts a CNS neuron. Acetylcholine is the main neurotransmitter released at these synapses.

Humans have 12 cranial nerves, nerves that emerge from or enter the skull (cranium), as opposed to the spinal nerves, which emerge from the vertebral column. Each cranial nerve is accorded a name, which are detailed in Figure **42.5.3**. Some cranial nerves transmit only sensory information. For example, the olfactory nerve transmits information about smells from the nose to the brainstem. Other cranial nerves transmit almost solely motor information. For example, the oculomotor nerve controls the opening and closing of the eyelid and some eye movements. Other cranial nerves contain a mix of sensory and motor fibers. For example, the glossopharyngeal nerve has a role in both taste (sensory) and swallowing (motor).

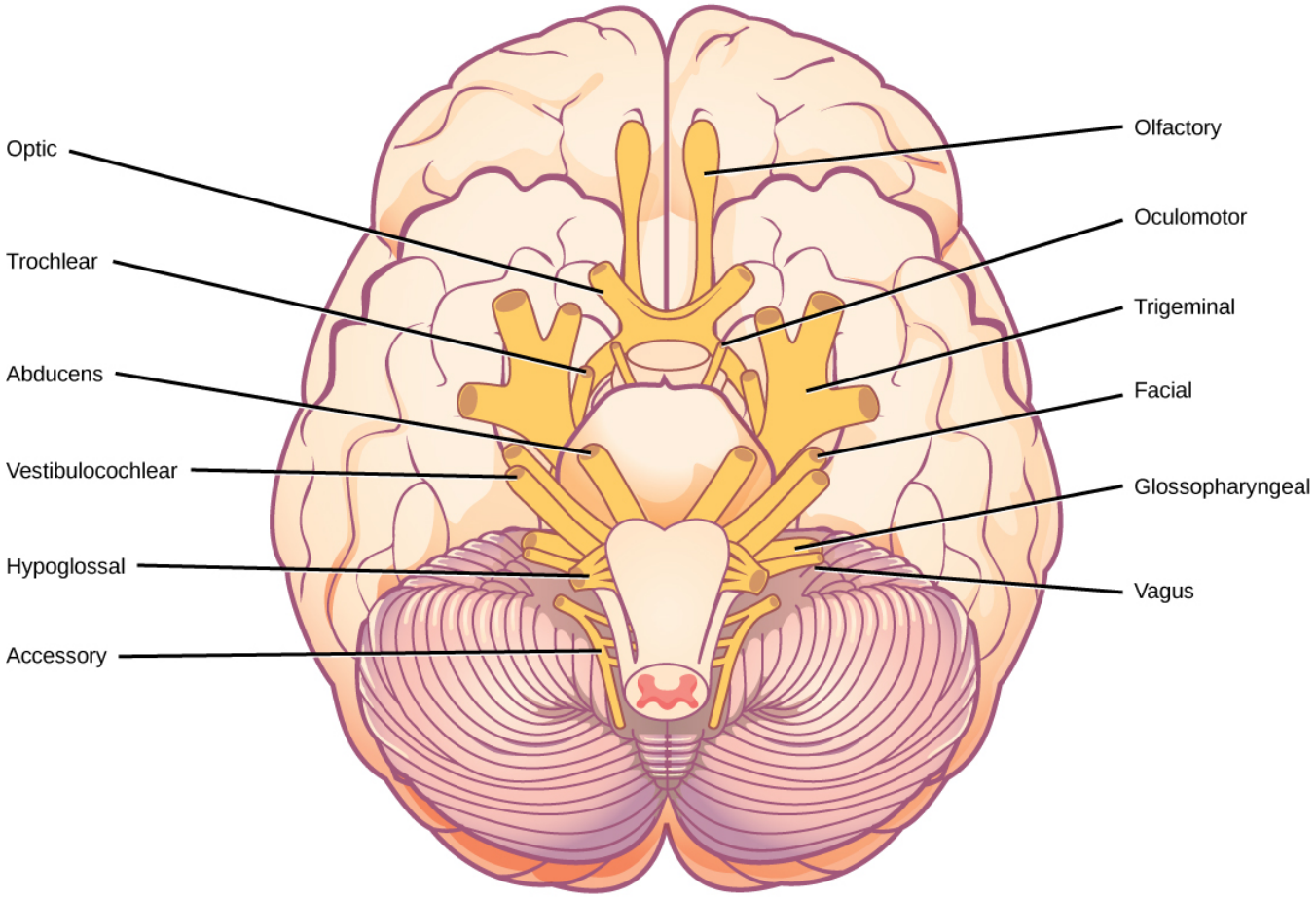


Figure **42.5.3**: The human brain contains 12 cranial nerves that receive sensory input and control motor output for the head and neck.

Spinal nerves transmit sensory and motor information between the spinal cord and the rest of the body. Each of the 31 spinal nerves (in humans) contains both sensory and motor axons. The sensory neuron cell bodies are grouped in structures called dorsal root ganglia and are shown in Figure **42.5.4**. Each sensory neuron has one projection—with a sensory receptor ending in skin, muscle, or sensory organs—and another that synapses with a neuron in the dorsal spinal cord. Motor neurons have cell bodies in the ventral gray matter of the spinal cord that project to muscle through the ventral root. These neurons are usually stimulated by interneurons within the spinal cord but are sometimes directly stimulated by sensory neurons.

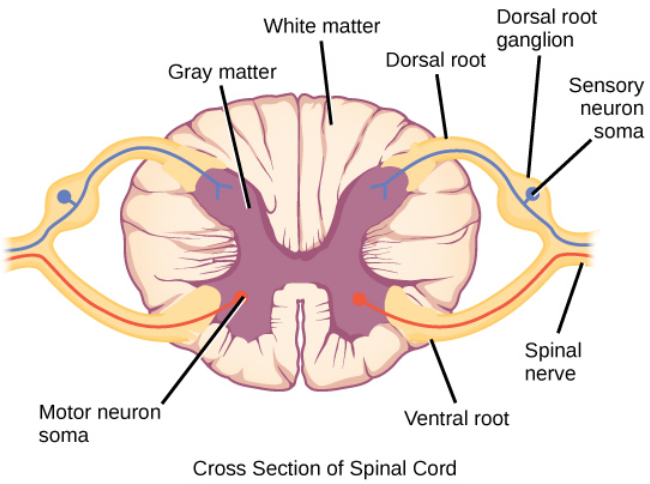


Figure **42.5.4**: Spinal nerves contain both sensory and motor axons. The somas of sensory neurons are located in dorsal root ganglia. The somas of motor neurons are found in the ventral portion of the gray matter of the spinal cord.

Summary

The peripheral nervous system contains both the autonomic and sensory-somatic nervous systems. The autonomic nervous system provides unconscious control over visceral functions and has two divisions: the sympathetic and parasympathetic nervous systems. The sympathetic nervous system is activated in stressful situations to prepare the animal for a “fight or flight” response. The parasympathetic nervous system is active during restful periods. The sensory-somatic nervous system is made of cranial and spinal nerves that transmit sensory information from skin and muscle to the CNS and motor commands from the CNS to the muscles.

Art Connections

Figure **42.5.1**: Which of the following statements is false?

A. The parasympathetic pathway is responsible for relaxing the body, while the sympathetic pathway is responsible for preparing for an emergency.
B. Most preganglionic neurons in the sympathetic pathway originate in the spinal cord.
C. Slowing of the heartbeat is a parasympathetic response.
D. Parasympathetic neurons are responsible for releasing norepinephrine on the target organ, while sympathetic neurons are responsible for releasing acetylcholine.

Answer

D

Glossary

acetylcholine
neurotransmitter released by neurons in the central nervous system and peripheral nervous system

autonomic nervous system
part of the peripheral nervous system that controls bodily functions

cranial nerve
sensory and/or motor nerve that emanates from the brain

norepinephrine
neurotransmitter and hormone released by activation of the sympathetic nervous system

parasympathetic nervous system

division of autonomic nervous system that regulates visceral functions during rest and digestion

sensory-somatic nervous system

system of sensory and motor nerves

spinal nerve

nerve projecting between skin or muscle and spinal cord

sympathetic nervous system

division of autonomic nervous system activated during stressful “fight or flight” situations

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CHAPTER OVERVIEW

43: Sensory Systems

43.1: Overview of Sensory Receptors

43.2: Thermoreceptors- Nociceptors, and Electromagnetic Receptors- Temperature

43.3: Mechanoreceptors 1- Touch, Pressure and Body Position

43.4: Mechanoreceptors 2- Hearing, Vibration and Balance

43.4.1: Hearing and Vestibular Sensation

43.5: Chemoreceptors- Taste, Smell and pH

43.6: Vision

43.7: Evolution and the Development of Eyes

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43.1: Overview of Sensory Receptors

Skills to Develop

- Identify the general and special senses in humans
- Describe three important steps in sensory perception
- Explain the concept of just-noticeable difference in sensory perception

Senses provide information about the body and its environment. Humans have five special senses: olfaction (smell), gustation (taste), equilibrium (balance and body position), vision, and hearing. Additionally, we possess general senses, also called somatosensation, which respond to stimuli like temperature, pain, pressure, and vibration. Vestibular sensation, which is an organism's sense of spatial orientation and balance, proprioception (position of bones, joints, and muscles), and the sense of limb position that is used to track kinesthesia (limb movement) are part of somatosensation. Although the sensory systems associated with these senses are very different, all share a common function: to convert a stimulus (such as light, or sound, or the position of the body) into an electrical signal in the nervous system. This process is called sensory transduction.

There are two broad types of cellular systems that perform sensory transduction. In one, a neuron works with a sensory receptor, a cell, or cell process that is specialized to engage with and detect a specific stimulus. Stimulation of the sensory receptor activates the associated afferent neuron, which carries information about the stimulus to the central nervous system. In the second type of sensory transduction, a sensory nerve ending responds to a stimulus in the internal or external environment: this neuron constitutes the sensory receptor. Free nerve endings can be stimulated by several different stimuli, thus showing little receptor specificity. For example, pain receptors in your gums and teeth may be stimulated by temperature changes, chemical stimulation, or pressure.

Reception

The first step in sensation is reception, which is the activation of sensory receptors by stimuli such as mechanical stimuli (being bent or squished, for example), chemicals, or temperature. The receptor can then respond to the stimuli. The region in space in which a given sensory receptor can respond to a stimulus, be it far away or in contact with the body, is that receptor's receptive field. Think for a moment about the differences in receptive fields for the different senses. For the sense of touch, a stimulus must come into contact with body. For the sense of hearing, a stimulus can be a moderate distance away (some baleen whale sounds can propagate for many kilometers). For vision, a stimulus can be very far away; for example, the visual system perceives light from stars at enormous distances.

Transduction

The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system. This takes place at the sensory receptor, and the change in electrical potential that is produced is called the receptor potential. How is sensory input, such as pressure on the skin, changed to a receptor potential? In this example, a type of receptor called a mechanoreceptor (as shown in Figure **43.1.1**) possesses specialized membranes that respond to pressure. Disturbance of these dendrites by compressing them or bending them opens gated ion channels in the plasma membrane of the sensory neuron, changing its electrical potential. Recall that in the nervous system, a positive change of a neuron's electrical potential (also called the membrane potential), depolarizes the neuron. Receptor potentials are graded potentials: the magnitude of these graded (receptor) potentials varies with the strength of the stimulus. If the magnitude of depolarization is sufficient (that is, if membrane potential reaches a threshold), the neuron will fire an action potential. In most cases, the correct stimulus impinging on a sensory receptor will drive membrane potential in a positive direction, although for some receptors, such as those in the visual system, this is not always the case.

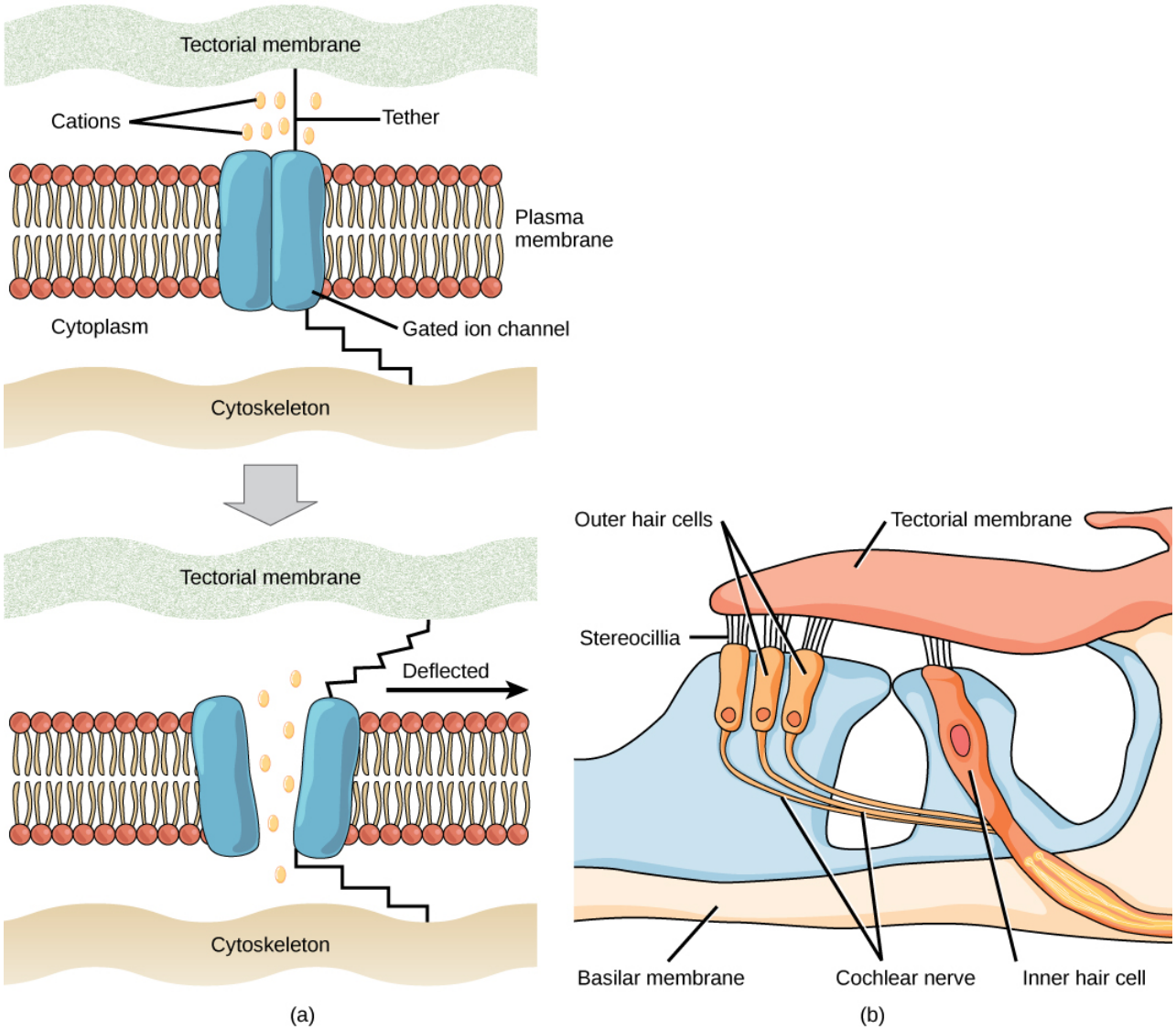


Figure **43.1.1**: (a) Mechanosensitive ion channels are gated ion channels that respond to mechanical deformation of the plasma membrane. A mechanosensitive channel is connected to the plasma membrane and the cytoskeleton by hair-like tethers. When pressure causes the extracellular matrix to move, the channel opens, allowing ions to enter or exit the cell. (b) Stereocilia in the human ear are connected to mechanosensitive ion channels. When a sound causes the stereocilia to move, mechanosensitive ion channels transduce the signal to the cochlear nerve.

Sensory receptors for different senses are very different from each other, and they are specialized according to the type of stimulus they sense: they have receptor specificity. For example, touch receptors, light receptors, and sound receptors are each activated by different stimuli. Touch receptors are not sensitive to light or sound; they are sensitive only to touch or pressure. However, stimuli may be combined at higher levels in the brain, as happens with olfaction, contributing to our sense of taste.

Encoding and Transmission of Sensory Information

Four aspects of sensory information are encoded by sensory systems: the type of stimulus, the location of the stimulus in the receptive field, the duration of the stimulus, and the relative intensity of the stimulus. Thus, action potentials transmitted over a sensory receptor's afferent axons encode one type of stimulus, and this segregation of the senses is preserved in other sensory circuits. For example, auditory receptors transmit signals over their own dedicated system, and electrical activity in the axons of the auditory receptors will be interpreted by the brain as an auditory stimulus—a sound.

The intensity of a stimulus is often encoded in the rate of action potentials produced by the sensory receptor. Thus, an intense stimulus will produce a more rapid train of action potentials, and reducing the stimulus will likewise slow the rate of production of

action potentials. A second way in which intensity is encoded is by the number of receptors activated. An intense stimulus might initiate action potentials in a large number of adjacent receptors, while a less intense stimulus might stimulate fewer receptors. Integration of sensory information begins as soon as the information is received in the CNS, and the brain will further process incoming signals.

Perception

Perception is an individual's interpretation of a sensation. Although perception relies on the activation of sensory receptors, perception happens not at the level of the sensory receptor, but at higher levels in the nervous system, in the brain. The brain distinguishes sensory stimuli through a sensory pathway: action potentials from sensory receptors travel along neurons that are dedicated to a particular stimulus. These neurons are dedicated to that particular stimulus and synapse with particular neurons in the brain or spinal cord.

All sensory signals, except those from the olfactory system, are transmitted though the central nervous system and are routed to the thalamus and to the appropriate region of the cortex. Recall that the thalamus is a structure in the forebrain that serves as a clearinghouse and relay station for sensory (as well as motor) signals. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex (Figure **43.1.2**) dedicated to processing that particular sense.

How are neural signals interpreted? Interpretation of sensory signals between individuals of the same species is largely similar, owing to the inherited similarity of their nervous systems; however, there are some individual differences. A good example of this is individual tolerances to a painful stimulus, such as dental pain, which certainly differ.

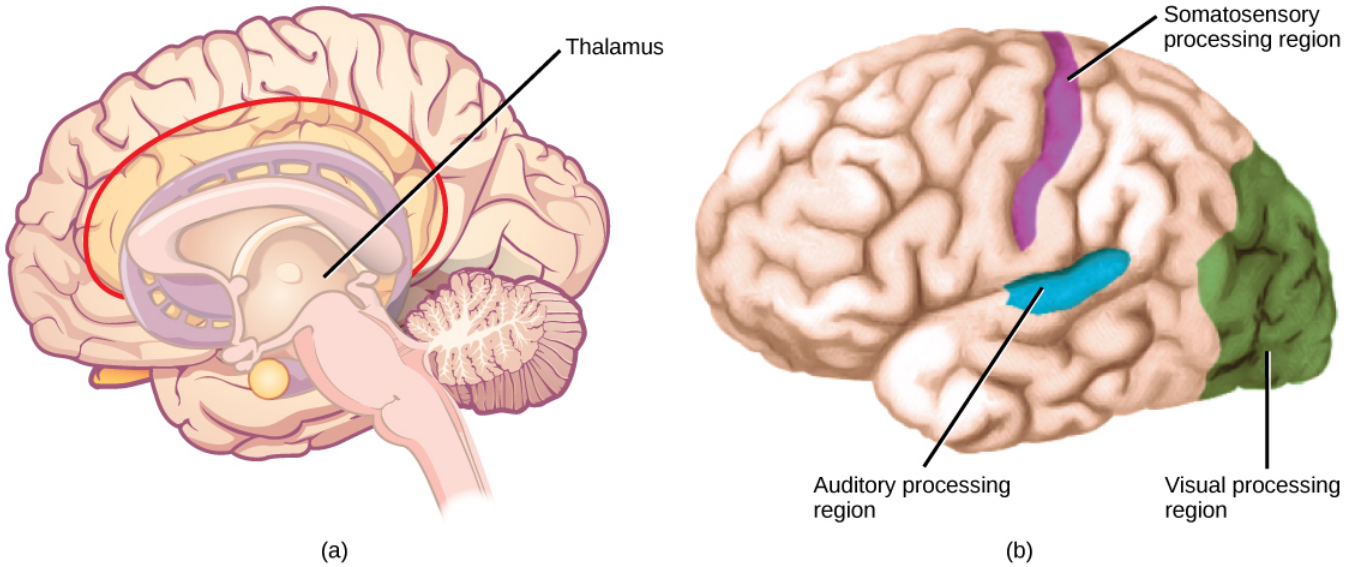


Figure **43.1.2:** In humans, with the exception of olfaction, all sensory signals are routed from the (a) thalamus to (b) final processing regions in the cortex of the brain. (credit b: modification of work by Polina Tishina)

Scientific Method Connection: Just-Noticeable Difference

It is easy to differentiate between a one-pound bag of rice and a two-pound bag of rice. There is a one-pound difference, and one bag is twice as heavy as the other. However, would it be as easy to differentiate between a 20- and a 21-pound bag?

Question: What is the smallest detectible weight difference between a one-pound bag of rice and a larger bag? What is the smallest detectible difference between a 20-pound bag and a larger bag? In both cases, at what weights are the differences detected? This smallest detectible difference in stimuli is known as the just-noticeable difference (JND).

Background: Research background literature on JND and on Weber's Law, a description of a proposed mathematical relationship between the overall magnitude of the stimulus and the JND. You will be testing JND of different weights of rice in bags. Choose a convenient increment that is to be stepped through while testing. For example, you could choose 10 percent increments between one and two pounds (1.1, 1.2, 1.3, 1.4, and so on) or 20 percent increments (1.2, 1.4, 1.6, and 1.8).

Hypothesis: Develop a hypothesis about JND in terms of percentage of the whole weight being tested (such as "the JND between the two small bags and between the two large bags is proportionally the same," or ". . . is not proportionally the same.") So, for the first hypothesis, if the JND between the one-pound bag and a larger bag is 0.2 pounds (that is, 20 percent; 1.0 pound feels the same as 1.1 pounds, but 1.0 pound feels less than 1.2 pounds), then the JND between the 20-pound bag and a larger bag will also be 20 percent. (So, 20 pounds feels the same as 22 pounds or 23 pounds, but 20 pounds feels less than 24 pounds.)

Test the hypothesis: Enlist 24 participants, and split them into two groups of 12. To set up the demonstration, assuming a 10 percent increment was selected, have the first group be the one-pound group. As a counter-balancing measure against a systematic error, however, six of the first group will compare one pound to two pounds, and step down in weight (1.0 to 2.0, 1.0 to 1.9, and so on.), while the other six will step up (1.0 to 1.1, 1.0 to 1.2, and so on). Apply the same principle to the 20-pound group (20 to 40, 20 to 38, and so on, and 20 to 22, 20 to 24, and so on). Given the large difference between 20 and 40 pounds, you may wish to use 30 pounds as your larger weight. In any case, use two weights that are easily detectable as different.

Record the observations: Record the data in a table similar to the table below. For the one-pound and 20-pound groups (base weights) record a plus sign (+) for each participant that detects a difference between the base weight and the step weight. Record a minus sign (-) for each participant that finds no difference. If one-tenth steps were not used, then replace the steps in the "Step Weight" columns with the step you are using.

Table 43.1.1: Results of JND Testing (+ = difference; – = no difference)

Step Weight	One pound	20 pounds	Step Weight
1.1			22
1.2			24
1.3			26
1.4			28
1.5			30
1.6			32
1.7			34
1.8			36
1.9			38
2.0			40

Analyze the data/report the results: What step weight did all participants find to be equal with one-pound base weight? What about the 20-pound group?

Draw a conclusion: Did the data support the hypothesis? Are the final weights proportionally the same? If not, why not? Do the findings adhere to Weber's Law? Weber's Law states that the concept that a just-noticeable difference in a stimulus is proportional to the magnitude of the original stimulus.

Summary

A sensory activation occurs when a physical or chemical stimulus is processed into a neural signal (sensory transduction) by a sensory receptor. Perception is an individual interpretation of a sensation and is a brain function. Humans have special senses: olfaction, gustation, equilibrium, and hearing, plus the general senses of somatosensation.

Sensory receptors are either specialized cells associated with sensory neurons or the specialized ends of sensory neurons that are a part of the peripheral nervous system, and they are used to receive information about the environment (internal or external). Each sensory receptor is modified for the type of stimulus it detects. For example, neither gustatory receptors nor auditory receptors are sensitive to light. Each sensory receptor is responsive to stimuli within a specific region in space, which is known as that receptor's receptive field. The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system.

All sensory signals, except those from the olfactory system, enter the central nervous system and are routed to the thalamus. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex dedicated to processing that particular sense.

Glossary

kinesthesia
sense of body movement

mechanoreceptor
sensory receptor modified to respond to mechanical disturbance such as being bent, touch, pressure, motion, and sound

perception
individual interpretation of a sensation; a brain function

proprioception
sense of limb position; used to track kinesthesia

reception
receipt of a signal (such as light or sound) by sensory receptors

receptive field
region in space in which a stimulus can activate a given sensory receptor

receptor potential
membrane potential in a sensory receptor in response to detection of a stimulus

sensory receptor
specialized neuron or other cells associated with a neuron that is modified to receive specific sensory input

sensory transduction
conversion of a sensory stimulus into electrical energy in the nervous system by a change in the membrane potential

vestibular sense
sense of spatial orientation and balance

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43.2: Thermoreceptors- Nociceptors, and Electromagnetic Receptors- Temperature

Skills to Develop

- Describe four important mechanoreceptors in human skin
- Describe the topographical distribution of somatosensory receptors between glabrous and hairy skin
- Explain why the perception of pain is subjective

Somatosensation is a mixed sensory category and includes all sensation received from the skin and mucous membranes, as well from as the limbs and joints. Somatosensation is also known as tactile sense, or more familiarly, as the sense of touch. Somatosensation occurs all over the exterior of the body and at some interior locations as well. A variety of receptor types—embedded in the skin, mucous membranes, muscles, joints, internal organs, and cardiovascular system—play a role.

Recall that the epidermis is the outermost layer of skin in mammals. It is relatively thin, is composed of keratin-filled cells, and has no blood supply. The epidermis serves as a barrier to water and to invasion by pathogens. Below this, the much thicker dermis contains blood vessels, sweat glands, hair follicles, lymph vessels, and lipid-secreting sebaceous glands (Figure **43.2.1**). Below the epidermis and dermis is the subcutaneous tissue, or hypodermis, the fatty layer that contains blood vessels, connective tissue, and the axons of sensory neurons. The hypodermis, which holds about 50 percent of the body's fat, attaches the dermis to the bone and muscle, and supplies nerves and blood vessels to the dermis.

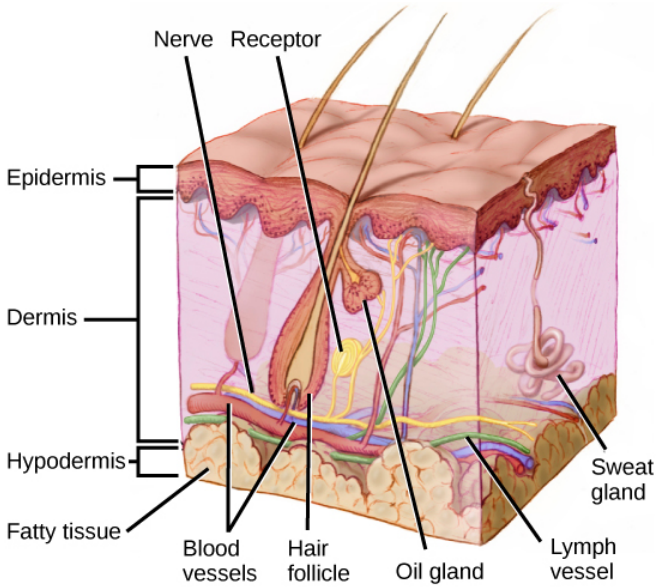


Figure **43.2.1**: Mammalian skin has three layers: an epidermis, a dermis, and a hypodermis. (credit: modification of work by Don Bliss, National Cancer Institute)

Somatosensory Receptors

Sensory receptors are classified into five categories: mechanoreceptors, thermoreceptors, proprioceptors, pain receptors, and chemoreceptors. These categories are based on the nature of stimuli each receptor class transduces. What is commonly referred to as "touch" involves more than one kind of stimulus and more than one kind of receptor. Mechanoreceptors in the skin are described as encapsulated (that is, surrounded by a capsule) or unencapsulated (a group that includes free nerve endings). A free nerve ending, as its name implies, is an unencapsulated dendrite of a sensory neuron. Free nerve endings are the most common nerve endings in skin, and they extend into the middle of the epidermis. Free nerve endings are sensitive to painful stimuli, to hot and cold, and to light touch. They are slow to adjust to a stimulus and so are less sensitive to abrupt changes in stimulation.

There are three classes of mechanoreceptors: tactile, proprioceptors, and baroreceptors. Mechanoreceptors sense stimuli due to physical deformation of their plasma membranes. They contain mechanically gated ion channels whose gates open or close in response to pressure, touch, stretching, and sound." There are four primary tactile mechanoreceptors in human skin: Merkel's disks, Meissner's corpuscles, Ruffini endings, and Pacinian corpuscle; two are located toward the surface of the skin and two are located

deeper. A fifth type of mechanoreceptor, Krause end bulbs, are found only in specialized regions. Merkel's disks (shown in Figure **43.2.2**) are found in the upper layers of skin near the base of the epidermis, both in skin that has hair and on glabrous skin, that is, the hairless skin found on the palms and fingers, the soles of the feet, and the lips of humans and other primates. Merkel's disks are densely distributed in the fingertips and lips. They are slow-adapting, unencapsulated nerve endings, and they respond to light touch. Light touch, also known as discriminative touch, is a light pressure that allows the location of a stimulus to be pinpointed. The receptive fields of Merkel's disks are small with well-defined borders. That makes them finely sensitive to edges and they come into use in tasks such as typing on a keyboard.

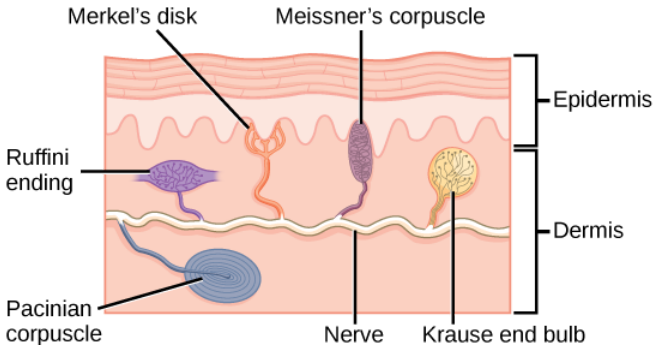


Figure **43.2.2**: Four of the primary mechanoreceptors in human skin are shown. Merkel's disks, which are unencapsulated, respond to light touch. Meissner's corpuscles, Ruffini endings, Pacinian corpuscles, and Krause end bulbs are all encapsulated. Meissner's corpuscles respond to touch and low-frequency vibration. Ruffini endings detect stretch, deformation within joints, and warmth. Pacinian corpuscles detect transient pressure and high-frequency vibration. Krause end bulbs detect cold.

Exercise

Which of the following statements about mechanoreceptors is false?

A. Pacini corpuscles are found in both glabrous and hairy skin.
B. Merkel's disks are abundant on the fingertips and lips.
C. Ruffini endings are encapsulated mechanoreceptors.
D. Meissner's corpuscles extend into the lower dermis.

Answer

D

Meissner's corpuscles, (shown in Figure **43.2.3**) also known as tactile corpuscles, are found in the upper dermis, but they project into the epidermis. They, too, are found primarily in the glabrous skin on the fingertips and eyelids. They respond to fine touch and pressure, but they also respond to low-frequency vibration or flutter. They are rapidly adapting, fluid-filled, encapsulated neurons with small, well-defined borders and are responsive to fine details. Like Merkel's disks, Meissner's corpuscles are not as plentiful in the palms as they are in the fingertips.

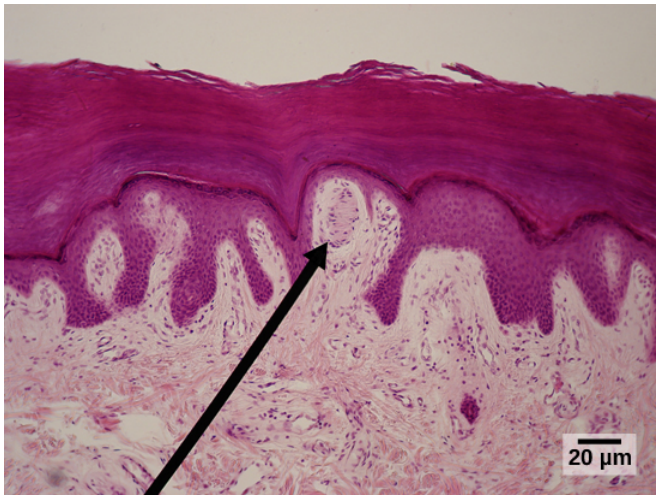


Figure **43.2.3**: Meissner corpuscles in the fingertips, such as the one viewed here using bright field light microscopy, allow for touch discrimination of fine detail. (credit: modification of work by "Wbensmith"/Wikimedia Commons; scale-bar data from Matt Russell)

Deeper in the epidermis, near the base, are Ruffini endings, which are also known as bulbous corpuscles. They are found in both glabrous and hairy skin. These are slow-adapting, encapsulated mechanoreceptors that detect skin stretch and deformations within joints, so they provide valuable feedback for gripping objects and controlling finger position and movement. Thus, they also contribute to proprioception and kinesthesia. Ruffini endings also detect warmth. Note that these warmth detectors are situated deeper in the skin than are the cold detectors. It is not surprising, then, that humans detect cold stimuli before they detect warm stimuli.

Pacinian corpuscles (seen in Figure **43.2.4**) are located deep in the dermis of both glabrous and hairy skin and are structurally similar to Meissner's corpuscles; they are found in the bone periosteum, joint capsules, pancreas and other viscera, breast, and genitals. They are rapidly adapting mechanoreceptors that sense deep transient (but not prolonged) pressure and high-frequency vibration. Pacinian receptors detect pressure and vibration by being compressed, stimulating their internal dendrites. There are fewer Pacinian corpuscles and Ruffini endings in skin than there are Merkel's disks and Meissner's corpuscles.

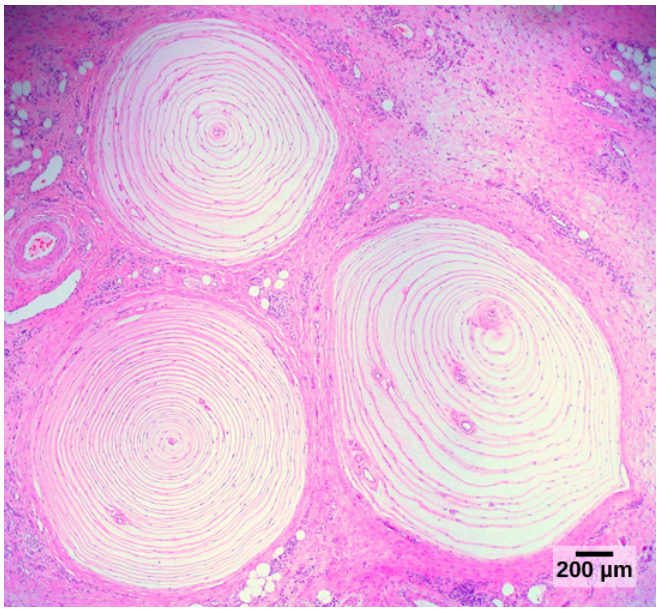


Figure **43.2.4**: Pacinian corpuscles, such as these visualized using bright field light microscopy, detect pressure (touch) and high-frequency vibration. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

In proprioception, proprioceptive and kinesthetic signals travel through myelinated afferent neurons running from the spinal cord to the medulla. Neurons are not physically connected, but communicate via neurotransmitters secreted into synapses or "gaps"

between communicating neurons. Once in the medulla, the neurons continue carrying the signals to the thalamus.

Muscle spindles are stretch receptors that detect the amount of stretch, or lengthening of muscles. Related to these are Golgi tendon organs, which are tension receptors that detect the force of muscle contraction. Proprioceptive and kinesthetic signals come from limbs. Unconscious proprioceptive signals run from the spinal cord to the cerebellum, the brain region that coordinates muscle contraction, rather than to the thalamus, like most other sensory information.

Barorecptors detect pressure changes in an organ. They are found in the walls of the carotid artery and the aorta where they monitor blood pressure, and in the lungs where they detect the degree of lung expansion. Stretch receptors are found at various sites in the digestive and urinary systems.

In addition to these two types of deeper receptors, there are also rapidly adapting hair receptors, which are found on nerve endings that wrap around the base of hair follicles. There are a few types of hair receptors that detect slow and rapid hair movement, and they differ in their sensitivity to movement. Some hair receptors also detect skin deflection, and certain rapidly adapting hair receptors allow detection of stimuli that have not yet touched the skin.

Integration of Signals from Mechanoreceptors

The configuration of the different types of receptors working in concert in human skin results in a very refined sense of touch. The nociceptive receptors—those that detect pain—are located near the surface. Small, finely calibrated mechanoreceptors—Merkel's disks and Meissner's corpuscles—are located in the upper layers and can precisely localize even gentle touch. The large mechanoreceptors—Pacinian corpuscles and Ruffini endings—are located in the lower layers and respond to deeper touch. (Consider that the deep pressure that reaches those deeper receptors would not need to be finely localized.) Both the upper and lower layers of the skin hold rapidly and slowly adapting receptors. Both primary somatosensory cortex and secondary cortical areas are responsible for processing the complex picture of stimuli transmitted from the interplay of mechanoreceptors.

Density of Mechanoreceptors

The distribution of touch receptors in human skin is not consistent over the body. In humans, touch receptors are less dense in skin covered with any type of hair, such as the arms, legs, torso, and face. Touch receptors are denser in glabrous skin (the type found on human fingertips and lips, for example), which is typically more sensitive and is thicker than hairy skin (4 to 5 mm versus 2 to 3 mm).

How is receptor density estimated in a human subject? The relative density of pressure receptors in different locations on the body can be demonstrated experimentally using a two-point discrimination test. In this demonstration, two sharp points, such as two thumbtacks, are brought into contact with the subject's skin (though not hard enough to cause pain or break the skin). The subject reports if he or she feels one point or two points. If the two points are felt as one point, it can be inferred that the two points are both in the receptive field of a single sensory receptor. If two points are felt as two separate points, each is in the receptive field of two separate sensory receptors. The points could then be moved closer and re-tested until the subject reports feeling only one point, and the size of the receptive field of a single receptor could be estimated from that distance.

Thermoreception

In addition to Krause end bulbs that detect cold and Ruffini endings that detect warmth, there are different types of cold receptors on some free nerve endings: thermoreceptors, located in the dermis, skeletal muscles, liver, and hypothalamus, that are activated by different temperatures. Their pathways into the brain run from the spinal cord through the thalamus to the primary somatosensory cortex. Warmth and cold information from the face travels through one of the cranial nerves to the brain. You know from experience that a tolerably cold or hot stimulus can quickly progress to a much more intense stimulus that is no longer tolerable. Any stimulus that is too intense can be perceived as pain because temperature sensations are conducted along the same pathways that carry pain sensations

Pain

Pain is the name given to nociception, which is the neural processing of injurious stimuli in response to tissue damage. Pain is caused by true sources of injury, such as contact with a heat source that causes a thermal burn or contact with a corrosive chemical. But pain also can be caused by harmless stimuli that mimic the action of damaging stimuli, such as contact with capsaicins, the

compounds that cause peppers to taste hot and which are used in self-defense pepper sprays and certain topical medications. Peppers taste “hot” because the protein receptors that bind capsaicin open the same calcium channels that are activated by warm receptors.

Nociception starts at the sensory receptors, but pain, inasmuch as it is the perception of nociception, does not start until it is communicated to the brain. There are several nociceptive pathways to and through the brain. Most axons carrying nociceptive information into the brain from the spinal cord project to the thalamus (as do other sensory neurons) and the neural signal undergoes final processing in the primary somatosensory cortex. Interestingly, one nociceptive pathway projects not to the thalamus but directly to the hypothalamus in the forebrain, which modulates the cardiovascular and neuroendocrine functions of the autonomic nervous system. Recall that threatening—or painful—stimuli stimulate the sympathetic branch of the visceral sensory system, readying a fight-or-flight response.

Link to Learning



View this video that animates the five phases of nociceptive pain.

Summary

Somatosensation includes all sensation received from the skin and mucous membranes, as well as from the limbs and joints. Somatosensation occurs all over the exterior of the body and at some interior locations as well, and a variety of receptor types, embedded in the skin and mucous membranes, play a role.

There are several types of specialized sensory receptors. Rapidly adapting free nerve endings detect nociception, hot and cold, and light touch. Slowly adapting, encapsulated Merkel’s disks are found in fingertips and lips, and respond to light touch. Meissner’s corpuscles, found in glabrous skin, are rapidly adapting, encapsulated receptors that detect touch, low-frequency vibration, and flutter. Ruffini endings are slowly adapting, encapsulated receptors that detect skin stretch, joint activity, and warmth. Hair receptors are rapidly adapting nerve endings wrapped around the base of hair follicles that detect hair movement and skin deflection. Finally, Pacinian corpuscles are encapsulated, rapidly adapting receptors that detect transient pressure and high-frequency vibration.

Glossary

free nerve ending
: ending of an afferent neuron that lacks a specialized structure for detection of sensory stimuli; some respond to touch, pain, or temperature

glabrous
: describes the non-hairy skin found on palms and fingers, soles of feet, and lips of humans and other primates

Golgi tendon organ
: muscular proprioceptive tension receptor that provides the sensory component of the Golgi tendon reflex

Meissner’s corpuscle

(also, tactile corpuscle) encapsulated, rapidly-adapting mechanoreceptor in the skin that responds to light touch

Merkel's disc

unencapsulated, slowly-adapting mechanoreceptor in the skin that responds to touch

muscle spindle

proprioceptive stretch receptor that lies within a muscle and that shortens the muscle to an optimal length for efficient contraction

nociception

neural processing of noxious (such as damaging) stimuli

Pacinian corpuscle

encapsulated mechanoreceptor in the skin that responds to deep pressure and vibration

Ruffini ending

(also, bulbous corpuscle) slowly-adapting mechanoreceptor in the skin that responds to skin stretch and joint position

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43.3: Mechanoreceptors 1- Touch, Pressure and Body Position

Skills to Develop

- Describe four important mechanoreceptors in human skin
- Describe the topographical distribution of somatosensory receptors between glabrous and hairy skin
- Explain why the perception of pain is subjective

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Recall that the epidermis is the outermost layer of skin in mammals. It is relatively thin, is composed of keratin-filled cells, and has no blood supply. The epidermis serves as a barrier to water and to invasion by pathogens. Below this, the much thicker dermis contains blood vessels, sweat glands, hair follicles, lymph vessels, and lipid-secreting sebaceous glands (Figure **43.3.1**). Below the epidermis and dermis is the subcutaneous tissue, or hypodermis, the fatty layer that contains blood vessels, connective tissue, and the axons of sensory neurons. The hypodermis, which holds about 50 percent of the body's fat, attaches the dermis to the bone and muscle, and supplies nerves and blood vessels to the dermis.

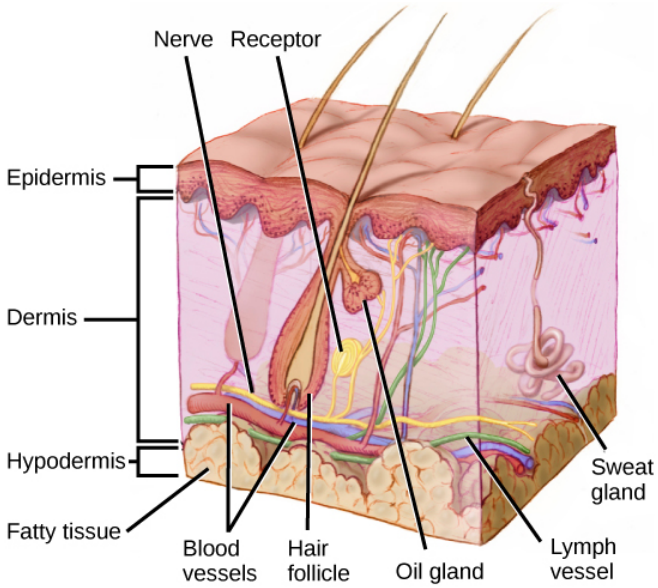


Figure **43.3.1**: Mammalian skin has three layers: an epidermis, a dermis, and a hypodermis. (credit: modification of work by Don Bliss, National Cancer Institute)

Somatosensory Receptors

Sensory receptors are classified into five categories: mechanoreceptors, thermoreceptors, proprioceptors, pain receptors, and chemoreceptors. These categories are based on the nature of stimuli each receptor class transduces. What is commonly referred to as "touch" involves more than one kind of stimulus and more than one kind of receptor. Mechanoreceptors in the skin are described as encapsulated (that is, surrounded by a capsule) or unencapsulated (a group that includes free nerve endings). A free nerve ending, as its name implies, is an unencapsulated dendrite of a sensory neuron. Free nerve endings are the most common nerve endings in skin, and they extend into the middle of the epidermis. Free nerve endings are sensitive to painful stimuli, to hot and cold, and to light touch. They are slow to adjust to a stimulus and so are less sensitive to abrupt changes in stimulation.

There are three classes of mechanoreceptors: tactile, proprioceptors, and baroreceptors. Mechanoreceptors sense stimuli due to physical deformation of their plasma membranes. They contain mechanically gated ion channels whose gates open or close in response to pressure, touch, stretching, and sound." There are four primary tactile mechanoreceptors in human skin: Merkel's disks, Meissner's corpuscles, Ruffini endings, and Pacinian corpuscle; two are located toward the surface of the skin and two are located

deeper. A fifth type of mechanoreceptor, Krause end bulbs, are found only in specialized regions. Merkel's disks (shown in Figure **43.3.2**) are found in the upper layers of skin near the base of the epidermis, both in skin that has hair and on glabrous skin, that is, the hairless skin found on the palms and fingers, the soles of the feet, and the lips of humans and other primates. Merkel's disks are densely distributed in the fingertips and lips. They are slow-adapting, unencapsulated nerve endings, and they respond to light touch. Light touch, also known as discriminative touch, is a light pressure that allows the location of a stimulus to be pinpointed. The receptive fields of Merkel's disks are small with well-defined borders. That makes them finely sensitive to edges and they come into use in tasks such as typing on a keyboard.

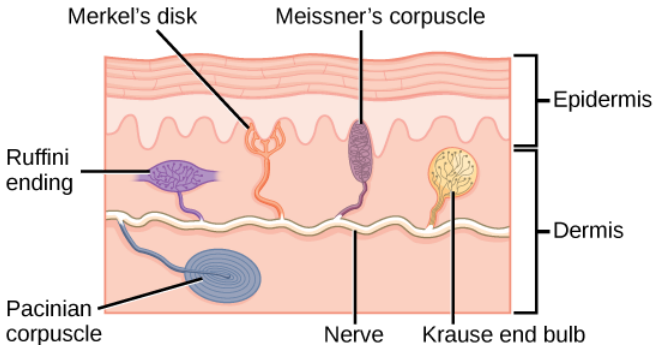


Figure **43.3.2**: Four of the primary mechanoreceptors in human skin are shown. Merkel's disks, which are unencapsulated, respond to light touch. Meissner's corpuscles, Ruffini endings, Pacinian corpuscles, and Krause end bulbs are all encapsulated. Meissner's corpuscles respond to touch and low-frequency vibration. Ruffini endings detect stretch, deformation within joints, and warmth. Pacinian corpuscles detect transient pressure and high-frequency vibration. Krause end bulbs detect cold.

Exercise

Which of the following statements about mechanoreceptors is false?

A. Pacini corpuscles are found in both glabrous and hairy skin.
B. Merkel's disks are abundant on the fingertips and lips.
C. Ruffini endings are encapsulated mechanoreceptors.
D. Meissner's corpuscles extend into the lower dermis.

Answer

D

Meissner's corpuscles, (shown in Figure **43.3.3**) also known as tactile corpuscles, are found in the upper dermis, but they project into the epidermis. They, too, are found primarily in the glabrous skin on the fingertips and eyelids. They respond to fine touch and pressure, but they also respond to low-frequency vibration or flutter. They are rapidly adapting, fluid-filled, encapsulated neurons with small, well-defined borders and are responsive to fine details. Like Merkel's disks, Meissner's corpuscles are not as plentiful in the palms as they are in the fingertips.

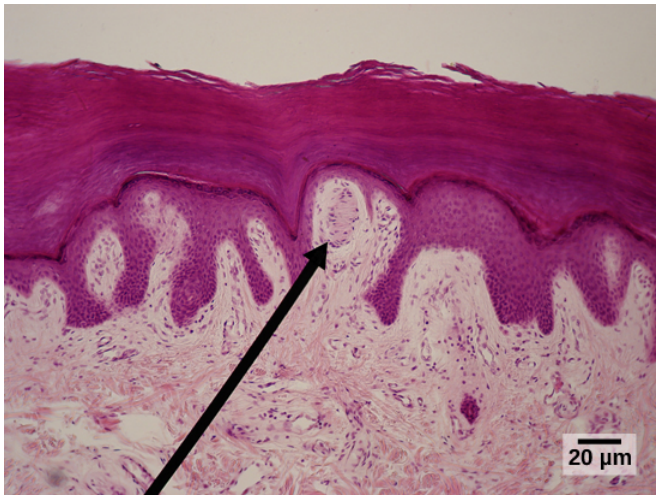


Figure **43.3.3**: Meissner corpuscles in the fingertips, such as the one viewed here using bright field light microscopy, allow for touch discrimination of fine detail. (credit: modification of work by "Wbensmith"/Wikimedia Commons; scale-bar data from Matt Russell)

Deeper in the epidermis, near the base, are Ruffini endings, which are also known as bulbous corpuscles. They are found in both glabrous and hairy skin. These are slow-adapting, encapsulated mechanoreceptors that detect skin stretch and deformations within joints, so they provide valuable feedback for gripping objects and controlling finger position and movement. Thus, they also contribute to proprioception and kinesthesia. Ruffini endings also detect warmth. Note that these warmth detectors are situated deeper in the skin than are the cold detectors. It is not surprising, then, that humans detect cold stimuli before they detect warm stimuli.

Pacinian corpuscles (seen in Figure **43.3.4**) are located deep in the dermis of both glabrous and hairy skin and are structurally similar to Meissner's corpuscles; they are found in the bone periosteum, joint capsules, pancreas and other viscera, breast, and genitals. They are rapidly adapting mechanoreceptors that sense deep transient (but not prolonged) pressure and high-frequency vibration. Pacinian receptors detect pressure and vibration by being compressed, stimulating their internal dendrites. There are fewer Pacinian corpuscles and Ruffini endings in skin than there are Merkel's disks and Meissner's corpuscles.

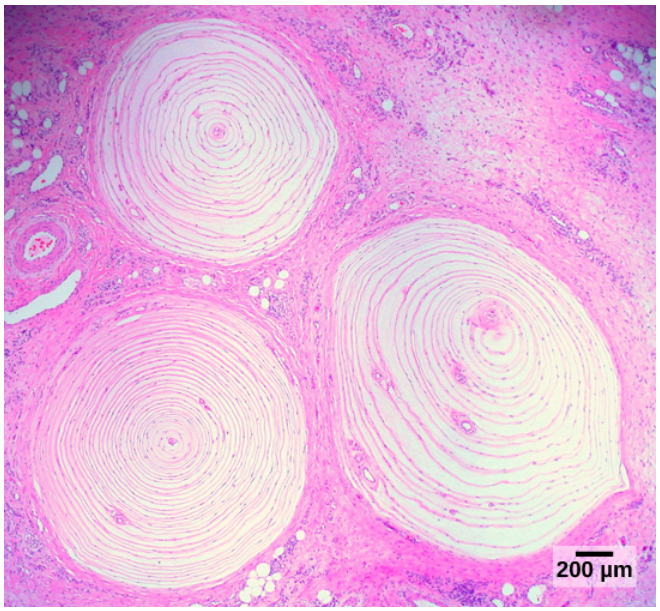


Figure **43.3.4**: Pacinian corpuscles, such as these visualized using bright field light microscopy, detect pressure (touch) and high-frequency vibration. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

In proprioception, proprioceptive and kinesthetic signals travel through myelinated afferent neurons running from the spinal cord to the medulla. Neurons are not physically connected, but communicate via neurotransmitters secreted into synapses or "gaps"

between communicating neurons. Once in the medulla, the neurons continue carrying the signals to the thalamus.

Muscle spindles are stretch receptors that detect the amount of stretch, or lengthening of muscles. Related to these are Golgi tendon organs, which are tension receptors that detect the force of muscle contraction. Proprioceptive and kinesthetic signals come from limbs. Unconscious proprioceptive signals run from the spinal cord to the cerebellum, the brain region that coordinates muscle contraction, rather than to the thalamus, like most other sensory information.

Barorecptors detect pressure changes in an organ. They are found in the walls of the carotid artery and the aorta where they monitor blood pressure, and in the lungs where they detect the degree of lung expansion. Stretch receptors are found at various sites in the digestive and urinary systems.

In addition to these two types of deeper receptors, there are also rapidly adapting hair receptors, which are found on nerve endings that wrap around the base of hair follicles. There are a few types of hair receptors that detect slow and rapid hair movement, and they differ in their sensitivity to movement. Some hair receptors also detect skin deflection, and certain rapidly adapting hair receptors allow detection of stimuli that have not yet touched the skin.

Integration of Signals from Mechanoreceptors

The configuration of the different types of receptors working in concert in human skin results in a very refined sense of touch. The nociceptive receptors—those that detect pain—are located near the surface. Small, finely calibrated mechanoreceptors—Merkel's disks and Meissner's corpuscles—are located in the upper layers and can precisely localize even gentle touch. The large mechanoreceptors—Pacinian corpuscles and Ruffini endings—are located in the lower layers and respond to deeper touch. (Consider that the deep pressure that reaches those deeper receptors would not need to be finely localized.) Both the upper and lower layers of the skin hold rapidly and slowly adapting receptors. Both primary somatosensory cortex and secondary cortical areas are responsible for processing the complex picture of stimuli transmitted from the interplay of mechanoreceptors.

Density of Mechanoreceptors

The distribution of touch receptors in human skin is not consistent over the body. In humans, touch receptors are less dense in skin covered with any type of hair, such as the arms, legs, torso, and face. Touch receptors are denser in glabrous skin (the type found on human fingertips and lips, for example), which is typically more sensitive and is thicker than hairy skin (4 to 5 mm versus 2 to 3 mm).

How is receptor density estimated in a human subject? The relative density of pressure receptors in different locations on the body can be demonstrated experimentally using a two-point discrimination test. In this demonstration, two sharp points, such as two thumbtacks, are brought into contact with the subject's skin (though not hard enough to cause pain or break the skin). The subject reports if he or she feels one point or two points. If the two points are felt as one point, it can be inferred that the two points are both in the receptive field of a single sensory receptor. If two points are felt as two separate points, each is in the receptive field of two separate sensory receptors. The points could then be moved closer and re-tested until the subject reports feeling only one point, and the size of the receptive field of a single receptor could be estimated from that distance.

Thermoreception

In addition to Krause end bulbs that detect cold and Ruffini endings that detect warmth, there are different types of cold receptors on some free nerve endings: thermoreceptors, located in the dermis, skeletal muscles, liver, and hypothalamus, that are activated by different temperatures. Their pathways into the brain run from the spinal cord through the thalamus to the primary somatosensory cortex. Warmth and cold information from the face travels through one of the cranial nerves to the brain. You know from experience that a tolerably cold or hot stimulus can quickly progress to a much more intense stimulus that is no longer tolerable. Any stimulus that is too intense can be perceived as pain because temperature sensations are conducted along the same pathways that carry pain sensations

Pain

Pain is the name given to nociception, which is the neural processing of injurious stimuli in response to tissue damage. Pain is caused by true sources of injury, such as contact with a heat source that causes a thermal burn or contact with a corrosive chemical. But pain also can be caused by harmless stimuli that mimic the action of damaging stimuli, such as contact with capsaicins, the

compounds that cause peppers to taste hot and which are used in self-defense pepper sprays and certain topical medications. Peppers taste “hot” because the protein receptors that bind capsaicin open the same calcium channels that are activated by warm receptors.

Nociception starts at the sensory receptors, but pain, inasmuch as it is the perception of nociception, does not start until it is communicated to the brain. There are several nociceptive pathways to and through the brain. Most axons carrying nociceptive information into the brain from the spinal cord project to the thalamus (as do other sensory neurons) and the neural signal undergoes final processing in the primary somatosensory cortex. Interestingly, one nociceptive pathway projects not to the thalamus but directly to the hypothalamus in the forebrain, which modulates the cardiovascular and neuroendocrine functions of the autonomic nervous system. Recall that threatening—or painful—stimuli stimulate the sympathetic branch of the visceral sensory system, readying a fight-or-flight response.

Link to Learning



View this video that animates the five phases of nociceptive pain.

Summary

Somatosensation includes all sensation received from the skin and mucous membranes, as well as from the limbs and joints. Somatosensation occurs all over the exterior of the body and at some interior locations as well, and a variety of receptor types, embedded in the skin and mucous membranes, play a role.

There are several types of specialized sensory receptors. Rapidly adapting free nerve endings detect nociception, hot and cold, and light touch. Slowly adapting, encapsulated Merkel’s disks are found in fingertips and lips, and respond to light touch. Meissner’s corpuscles, found in glabrous skin, are rapidly adapting, encapsulated receptors that detect touch, low-frequency vibration, and flutter. Ruffini endings are slowly adapting, encapsulated receptors that detect skin stretch, joint activity, and warmth. Hair receptors are rapidly adapting nerve endings wrapped around the base of hair follicles that detect hair movement and skin deflection. Finally, Pacinian corpuscles are encapsulated, rapidly adapting receptors that detect transient pressure and high-frequency vibration.

Glossary

free nerve ending
: ending of an afferent neuron that lacks a specialized structure for detection of sensory stimuli; some respond to touch, pain, or temperature

glabrous
: describes the non-hairy skin found on palms and fingers, soles of feet, and lips of humans and other primates

Golgi tendon organ
: muscular proprioceptive tension receptor that provides the sensory component of the Golgi tendon reflex

Meissner’s corpuscle

(also, tactile corpuscle) encapsulated, rapidly-adapting mechanoreceptor in the skin that responds to light touch

Merkel's disc

unencapsulated, slowly-adapting mechanoreceptor in the skin that responds to touch

muscle spindle

proprioceptive stretch receptor that lies within a muscle and that shortens the muscle to an optimal length for efficient contraction

nociception

neural processing of noxious (such as damaging) stimuli

Pacinian corpuscle

encapsulated mechanoreceptor in the skin that responds to deep pressure and vibration

Ruffini ending

(also, bulbous corpuscle) slowly-adapting mechanoreceptor in the skin that responds to skin stretch and joint position

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43.4: Mechanoreceptors 2- Hearing, Vibration and Balance

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43.4.1: Hearing and Vestibular Sensation

Skills to Develop

- Describe the relationship of amplitude and frequency of a sound wave to attributes of sound
- Trace the path of sound through the auditory system to the site of transduction of sound
- Identify the structures of the vestibular system that respond to gravity

Audition, or hearing, is important to humans and to other animals for many different interactions. It enables an organism to detect and receive information about danger, such as an approaching predator, and to participate in communal exchanges like those concerning territories or mating. On the other hand, although it is physically linked to the auditory system, the vestibular system is not involved in hearing. Instead, an animal's vestibular system detects its own movement, both linear and angular acceleration and deceleration, and balance.

Sound

Auditory stimuli are sound waves, which are mechanical, pressure waves that move through a medium, such as air or water. There are no sound waves in a vacuum since there are no air molecules to move in waves. The speed of sound waves differs, based on altitude, temperature, and medium, but at sea level and a temperature of 20º C (68º F), sound waves travel in the air at about 343 meters per second.

As is true for all waves, there are four main characteristics of a sound wave: frequency, wavelength, period, and amplitude. Frequency is the number of waves per unit of time, and in sound is heard as pitch. High-frequency (≥15.000Hz) sounds are higher-pitched (short wavelength) than low-frequency (long wavelengths; ≤100Hz) sounds. Frequency is measured in cycles per second, and for sound, the most commonly used unit is hertz (Hz), or cycles per second. Most humans can perceive sounds with frequencies between 30 and 20,000 Hz. Women are typically better at hearing high frequencies, but everyone's ability to hear high frequencies decreases with age. Dogs detect up to about 40,000 Hz; cats, 60,000 Hz; bats, 100,000 Hz; and dolphins 150,000 Hz, and American shad (*Alosa sapidissima*), a fish, can hear 180,000 Hz. Those frequencies above the human range are called ultrasound.

Amplitude, or the dimension of a wave from peak to trough, in sound is heard as volume and is illustrated in Figure **43.4.1.1**. The sound waves of louder sounds have greater amplitude than those of softer sounds. For sound, volume is measured in decibels (dB). The softest sound that a human can hear is the zero point. Humans speak normally at 60 decibels.

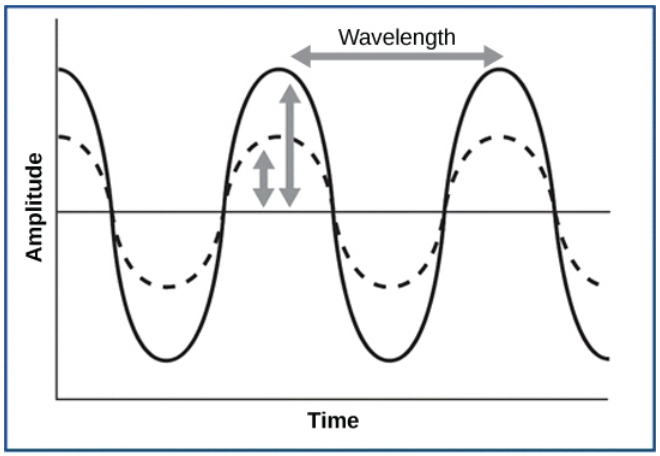


Figure **43.4.1.1**: For sound waves, wavelength corresponds to pitch. Amplitude of the wave corresponds to volume. The sound wave shown with a dashed line is softer in volume than the sound wave shown with a solid line. (credit: NIH)

Reception of Sound

In mammals, sound waves are collected by the external, cartilaginous part of the ear called the pinna, then travel through the auditory canal and cause vibration of the thin diaphragm called the tympanum or ear drum, the innermost part of the outer ear (illustrated in Figure **43.4.1.2**). Interior to the tympanum is the middle ear. The middle ear holds three small bones called the

ossicles, which transfer energy from the moving tympanum to the inner ear. The three ossicles are the malleus (also known as the hammer), the incus (the anvil), and stapes (the stirrup). The aptly named stapes looks very much like a stirrup. The three ossicles are unique to mammals, and each plays a role in hearing. The malleus attaches at three points to the interior surface of the tympanic membrane. The incus attaches the malleus to the stapes. In humans, the stapes is not long enough to reach the tympanum. If we did not have the malleus and the incus, then the vibrations of the tympanum would never reach the inner ear. These bones also function to collect force and amplify sounds. The ear ossicles are homologous to bones in a fish mouth: the bones that support gills in fish are thought to be adapted for use in the vertebrate ear over evolutionary time. Many animals (frogs, reptiles, and birds, for example) use the stapes of the middle ear to transmit vibrations to the middle ear.

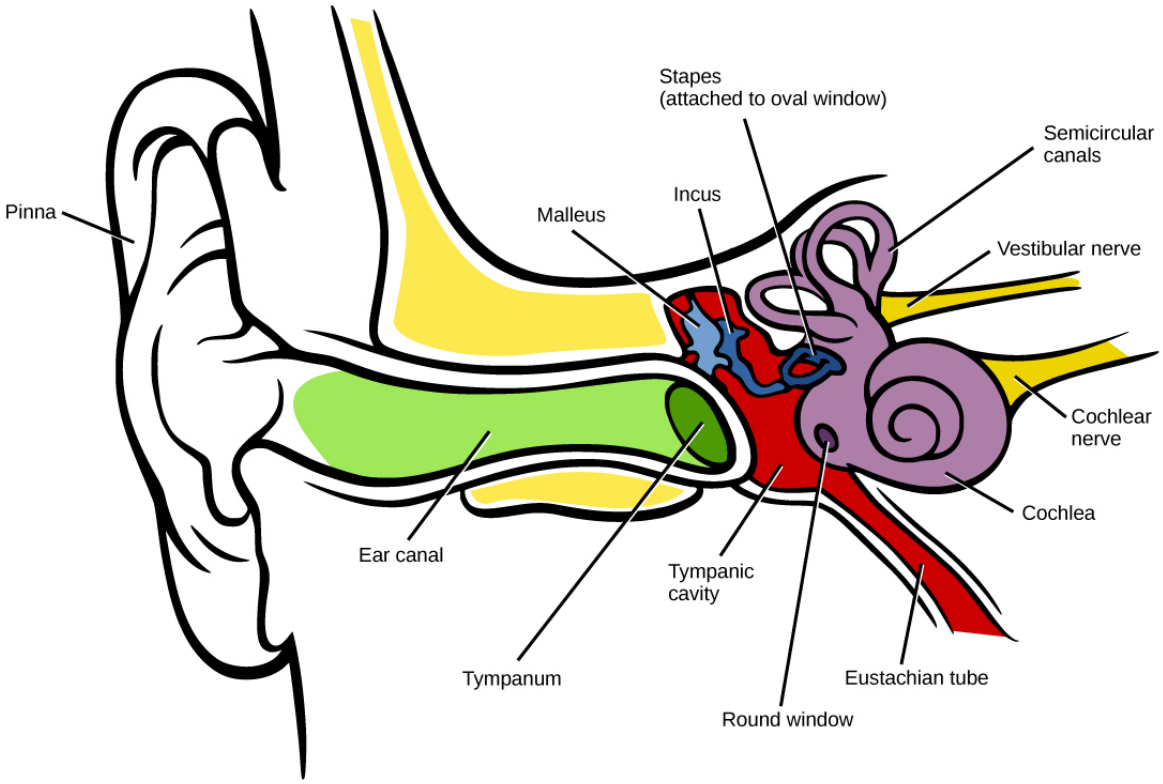


Figure **43.4.1.2**: Sound travels through the outer ear to the middle ear, which is bounded on its exterior by the tympanic membrane. The middle ear contains three bones called ossicles that transfer the sound wave to the oval window, the exterior boundary of the inner ear. The organ of Corti, which is the organ of sound transduction, lies inside the cochlea. (credit: modification of work by Lars Chittka, Axel Brockmann)

Transduction of Sound

Vibrating objects, such as vocal cords, create sound waves or pressure waves in the air. When these pressure waves reach the ear, the ear transduces this mechanical stimulus (pressure wave) into a nerve impulse (electrical signal) that the brain perceives as sound. The pressure waves strike the tympanum, causing it to vibrate. The mechanical energy from the moving tympanum transmits the vibrations to the three bones of the middle ear. The stapes transmits the vibrations to a thin diaphragm called the oval window, which is the outermost structure of the inner ear. The structures of the inner ear are found in the labyrinth, a bony, hollow structure that is the most interior portion of the ear. Here, the energy from the sound wave is transferred from the stapes through the flexible oval window and to the fluid of the cochlea. The vibrations of the oval window create pressure waves in the fluid (perilymph) inside the cochlea. The cochlea is a whorled structure, like the shell of a snail, and it contains receptors for transduction of the mechanical wave into an electrical signal (as illustrated in Figure **43.4.1.3**). Inside the cochlea, the basilar membrane is a mechanical analyzer that runs the length of the cochlea, curling toward the cochlea's center.

The mechanical properties of the basilar membrane change along its length, such that it is thicker, tauter, and narrower at the outside of the whorl (where the cochlea is largest), and thinner, floppier, and broader toward the apex, or center, of the whorl (where the cochlea is smallest). Different regions of the basilar membrane vibrate according to the frequency of the sound wave conducted through the fluid in the cochlea. For these reasons, the fluid-filled cochlea detects different wave frequencies (pitches) at

different regions of the membrane. When the sound waves in the cochlear fluid contact the basilar membrane, it flexes back and forth in a wave-like fashion. Above the basilar membrane is the tectorial membrane.

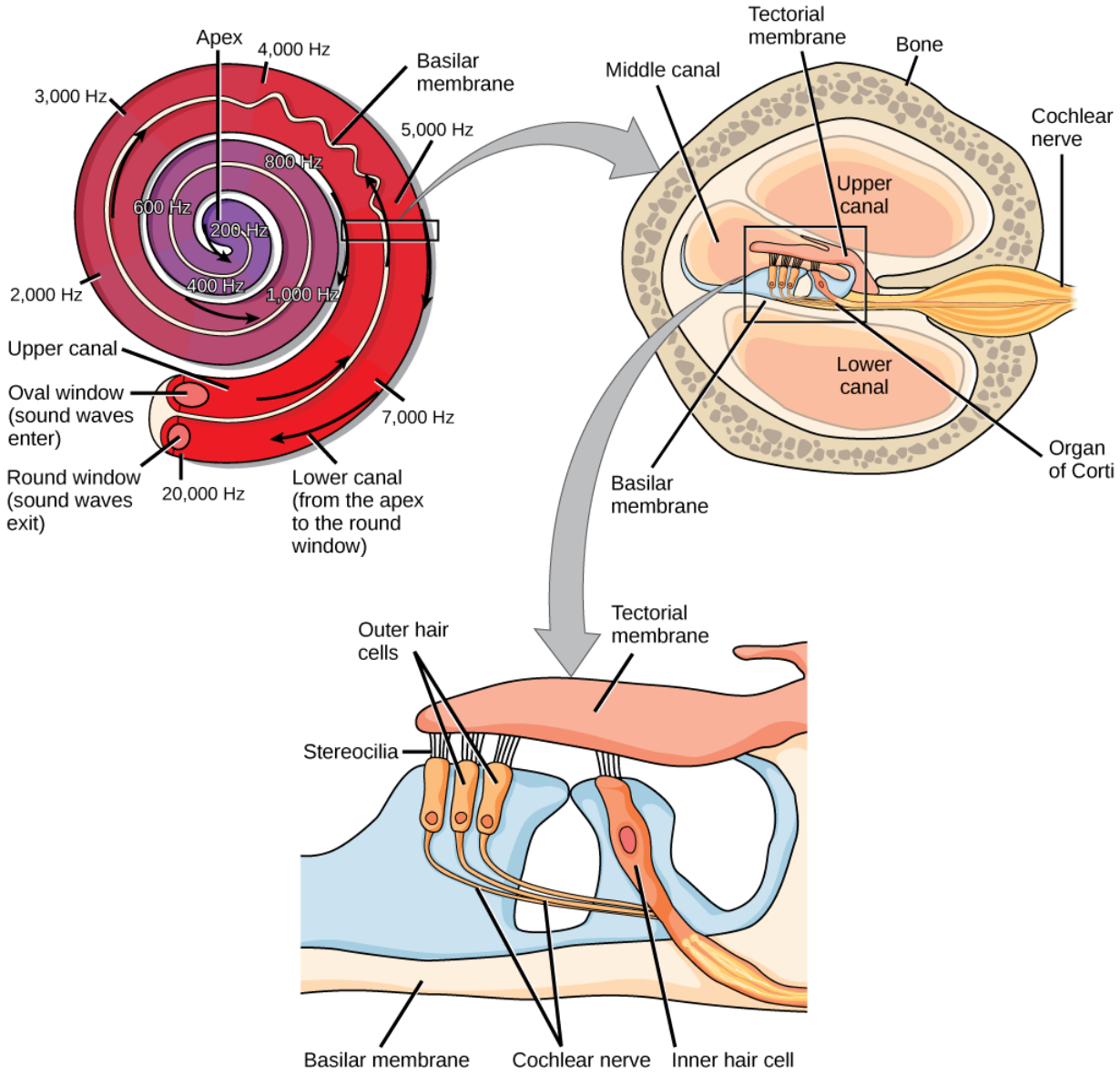


Figure **43.4.1.3**: In the human ear, sound waves cause the stapes to press against the oval window. Vibrations travel up the fluid-filled interior of the cochlea. The basilar membrane that lines the cochlea gets continuously thinner toward the apex of the cochlea. Different thicknesses of membrane vibrate in response to different frequencies of sound. Sound waves then exit through the round window. In the cross section of the cochlea (top right figure), note that in addition to the upper canal and lower canal, the cochlea also has a middle canal. The organ of Corti (bottom image) is the site of sound transduction. Movement of stereocilia on hair cells results in an action potential that travels along the auditory nerve.

Exercise

Cochlear implants can restore hearing in people who have a nonfunctional cochlear. The implant consists of a microphone that picks up sound. A speech processor selects sounds in the range of human speech, and a transmitter converts these sounds to electrical impulses, which are then sent to the auditory nerve. Which of the following types of hearing loss would not be restored by a cochlear implant?

A. Hearing loss resulting from absence or loss of hair cells in the organ of Corti.
B. Hearing loss resulting from an abnormal auditory nerve.
C. Hearing loss resulting from fracture of the cochlea.

D. Hearing loss resulting from damage to bones of the middle ear.

Answer

B

The site of transduction is in the organ of Corti (spiral organ). It is composed of hair cells held in place above the basilar membrane like flowers projecting up from soil, with their exposed short, hair-like stereocilia contacting or embedded in the tectorial membrane above them. The inner hair cells are the primary auditory receptors and exist in a single row, numbering approximately 3,500. The stereocilia from inner hair cells extend into small dimples on the tectorial membrane's lower surface. The outer hair cells are arranged in three or four rows. They number approximately 12,000, and they function to fine tune incoming sound waves. The longer stereocilia that project from the outer hair cells actually attach to the tectorial membrane. All of the stereocilia are mechanoreceptors, and when bent by vibrations they respond by opening a gated ion channel. As a result, the hair cell membrane is depolarized, and a signal is transmitted to the chochlear nerve. Intensity (volume) of sound is determined by how many hair cells at a particular location are stimulated.

The hair cells are arranged on the basilar membrane in an orderly way. The basilar membrane vibrates in different regions, according to the frequency of the sound waves impinging on it. Likewise, the hair cells that lay above it are most sensitive to a specific frequency of sound waves. Hair cells can respond to a small range of similar frequencies, but they require stimulation of greater intensity to fire at frequencies outside of their optimal range. The difference in response frequency between adjacent inner hair cells is about 0.2 percent. Compare that to adjacent piano strings, which are about six percent different. Place theory, which is the model for how biologists think pitch detection works in the human ear, states that high frequency sounds selectively vibrate the basilar membrane of the inner ear near the entrance port (the oval window). Lower frequencies travel farther along the membrane before causing appreciable excitation of the membrane. The basic pitch-determining mechanism is based on the location along the membrane where the hair cells are stimulated. The place theory is the first step toward an understanding of pitch perception. Considering the extreme pitch sensitivity of the human ear, it is thought that there must be some auditory "sharpening" mechanism to enhance the pitch resolution.

When sound waves produce fluid waves inside the cochlea, the basilar membrane flexes, bending the stereocilia that attach to the tectorial membrane. Their bending results in action potentials in the hair cells, and auditory information travels along the neural endings of the bipolar neurons of the hair cells (collectively, the auditory nerve) to the brain. When the hairs bend, they release an excitatory neurotransmitter at a synapse with a sensory neuron, which then conducts action potentials to the central nervous system. The cochlear branch of the vestibulocochlear cranial nerve sends information on hearing. The auditory system is very refined, and there is some modulation or "sharpening" built in. The brain can send signals back to the cochlea, resulting in a change of length in the outer hair cells, sharpening or dampening the hair cells' response to certain frequencies.

Higher Processing

The inner hair cells are most important for conveying auditory information to the brain. About 90 percent of the afferent neurons carry information from inner hair cells, with each hair cell synapsing with 10 or so neurons. Outer hair cells connect to only 10 percent of the afferent neurons, and each afferent neuron innervates many hair cells. The afferent, bipolar neurons that convey auditory information travel from the cochlea to the medulla, through the pons and midbrain in the brainstem, finally reaching the primary auditory cortex in the temporal lobe.

Vestibular Information

The stimuli associated with the vestibular system are linear acceleration (gravity) and angular acceleration and deceleration. Gravity, acceleration, and deceleration are detected by evaluating the inertia on receptive cells in the vestibular system. Gravity is detected through head position. Angular acceleration and deceleration are expressed through turning or tilting of the head.

The vestibular system has some similarities with the auditory system. It utilizes hair cells just like the auditory system, but it excites them in different ways. There are five vestibular receptor organs in the inner ear: the utricle, the saccule, and three semicircular canals. Together, they make up what's known as the vestibular labyrinth that is shown in Figure **43.4.1.4**. The utricle and saccule respond to acceleration in a straight line, such as gravity. The roughly 30,000 hair cells in the utricle and 16,000 hair

cells in the saccule lie below a gelatinous layer, with their stereocilia projecting into the gelatin. Embedded in this gelatin are calcium carbonate crystals—like tiny rocks. When the head is tilted, the crystals continue to be pulled straight down by gravity, but the new angle of the head causes the gelatin to shift, thereby bending the stereocilia. The bending of the stereocilia stimulates the neurons, and they signal to the brain that the head is tilted, allowing the maintenance of balance. It is the vestibular branch of the vestibulocochlear cranial nerve that deals with balance.

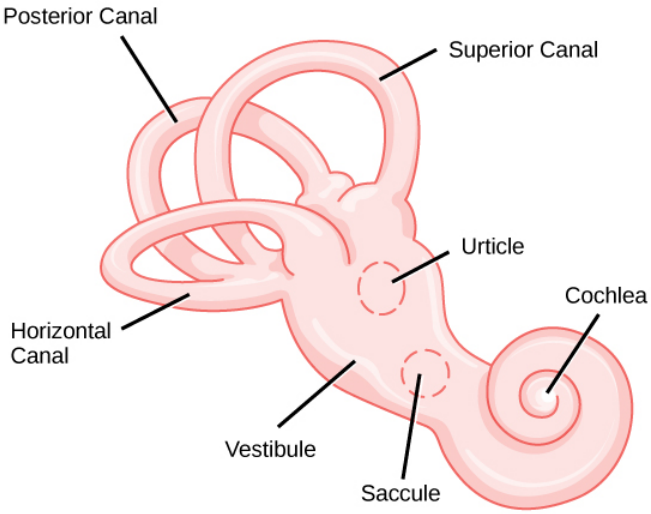


Figure **43.4.1.4**: The structure of the vestibular labyrinth is shown. (credit: modification of work by NIH)

The fluid-filled semicircular canals are tubular loops set at oblique angles. They are arranged in three spatial planes. The base of each canal has a swelling that contains a cluster of hair cells. The hairs project into a gelatinous cap called the cupula and monitor angular acceleration and deceleration from rotation. They would be stimulated by driving your car around a corner, turning your head, or falling forward. One canal lies horizontally, while the other two lie at about 45 degree angles to the horizontal axis. When the brain processes input from all three canals together, it can detect angular acceleration or deceleration in three dimensions. When the head turns, the fluid in the canals shifts, thereby bending stereocilia and sending signals to the brain. Upon cessation accelerating or decelerating—or just moving—the movement of the fluid within the canals slows or stops. For example, imagine holding a glass of water. When moving forward, water may splash backwards onto the hand, and when motion has stopped, water may splash forward onto the fingers. While in motion, the water settles in the glass and does not splash. Note that the canals are not sensitive to velocity itself, but to changes in velocity, so moving forward at 60mph with your eyes closed would not give the sensation of movement, but suddenly accelerating or braking would stimulate the receptors.

Higher Processing

Hair cells from the utricle, saccule, and semicircular canals also communicate through bipolar neurons to the cochlear nucleus in the medulla. Cochlear neurons send descending projections to the spinal cord and ascending projections to the pons, thalamus, and cerebellum. Connections to the cerebellum are important for coordinated movements. There are also projections to the temporal cortex, which account for feelings of dizziness; projections to autonomic nervous system areas in the brainstem, which account for motion sickness; and projections to the primary somatosensory cortex, which monitors subjective measurements of the external world and self-movement. People with lesions in the vestibular area of the somatosensory cortex see vertical objects in the world as being tilted. Finally, the vestibular signals project to certain optic muscles to coordinate eye and head movements.

Link to Learning



Click through this interactive tutorial to review the parts of the ear and how they function to process sound.

Summary

Audition is important for territory defense, predation, predator defense, and communal exchanges. The vestibular system, which is not auditory, detects linear acceleration and angular acceleration and deceleration. Both the auditory system and vestibular system use hair cells as their receptors.

Auditory stimuli are sound waves. The sound wave energy reaches the outer ear (pinna, canal, tympanum), and vibrations of the tympanum send the energy to the middle ear. The middle ear bones shift and the stapes transfers mechanical energy to the oval window of the fluid-filled inner ear cochlea. Once in the cochlea, the energy causes the basilar membrane to flex, thereby bending the stereocilia on receptor hair cells. This activates the receptors, which send their auditory neural signals to the brain.

The vestibular system has five parts that work together to provide the sense of direction, thus helping to maintain balance. The utricle and saccule measure head orientation: their calcium carbonate crystals shift when the head is tilted, thereby activating hair cells. The semicircular canals work similarly, such that when the head is turned, the fluid in the canals bends stereocilia on hair cells. The vestibular hair cells also send signals to the thalamus and to somatosensory cortex, but also to the cerebellum, the structure above the brainstem that plays a large role in timing and coordination of movement.

Glossary

audition
sense of hearing

basilar membrane
stiff structure in the cochlea that indirectly anchors auditory receptors

cochlea
whorled structure that contains receptors for transduction of the mechanical wave into an electrical signal

incus
(also, anvil) second of the three bones of the middle ear

inner ear
innermost part of the ear; consists of the cochlea and the vestibular system

labyrinth
bony, hollow structure that is the most internal part of the ear; contains the sites of transduction of auditory and vestibular information

malleus
(also, hammer) first of the three bones of the middle ear

middle ear
part of the hearing apparatus that functions to transfer energy from the tympanum to the oval window of the inner ear

organ of Corti

in the basilar membrane, the site of the transduction of sound, a mechanical wave, to a neural signal

ossicle
one of the three bones of the middle ear

outer ear
part of the ear that consists of the pinna, ear canal, and tympanum and which conducts sound waves into the middle ear

oval window
thin diaphragm between the middle and inner ears that receives sound waves from contact with the stapes bone of the middle ear

pinna
cartilaginous outer ear

semicircular canal
one of three half-circular, fluid-filled tubes in the vestibular labyrinth that monitors angular acceleration and deceleration

stapes
(also, stirrup) third of the three bones of the middle ear

stereocilia
in the auditory system, hair-like projections from hair cells that help detect sound waves

tectorial membrane
cochlear structure that lies above the hair cells and participates in the transduction of sound at the hair cells

tympanum
(also, tympanic membrane or ear drum) thin diaphragm between the outer and middle ears

ultrasound
sound frequencies above the human detectable ceiling of approximately 20,000 Hz

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43.5: Chemoreceptors- Taste, Smell and pH

Skills to Develop

- Explain in what way smell and taste stimuli differ from other sensory stimuli
- Identify the five primary tastes that can be distinguished by humans
- Explain in anatomical terms why a dog's sense of smell is more acute than a human's

Taste, also called gustation, and smell, also called olfaction, are the most interconnected senses in that both involve molecules of the stimulus entering the body and bonding to receptors. Smell lets an animal sense the presence of food or other animals—whether potential mates, predators, or prey—or other chemicals in the environment that can impact their survival. Similarly, the sense of taste allows animals to discriminate between types of foods. While the value of a sense of smell is obvious, what is the value of a sense of taste? Different tasting foods have different attributes, both helpful and harmful. For example, sweet-tasting substances tend to be highly caloric, which could be necessary for survival in lean times. Bitterness is associated with toxicity, and sourness is associated with spoiled food. Salty foods are valuable in maintaining homeostasis by helping the body retain water and by providing ions necessary for cells to function.

Tastes and Odors

Both taste and odor stimuli are molecules taken in from the environment. The primary tastes detected by humans are sweet, sour, bitter, salty and umami. The first four tastes need little explanation. The identification of umami as a fundamental taste occurred fairly recently—it was identified in 1908 by Japanese scientist Kikunae Ikeda while he worked with seaweed broth, but it was not widely accepted as a taste that could be physiologically distinguished until many years later. The taste of umami, also known as savoriness, is attributable to the taste of the amino acid L-glutamate. In fact, monosodium glutamate, or MSG, is often used in cooking to enhance the savory taste of certain foods. What is the adaptive value of being able to distinguish umami? Savory substances tend to be high in protein.

All odors that we perceive are molecules in the air we breathe. If a substance does not release molecules into the air from its surface, it has no smell. And if a human or other animal does not have a receptor that recognizes a specific molecule, then that molecule has no smell. Humans have about 350 olfactory receptor subtypes that work in various combinations to allow us to sense about 10,000 different odors. Compare that to mice, for example, which have about 1,300 olfactory receptor types, and therefore probably sense more odors. Both odors and tastes involve molecules that stimulate specific chemoreceptors. Although humans commonly distinguish taste as one sense and smell as another, they work together to create the perception of flavor. A person's perception of flavor is reduced if he or she has congested nasal passages.

Reception and Transduction

Odorants (odor molecules) enter the nose and dissolve in the olfactory epithelium, the mucosa at the back of the nasal cavity (as illustrated in Figure **43.5.1**). The olfactory epithelium is a collection of specialized olfactory receptors in the back of the nasal cavity that spans an area about 5 cm^2 in humans. Recall that sensory cells are neurons. An olfactory receptor, which is a dendrite of a specialized neuron, responds when it binds certain molecules inhaled from the environment by sending impulses directly to the olfactory bulb of the brain. Humans have about 12 million olfactory receptors, distributed among hundreds of different receptor types that respond to different odors. Twelve million seems like a large number of receptors, but compare that to other animals: rabbits have about 100 million, most dogs have about 1 billion, and bloodhounds—dogs selectively bred for their sense of smell—have about 4 billion. The overall size of the olfactory epithelium also differs between species, with that of bloodhounds, for example, being many times larger than that of humans.

Olfactory neurons are bipolar neurons (neurons with two processes from the cell body). Each neuron has a single dendrite buried in the olfactory epithelium, and extending from this dendrite are 5 to 20 receptor-laden, hair-like cilia that trap odorant molecules. The sensory receptors on the cilia are proteins, and it is the variations in their amino acid chains that make the receptors sensitive to different odorants. Each olfactory sensory neuron has only one type of receptor on its cilia, and the receptors are specialized to detect specific odorants, so the bipolar neurons themselves are specialized. When an odorant binds with a receptor that recognizes

it, the sensory neuron associated with the receptor is stimulated. Olfactory stimulation is the only sensory information that directly reaches the cerebral cortex, whereas other sensations are relayed through the thalamus.

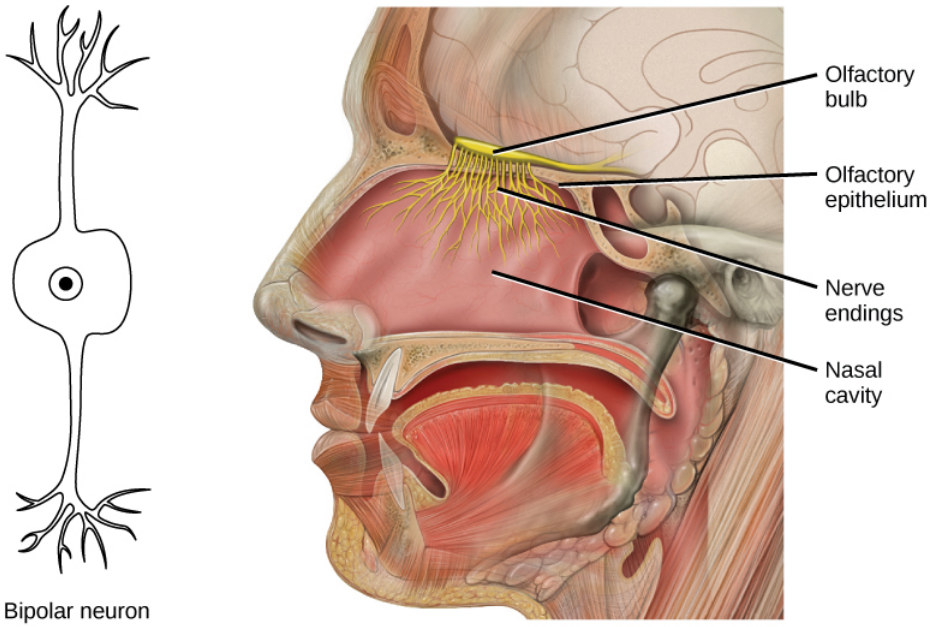


Figure **43.5.1**: In the human olfactory system, (a) bipolar olfactory neurons extend from (b) the olfactory epithelium, where olfactory receptors are located, to the olfactory bulb. (credit: modification of work by Patrick J. Lynch, medical illustrator; C. Carl Jaffe, MD, cardiologist)

Evolution Connection: Pheromones

A pheromone is a chemical released by an animal that affects the behavior or physiology of animals of the same species. Pheromonal signals can have profound effects on animals that inhale them, but pheromones apparently are not consciously perceived in the same way as other odors. There are several different types of pheromones, which are released in urine or as glandular secretions. Certain pheromones are attractants to potential mates, others are repellants to potential competitors of the same sex, and still others play roles in mother-infant attachment. Some pheromones can also influence the timing of puberty, modify reproductive cycles, and even prevent embryonic implantation. While the roles of pheromones in many nonhuman species are important, pheromones have become less important in human behavior over evolutionary time compared to their importance to organisms with more limited behavioral repertoires.

The vomeronasal organ (VNO, or Jacobson's organ) is a tubular, fluid-filled, olfactory organ present in many vertebrate animals that sits adjacent to the nasal cavity. It is very sensitive to pheromones and is connected to the nasal cavity by a duct. When molecules dissolve in the mucosa of the nasal cavity, they then enter the VNO where the pheromone molecules among them bind with specialized pheromone receptors. Upon exposure to pheromones from their own species or others, many animals, including cats, may display the flehmen response (Figure **43.5.2**), a curling of the upper lip that helps pheromone molecules enter the VNO.



Figure **43.5.2**: The flehmen response in this tiger results in the curling of the upper lip and helps airborne pheromone molecules enter the vomeronasal organ. (credit: modification of work by "chadh"/Flickr)

Pheromonal signals are sent, not to the main olfactory bulb, but to a different neural structure that projects directly to the amygdala (recall that the amygdala is a brain center important in emotional reactions, such as fear). The pheromonal signal then continues to areas of the hypothalamus that are key to reproductive physiology and behavior. While some scientists assert that the VNO is apparently functionally vestigial in humans, even though there is a similar structure located near human nasal cavities, others are researching it as a possible functional system that may, for example, contribute to synchronization of menstrual cycles in women living in close proximity.

Taste

Detecting a taste (gustation) is fairly similar to detecting an odor (olfaction), given that both taste and smell rely on chemical receptors being stimulated by certain molecules. The primary organ of taste is the taste bud. A taste bud is a cluster of gustatory receptors (taste cells) that are located within the bumps on the tongue called papillae (singular: papilla) (illustrated in Figure **43.5.3**). There are several structurally distinct papillae. Filiform papillae, which are located across the tongue, are tactile, providing friction that helps the tongue move substances, and contain no taste cells. In contrast, fungiform papillae, which are located mainly on the anterior two-thirds of the tongue, each contain one to eight taste buds and also have receptors for pressure and temperature. The large circumvallate papillae contain up to 100 taste buds and form a V near the posterior margin of the tongue.

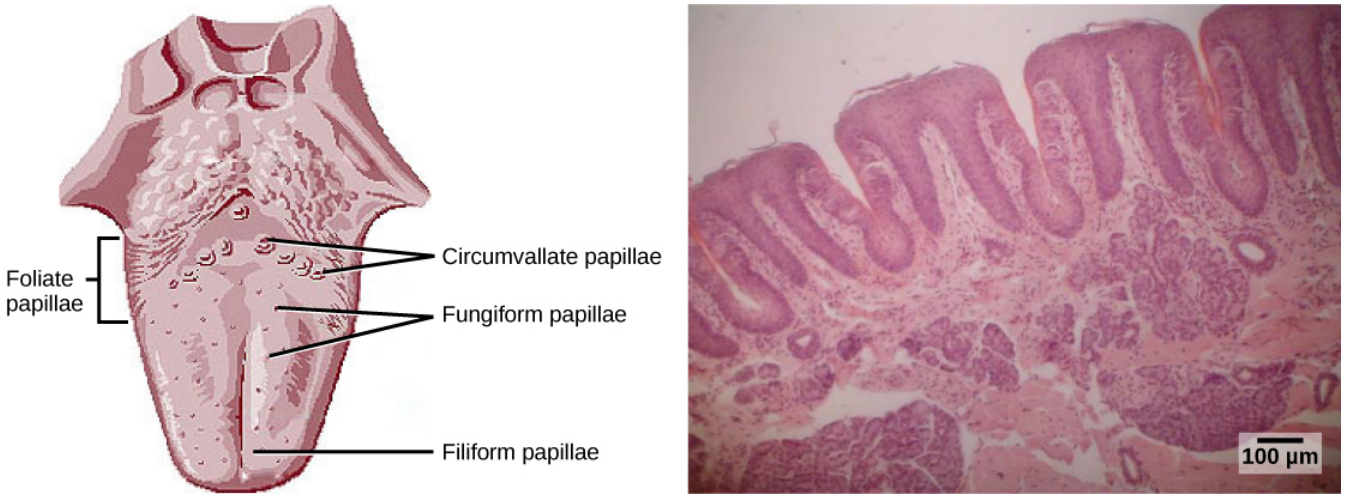


Figure **43.5.3**: (a) Foliate, circumvallate, and fungiform papillae are located on different regions of the tongue. (b) Foliate papillae are prominent protrusions on this light micrograph. (credit a: modification of work by NCI; scale-bar data from Matt Russell)

In addition to those two types of chemically and mechanically sensitive papillae are foliate papillae—leaf-like papillae located in parallel folds along the edges and toward the back of the tongue, as seen in the micrograph. Foliate papillae contain about 1,300

taste buds within their folds. Finally, there are circumvallate papillae, which are wall-like papillae in the shape of an inverted “V” at the back of the tongue. Each of these papillae is surrounded by a groove and contains about 250 taste buds.

Each taste bud’s taste cells are replaced every 10 to 14 days. These are elongated cells with hair-like processes called microvilli at the tips that extend into the taste bud pore (illustrated in Figure **43.5.4**). Food molecules (tastants) are dissolved in saliva, and they bind with and stimulate the receptors on the microvilli. The receptors for tastants are located across the outer portion and front of the tongue, outside of the middle area where the filiform papillae are most prominent.

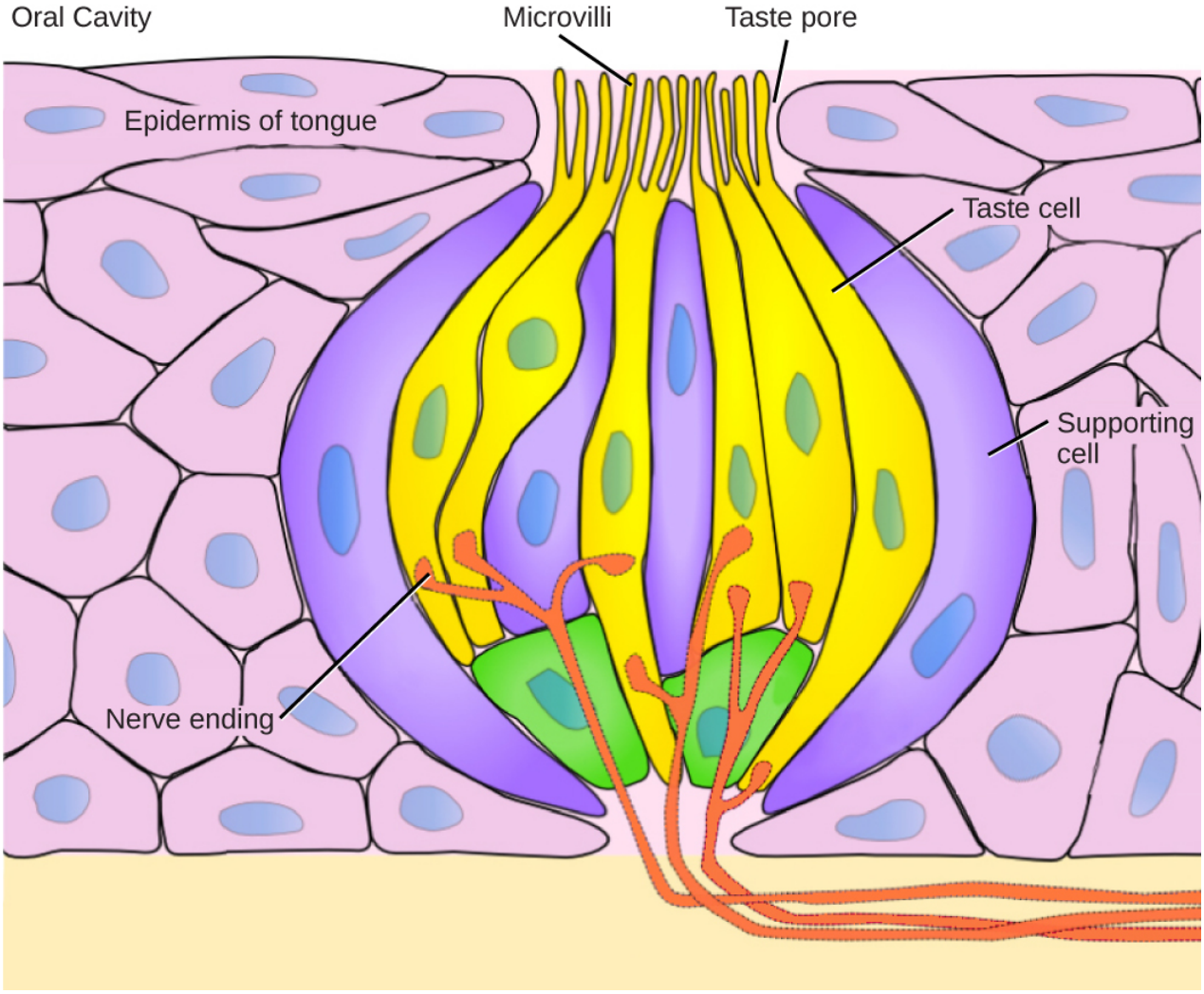


Figure **43.5.4**: Pores in the tongue allow tastants to enter taste pores in the tongue. (credit: modification of work by Vincenzo Rizzo)

In humans, there are five primary tastes, and each taste has only one corresponding type of receptor. Thus, like olfaction, each receptor is specific to its stimulus (tastant). Transduction of the five tastes happens through different mechanisms that reflect the molecular composition of the tastant. A salty tastant (containing NaCl) provides the sodium ions (Na^+) that enter the taste neurons and excite them directly. Sour tastants are acids and belong to the thermoreceptor protein family. Binding of an acid or other sour-tasting molecule triggers a change in the ion channel and these increase hydrogen ion (H^+) concentrations in the taste neurons, thus depolarizing them. Sweet, bitter, and umami tastants require a G-protein coupled receptor. These tastants bind to their respective receptors, thereby exciting the specialized neurons associated with them.

Both tasting abilities and sense of smell change with age. In humans, the senses decline dramatically by age 50 and continue to decline. A child may find a food to be too spicy, whereas an elderly person may find the same food to be bland and unappetizing.

Link to Learning



View this animation that shows how the sense of taste works.

Smell and Taste in the Brain

Olfactory neurons project from the olfactory epithelium to the olfactory bulb as thin, unmyelinated axons. The olfactory bulb is composed of neural clusters called glomeruli, and each glomerulus receives signals from one type of olfactory receptor, so each glomerulus is specific to one odorant. From glomeruli, olfactory signals travel directly to the olfactory cortex and then to the frontal cortex and the thalamus. Recall that this is a different path from most other sensory information, which is sent directly to the thalamus before ending up in the cortex. Olfactory signals also travel directly to the amygdala, thereafter reaching the hypothalamus, thalamus, and frontal cortex. The last structure that olfactory signals directly travel to is a cortical center in the temporal lobe structure important in spatial, autobiographical, declarative, and episodic memories. Olfaction is finally processed by areas of the brain that deal with memory, emotions, reproduction, and thought.

Taste neurons project from taste cells in the tongue, esophagus, and palate to the medulla, in the brainstem. From the medulla, taste signals travel to the thalamus and then to the primary gustatory cortex. Information from different regions of the tongue is segregated in the medulla, thalamus, and cortex.

Summary

There are five primary tastes in humans: sweet, sour, bitter, salty, and umami. Each taste has its own receptor type that responds only to that taste. Tastants enter the body and are dissolved in saliva. Taste cells are located within taste buds, which are found on three of the four types of papillae in the mouth.

Regarding olfaction, there are many thousands of odorants, but humans detect only about 10,000. Like taste receptors, olfactory receptors are each responsive to only one odorant. Odorants dissolve in nasal mucosa, where they excite their corresponding olfactory sensory cells. When these cells detect an odorant, they send their signals to the main olfactory bulb and then to other locations in the brain, including the olfactory cortex.

Glossary

bipolar neuron

neuron with two processes from the cell body, typically in opposite directions

glomerulus

in the olfactory bulb, one of the two neural clusters that receives signals from one type of olfactory receptor

gustation

sense of taste

odorant
airborne molecule that stimulates an olfactory receptor

olfaction
sense of smell

olfactory bulb
neural structure in the vertebrate brain that receives signals from olfactory receptors

olfactory epithelium
specialized tissue in the nasal cavity where olfactory receptors are located

olfactory receptor
dendrite of a specialized neuron

papilla
one of the small bump-like projections from the tongue

pheromone
substance released by an animal that can affect the physiology or behavior of other animals

tastant
food molecule that stimulates gustatory receptors

taste bud
clusters of taste cells

umami
one of the five basic tastes, which is described as “savory” and which may be largely the taste of L-glutamate

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43.6: Vision

Skills to Develop

- Explain how electromagnetic waves differs from sound waves
- Trace the path of light through the eye to the point of the optic nerve
- Explain tonic activity as it is manifested in photoreceptors in the retina

Vision is the ability to detect light patterns from the outside environment and interpret them into images. Animals are bombarded with sensory information, and the sheer volume of visual information can be problematic. Fortunately, the visual systems of species have evolved to attend to the most-important stimuli. The importance of vision to humans is further substantiated by the fact that about one-third of the human cerebral cortex is dedicated to analyzing and perceiving visual information.

Light

As with auditory stimuli, light travels in waves. The compression waves that compose sound must travel in a medium—a gas, a liquid, or a solid. In contrast, light is composed of electromagnetic waves and needs no medium; light can travel in a vacuum (Figure **43.6.1**). The behavior of light can be discussed in terms of the behavior of waves and also in terms of the behavior of the fundamental unit of light—a packet of electromagnetic radiation called a photon. A glance at the electromagnetic spectrum shows that visible light for humans is just a small slice of the entire spectrum, which includes radiation that we cannot see as light because it is below the frequency of visible red light and above the frequency of visible violet light.

Certain variables are important when discussing perception of light. Wavelength (which varies inversely with frequency) manifests itself as hue. Light at the red end of the visible spectrum has longer wavelengths (and is lower frequency), while light at the violet end has shorter wavelengths (and is higher frequency). The wavelength of light is expressed in nanometers (nm); one nanometer is one billionth of a meter. Humans perceive light that ranges between approximately 380 nm and 740 nm. Some other animals, though, can detect wavelengths outside of the human range. For example, bees see near-ultraviolet light in order to locate nectar guides on flowers, and some non-avian reptiles sense infrared light (heat that prey gives off).

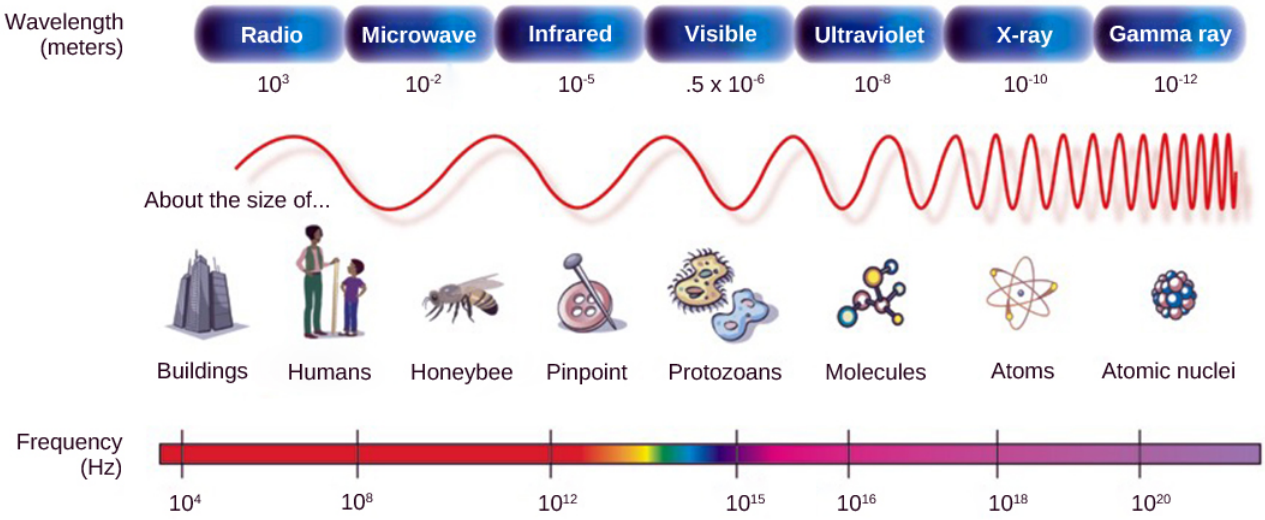


Figure **43.6.1**: In the electromagnetic spectrum, visible light lies between 380 nm and 740 nm. (credit: modification of work by NASA)

Wave amplitude is perceived as luminous intensity, or brightness. The standard unit of intensity of light is the candela, which is approximately the luminous intensity of a one common candle.

Light waves travel 299,792 km per second in a vacuum, (and somewhat slower in various media such as air and water), and those waves arrive at the eye as long (red), medium (green), and short (blue) waves. What is termed “white light” is light that is perceived as white by the human eye. This effect is produced by light that stimulates equally the color receptors in the human eye.

The apparent color of an object is the color (or colors) that the object reflects. Thus a red object reflects the red wavelengths in mixed (white) light and absorbs all other wavelengths of light.

Anatomy of the Eye

The photoreceptive cells of the eye, where transduction of light to nervous impulses occurs, are located in the retina (shown in Figure **43.6.2**) on the inner surface of the back of the eye. But light does not impinge on the retina unaltered. It passes through other layers that process it so that it can be interpreted by the retina (Figure **43.6.2b**). The cornea, the front transparent layer of the eye, and the crystalline lens, a transparent convex structure behind the cornea, both refract (bend) light to focus the image on the retina. The iris, which is conspicuous as the colored part of the eye, is a circular muscular ring lying between the lens and cornea that regulates the amount of light entering the eye. In conditions of high ambient light, the iris contracts, reducing the size of the pupil at its center. In conditions of low light, the iris relaxes and the pupil enlarges.

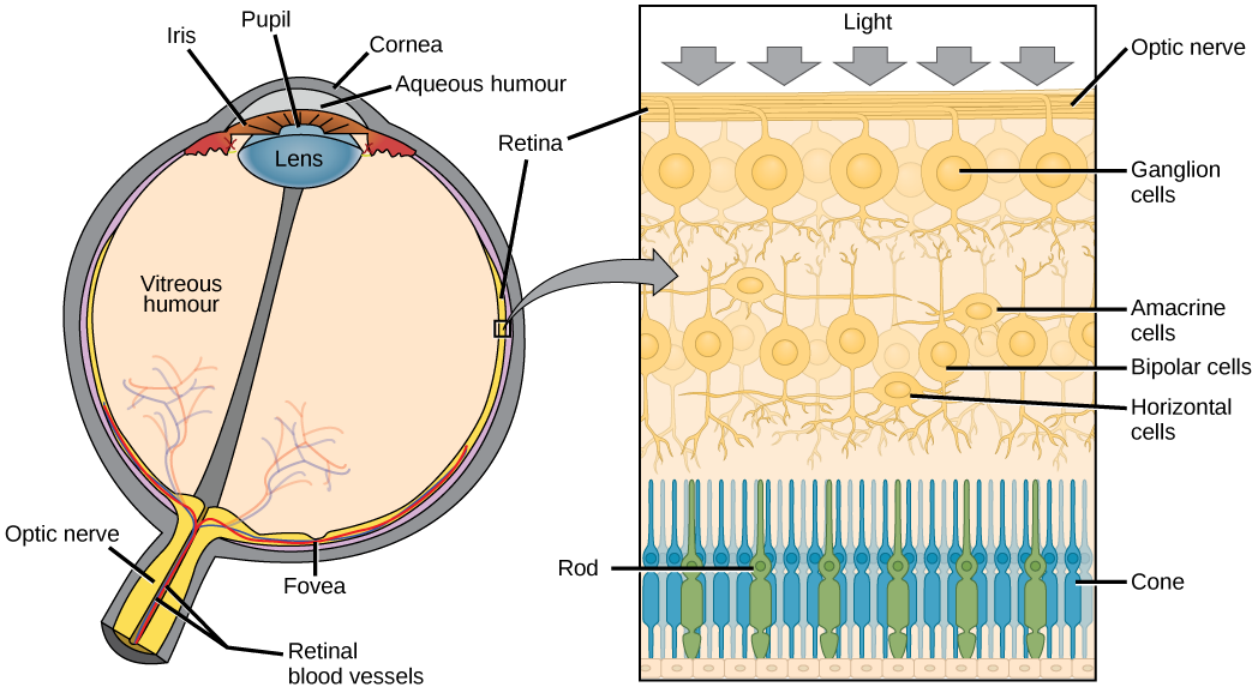


Figure **43.6.2**: (a) The human eye is shown in cross section. (b) A blowup shows the layers of the retina.

Exercise

Which of the following statements about the human eye is false?

A. Rods detect color, while cones detect only shades of gray.
B. When light enters the retina, it passes the ganglion cells and bipolar cells before reaching photoreceptors at the rear of the eye.
C. The iris adjusts the amount of light coming into the eye.
D. The cornea is a protective layer on the front of the eye.

Answer

A

The main function of the lens is to focus light on the retina and fovea centralis. The lens is dynamic, focusing and re-focusing light as the eye rests on near and far objects in the visual field. The lens is operated by muscles that stretch it flat or allow it to thicken, changing the focal length of light coming through it to focus it sharply on the retina. With age comes the loss of the flexibility of the lens, and a form of farsightedness called presbyopia results. Presbyopia occurs because the image focuses behind the retina. Presbyopia is a deficit similar to a different type of farsightedness called hyperopia caused by an eyeball that is too short. For both

defects, images in the distance are clear but images nearby are blurry. Myopia (nearsightedness) occurs when an eyeball is elongated and the image focus falls in front of the retina. In this case, images in the distance are blurry but images nearby are clear.

There are two types of photoreceptors in the retina: rods and cones, named for their general appearance as illustrated in Figure **43.6.3**. Rods are strongly photosensitive and are located in the outer edges of the retina. They detect dim light and are used primarily for peripheral and nighttime vision. Cones are weakly photosensitive and are located near the center of the retina. They respond to bright light, and their primary role is in daytime, color vision.

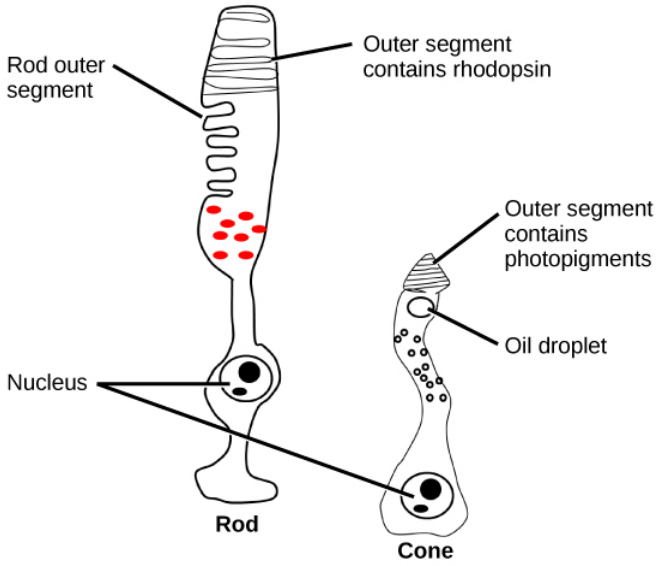


Figure **43.6.3**: Rods and cones are photoreceptors in the retina. Rods respond in low light and can detect only shades of gray. Cones respond in intense light and are responsible for color vision. (credit: modification of work by Piotr Sliwa)

The fovea is the region in the center back of the eye that is responsible for acute vision. The fovea has a high density of cones. When you bring your gaze to an object to examine it intently in bright light, the eyes orient so that the object's image falls on the fovea. However, when looking at a star in the night sky or other object in dim light, the object can be better viewed by the peripheral vision because it is the rods at the edges of the retina, rather than the cones at the center, that operate better in low light. In humans, cones far outnumber rods in the fovea.

Link to Learning

Review the anatomical structure of the eye, clicking on each part to practice identification.

Transduction of Light

The rods and cones are the site of transduction of light to a neural signal. Both rods and cones contain photopigments. In vertebrates, the main photopigment, rhodopsin, has two main parts Figure **43.6.4**): an opsin, which is a membrane protein (in the form of a cluster of α-helices that span the membrane), and retinal—a molecule that absorbs light.

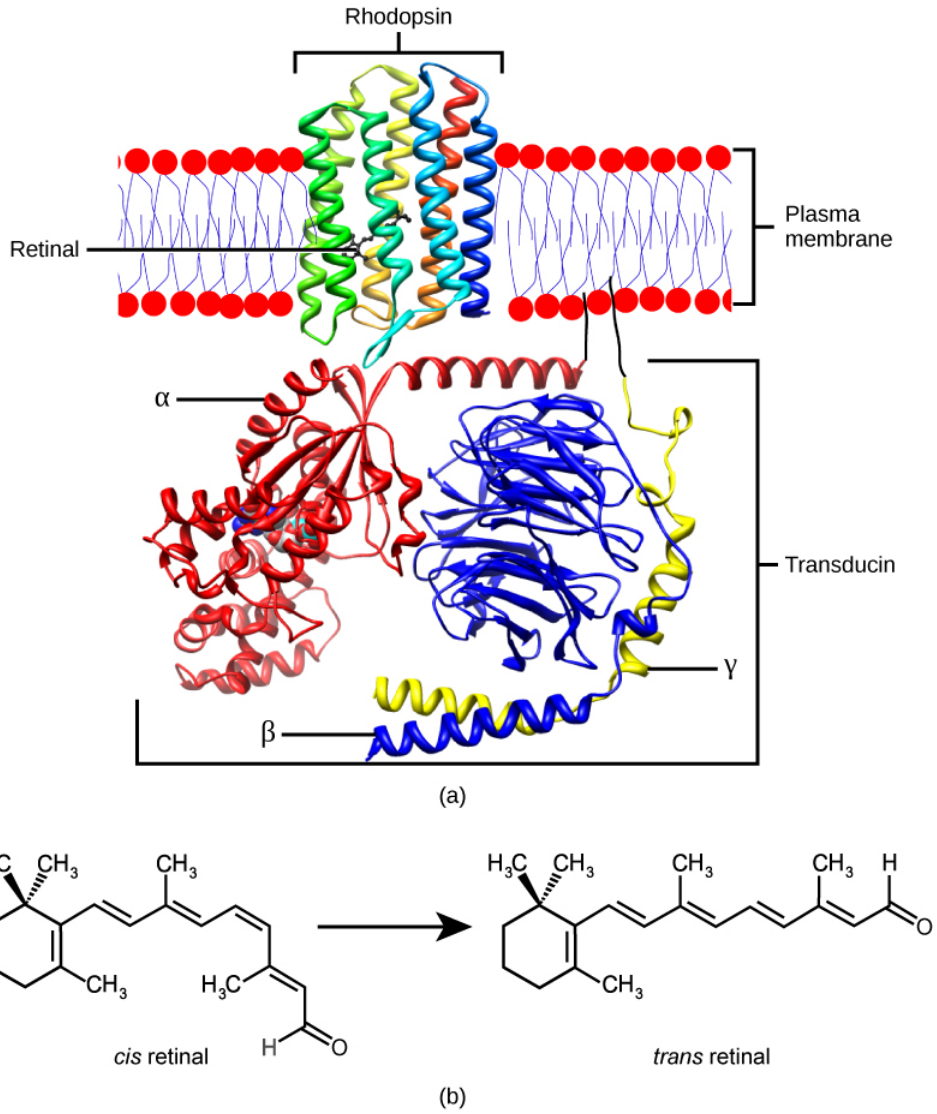


Figure 43.6.4: (a) Rhodopsin, the photoreceptor in vertebrates, has two parts: the trans-membrane protein opsin, and retinal. When light strikes retinal, it changes shape from (b) a *cis* to a *trans* form. The signal is passed to a G-protein called transducin, triggering a series of downstream events.

When light hits a photoreceptor, it causes a shape change in the retinal, altering its structure from a bent (*cis*) form of the molecule to its linear (*trans*) isomer. This isomerization of retinal activates the rhodopsin, starting a cascade of events that ends with the closing of Na^+ channels in the membrane of the photoreceptor. Thus, unlike most other sensory neurons (which become depolarized by exposure to a stimulus) visual receptors become hyperpolarized and thus driven away from threshold (Figure 43.6.5).

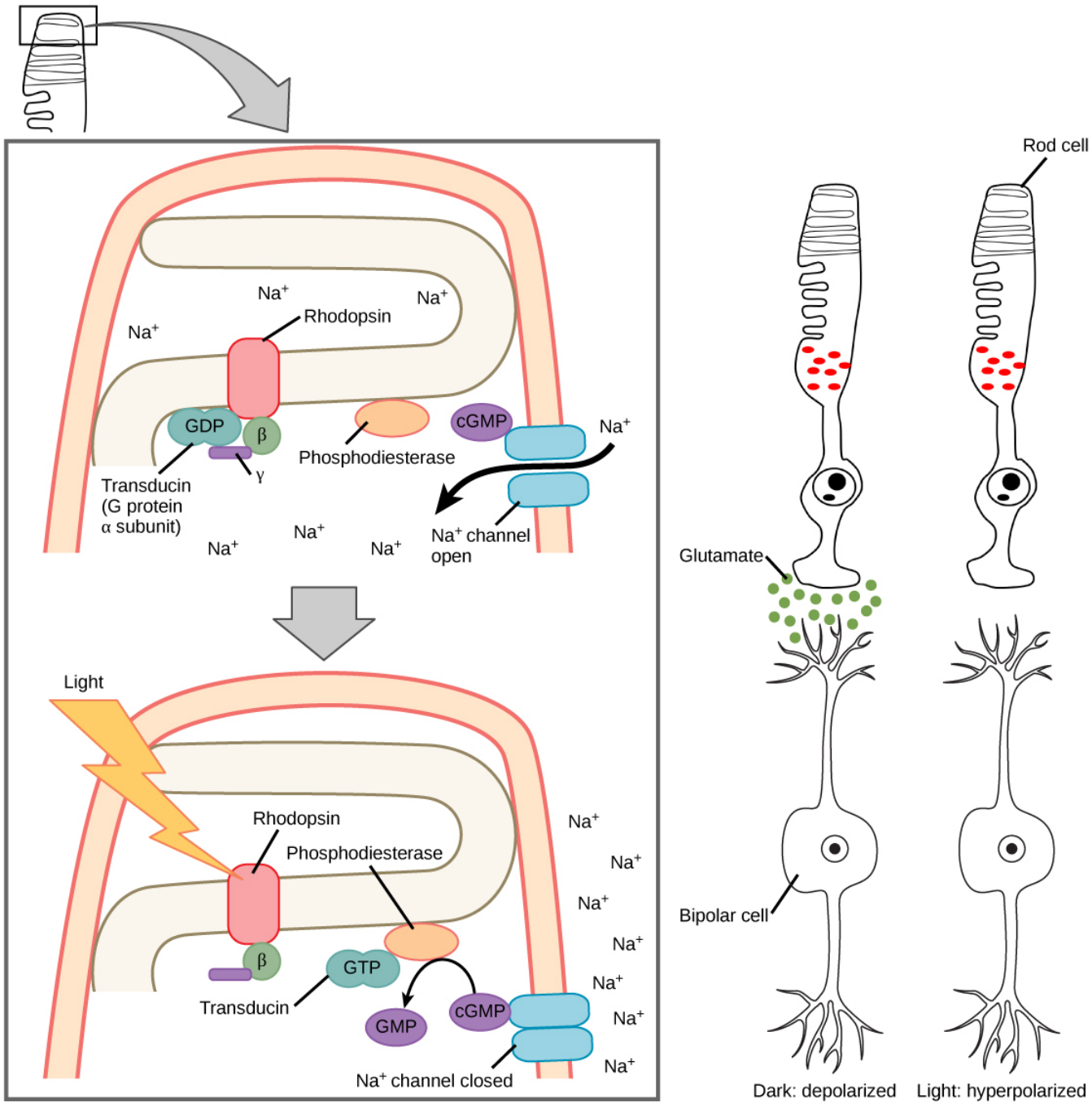


Figure **43.6.5**: When light strikes rhodopsin, the G-protein transducin is activated, which in turn activates phosphodiesterase. Phosphodiesterase converts cGMP to GMP, thereby closing sodium channels. As a result, the membrane becomes hyperpolarized. The hyperpolarized membrane does not release glutamate to the bipolar cell.

Trichromatic Coding

There are three types of cones (with different photopsins), and they differ in the wavelength to which they are most responsive, as shown in Figure **43.6.6**. Some cones are maximally responsive to short light waves of 420 nm, so they are called S cones ("S" for "short"); others respond maximally to waves of 530 nm (M cones, for "medium"); a third group responds maximally to light of longer wavelengths, at 560 nm (L, or "long" cones). With only one type of cone, color vision would not be possible, and a two-cone (dichromatic) system has limitations. Primates use a three-cone (trichromatic) system, resulting in full color vision.

The color we perceive is a result of the ratio of activity of our three types of cones. The colors of the visual spectrum, running from long-wavelength light to short, are red (700 nm), orange (600 nm), yellow (565 nm), green (497 nm), blue (470 nm), indigo (450

nm), and violet (425 nm). Humans have very sensitive perception of color and can distinguish about 500 levels of brightness, 200 different hues, and 20 steps of saturation, or about 2 million distinct colors.

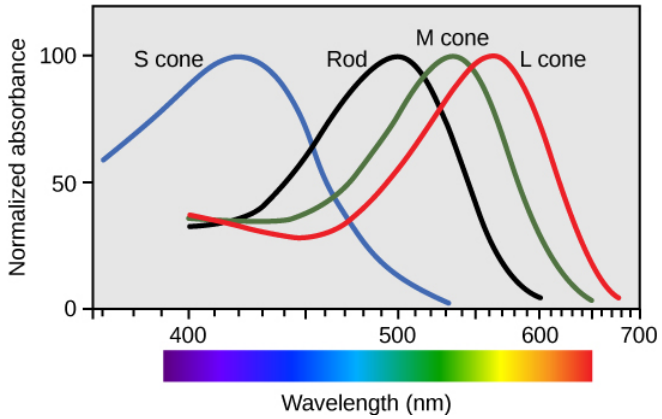


Figure **43.6.6**: Human rod cells and the different types of cone cells each have an optimal wavelength. However, there is considerable overlap in the wavelengths of light detected.

Retinal Processing

Visual signals leave the cones and rods, travel to the bipolar cells, and then to ganglion cells. A large degree of processing of visual information occurs in the retina itself, before visual information is sent to the brain.

Photoreceptors in the retina continuously undergo tonic activity. That is, they are always slightly active even when not stimulated by light. In neurons that exhibit tonic activity, the absence of stimuli maintains a firing rate at a baseline; while some stimuli increase firing rate from the baseline, and other stimuli decrease firing rate. In the absence of light, the bipolar neurons that connect rods and cones to ganglion cells are continuously and actively inhibited by the rods and cones. Exposure of the retina to light hyperpolarizes the rods and cones and removes their inhibition of bipolar cells. The now active bipolar cells in turn stimulate the ganglion cells, which send action potentials along their axons (which leave the eye as the optic nerve). Thus, the visual system relies on change in retinal activity, rather than the absence or presence of activity, to encode visual signals for the brain. Sometimes horizontal cells carry signals from one rod or cone to other photoreceptors and to several bipolar cells. When a rod or cone stimulates a horizontal cell, the horizontal cell inhibits more distant photoreceptors and bipolar cells, creating lateral inhibition. This inhibition sharpens edges and enhances contrast in the images by making regions receiving light appear lighter and dark surroundings appear darker. Amacrine cells can distribute information from one bipolar cell to many ganglion cells.

You can demonstrate this using an easy demonstration to “trick” your retina and brain about the colors you are observing in your visual field. Look fixedly at Figure **43.6.7** for about 45 seconds. Then quickly shift your gaze to a sheet of blank white paper or a white wall. You should see an afterimage of the Norwegian flag in its correct colors. At this point, close your eyes for a moment, then reopen them, looking again at the white paper or wall; the afterimage of the flag should continue to appear as red, white, and blue. What causes this? According to an explanation called opponent process theory, as you gazed fixedly at the green, black, and yellow flag, your retinal ganglion cells that respond positively to green, black, and yellow increased their firing dramatically. When you shifted your gaze to the neutral white ground, these ganglion cells abruptly decreased their activity and the brain interpreted this abrupt downshift as if the ganglion cells were responding now to their “opponent” colors: red, white, and blue, respectively, in the visual field. Once the ganglion cells return to their baseline activity state, the false perception of color will disappear.

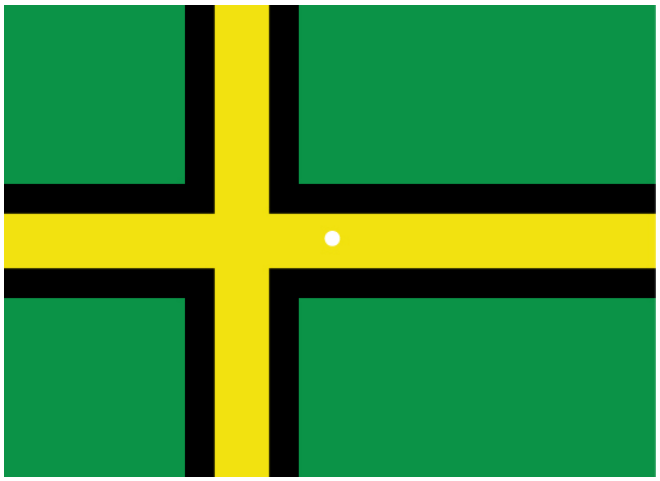


Figure **43.6.7**: View this flag to understand how retinal processing works. Stare at the center of the flag (indicated by the white dot) for 45 seconds, and then quickly look at a white background, noticing how colors appear.

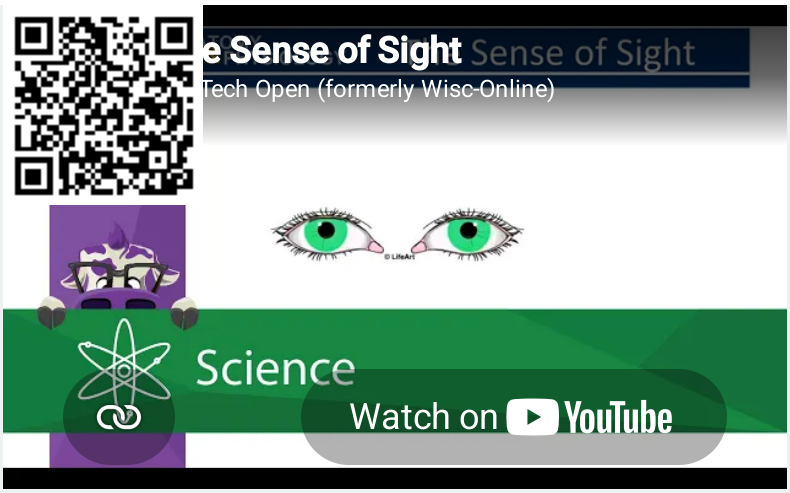
Higher Processing

The myelinated axons of ganglion cells make up the optic nerves. Within the nerves, different axons carry different qualities of the visual signal. Some axons constitute the magnocellular (big cell) pathway, which carries information about form, movement, depth, and differences in brightness. Other axons constitute the parvocellular (small cell) pathway, which carries information on color and fine detail. Some visual information projects directly back into the brain, while other information crosses to the opposite side of the brain. This crossing of optical pathways produces the distinctive optic chiasma (Greek, for “crossing”) found at the base of the brain and allows us to coordinate information from both eyes.

Once in the brain, visual information is processed in several places, and its routes reflect the complexity and importance of visual information to humans and other animals. One route takes the signals to the thalamus, which serves as the routing station for all incoming sensory impulses except olfaction. In the thalamus, the magnocellular and parvocellular distinctions remain intact, and there are different layers of the thalamus dedicated to each. When visual signals leave the thalamus, they travel to the primary visual cortex at the rear of the brain. From the visual cortex, the visual signals travel in two directions. One stream that projects to the parietal lobe, in the side of the brain, carries magnocellular (“where”) information. A second stream projects to the temporal lobe and carries both magnocellular (“where”) and parvocellular (“what”) information.

Another important visual route is a pathway from the retina to the superior colliculus in the midbrain, where eye movements are coordinated and integrated with auditory information. Finally, there is the pathway from the retina to the suprachiasmatic nucleus (SCN) of the hypothalamus. The SCN is a cluster of cells that is considered to be the body’s internal clock, which controls our circadian (day-long) cycle. The SCN sends information to the pineal gland, which is important in sleep/wake patterns and annual cycles.

Link to Learning



View this interactive presentation to review what you have learned about how vision functions.

Summary

Vision is the only photo responsive sense. Visible light travels in waves and is a very small slice of the electromagnetic radiation spectrum. Light waves differ based on their frequency (wavelength = hue) and amplitude (intensity = brightness).

In the vertebrate retina, there are two types of light receptors (photoreceptors): cones and rods. Cones, which are the source of color vision, exist in three forms—L, M, and S—and they are differentially sensitive to different wavelengths. Cones are located in the retina, along with the dim-light, achromatic receptors (rods). Cones are found in the fovea, the central region of the retina, whereas rods are found in the peripheral regions of the retina.

Visual signals travel from the eye over the axons of retinal ganglion cells, which make up the optic nerves. Ganglion cells come in several versions. Some ganglion cell axons carry information on form, movement, depth, and brightness, while other axons carry information on color and fine detail. Visual information is sent to the superior colliculi in the midbrain, where coordination of eye movements and integration of auditory information takes place. Visual information is also sent to the suprachiasmatic nucleus (SCN) of the hypothalamus, which plays a role in the circadian cycle.

Glossary

candela
(cd) unit of measurement of luminous intensity (brightness)

circadian
describes a time cycle about one day in length

cone
weakly photosensitive, chromatic, cone-shaped neuron in the fovea of the retina that detects bright light and is used in daytime color vision

cornea
transparent layer over the front of the eye that helps focus light waves

fovea
region in the center of the retina with a high density of photoreceptors and which is responsible for acute vision

hyperopia
(also, farsightedness) visual defect in which the image focus falls behind the retina, thereby making images in the distance clear, but close-up images blurry

iris
: pigmented, circular muscle at the front of the eye that regulates the amount of light entering the eye

lens
: transparent, convex structure behind the cornea that helps focus light waves on the retina

myopia
: (also, nearsightedness) visual defect in which the image focus falls in front of the retina, thereby making images in the distance blurry, but close-up images clear

presbyopia
: visual defect in which the image focus falls behind the retina, thereby making images in the distance clear, but close-up images blurry; caused by age-based changes in the lens

pupil
: small opening though which light enters

retina
: layer of photoreceptive and supporting cells on the inner surface of the back of the eye

rhodopsin
: main photopigment in vertebrates

rod
: strongly photosensitive, achromatic, cylindrical neuron in the outer edges of the retina that detects dim light and is used in peripheral and nighttime vision

superior colliculus
: paired structure in the top of the midbrain, which manages eye movements and auditory integration

suprachiasmatic nucleus
: cluster of cells in the hypothalamus that plays a role in the circadian cycle

tonic activity
: in a neuron, slight continuous activity while at rest

vision
: sense of sight

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43.7: Evolution and the Development of Eyes



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CHAPTER OVERVIEW

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44.1: Regulation of Body Processes by Chemical Messengers

Skills to Develop

- Describe four types of signaling found in multicellular organisms
- Compare internal receptors with cell-surface receptors
- Recognize the relationship between a ligand’s structure and its mechanism of action

There are two kinds of communication in the world of living cells. Communication between cells is called intercellular signaling, and communication within a cell is called intracellular signaling. An easy way to remember the distinction is by understanding the Latin origin of the prefixes: inter- means "between" (for example, intersecting lines are those that cross each other) and intra- means "inside" (like intravenous).

Chemical signals are released by signaling cells in the form of small, usually volatile or soluble molecules called ligands. A ligand is a molecule that binds another specific molecule, in some cases, delivering a signal in the process. Ligands can thus be thought of as signaling molecules. Ligands interact with proteins in target cells, which are cells that are affected by chemical signals; these proteins are also called receptors. Ligands and receptors exist in several varieties; however, a specific ligand will have a specific receptor that typically binds only that ligand.

Forms of Signaling

There are four categories of chemical signaling found in multicellular organisms: paracrine signaling, endocrine signaling, autocrine signaling, and direct signaling across gap junctions (Figure **44.1.1**). The main difference between the different categories of signaling is the distance that the signal travels through the organism to reach the target cell. Not all cells are affected by the same signals.

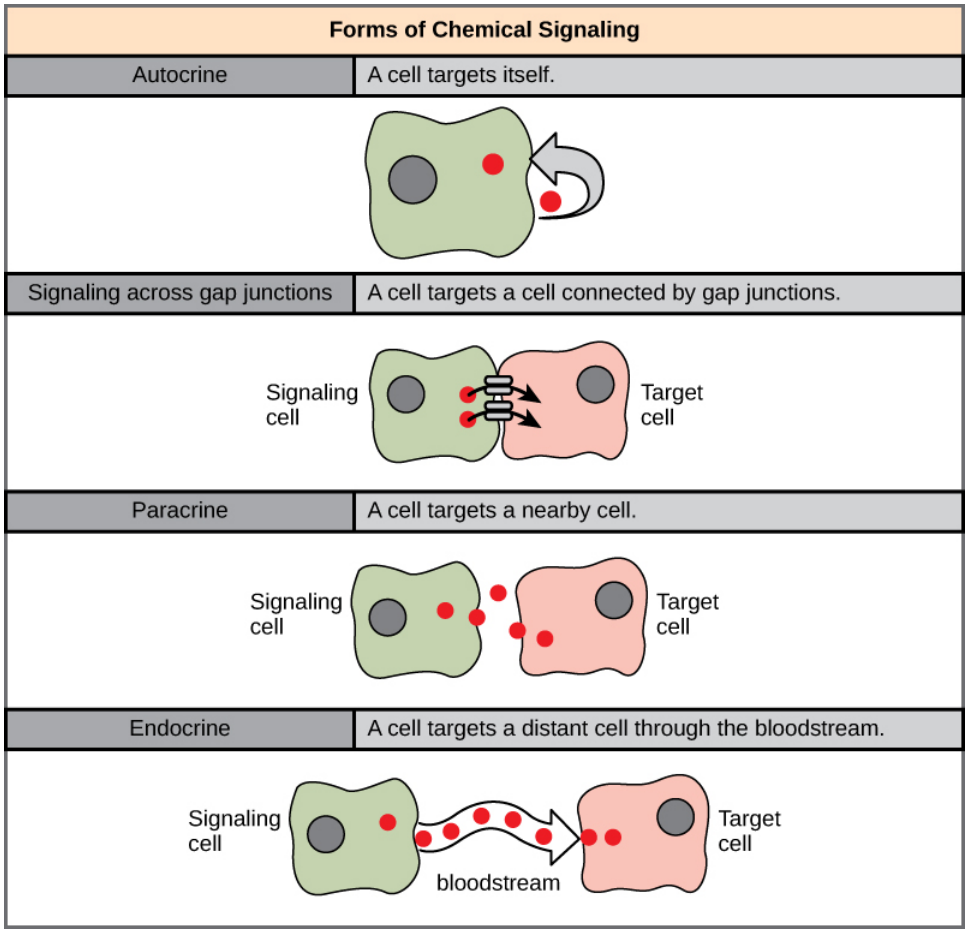


Figure **44.1.1**: In chemical signaling, a cell may target itself (autocrine signaling), a cell connected by gap junctions, a nearby cell (paracrine signaling), or a distant cell (endocrine signaling). Paracrine signaling acts on nearby cells, endocrine signaling uses the circulatory system to transport ligands, and autocrine signaling acts on the signaling cell. Signaling via gap junctions involves signaling molecules moving directly between adjacent cells.

Paracrine Signaling

Signals that act locally between cells that are close together are called *paracrine signals*. Paracrine signals move by diffusion through the extracellular matrix. These types of signals usually elicit quick responses that last only a short amount of time. In order to keep the response localized, paracrine ligand molecules are normally quickly degraded by enzymes or removed by neighboring cells. Removing the signals will reestablish the concentration gradient for the signal, allowing them to quickly diffuse through the intracellular space if released again.

One example of paracrine signaling is the transfer of signals across synapses between nerve cells. A nerve cell consists of a cell body, several short, branched extensions called dendrites that receive stimuli, and a long extension called an axon, which transmits signals to other nerve cells or muscle cells. The junction between nerve cells where signal transmission occurs is called a synapse. A synaptic signal is a chemical signal that travels between nerve cells. Signals within the nerve cells are propagated by fast-moving electrical impulses. When these impulses reach the end of the axon, the signal continues on to a dendrite of the next cell by the release of chemical ligands called neurotransmitters by the presynaptic cell (the cell emitting the signal). The neurotransmitters are transported across the very small distances between nerve cells, which are called chemical synapses (Figure **44.1.2**). The small distance between nerve cells allows the signal to travel quickly; this enables an immediate response, such as, Take your hand off the stove!

When the neurotransmitter binds the receptor on the surface of the postsynaptic cell, the electrochemical potential of the target cell changes, and the next electrical impulse is launched. The neurotransmitters that are released into the chemical synapse are degraded quickly or get reabsorbed by the presynaptic cell so that the recipient nerve cell can recover quickly and be prepared to respond rapidly to the next synaptic signal.

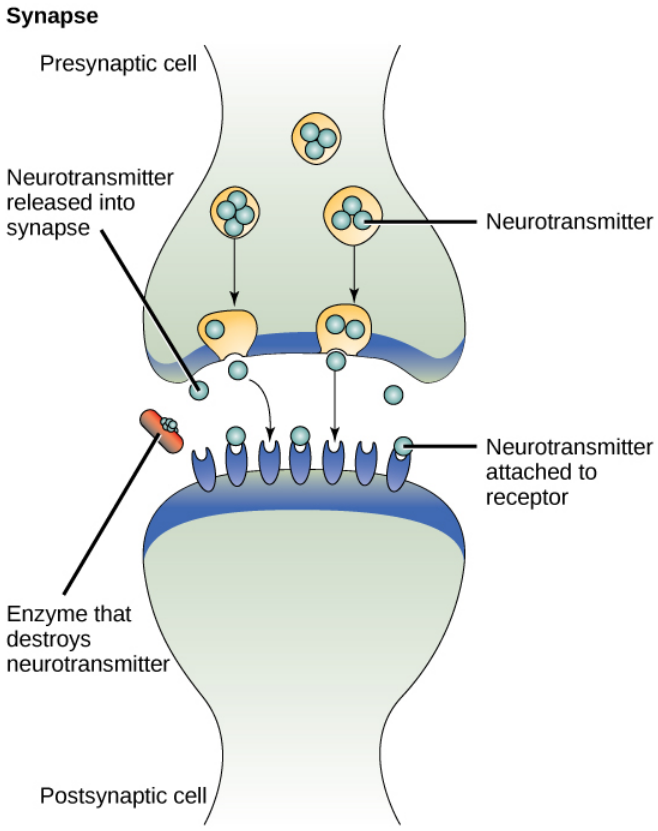


Figure **44.1.2**: The distance between the presynaptic cell and the postsynaptic cell—called the synaptic gap—is very small and allows for rapid diffusion of the neurotransmitter. Enzymes in the synapatic cleft degrade some types of neurotransmitters to terminate the signal.

Endocrine Signaling

Signals from distant cells are called endocrine signals, and they originate from endocrine cells. (In the body, many endocrine cells are located in endocrine glands, such as the thyroid gland, the hypothalamus, and the pituitary gland.) These types of signals usually produce a slower response but have a longer-lasting effect. The ligands released in endocrine signaling are called hormones, signaling molecules that are produced in one part of the body but affect other body regions some distance away.

Hormones travel the large distances between endocrine cells and their target cells via the bloodstream, which is a relatively slow way to move throughout the body. Because of their form of transport, hormones get diluted and are present in low concentrations when they act on their target cells. This is different from paracrine signaling, in which local concentrations of ligands can be very high.

Autocrine Signaling

Autocrine signals are produced by signaling cells that can also bind to the ligand that is released. This means the signaling cell and the target cell can be the same or a similar cell (the prefix *auto-* means self, a reminder that the signaling cell sends a signal to itself). This type of signaling often occurs during the early development of an organism to ensure that cells develop into the correct tissues and take on the proper function. Autocrine signaling also regulates pain sensation and inflammatory responses. Further, if a cell is infected with a virus, the cell can signal itself to undergo programmed cell death, killing the virus in the process. In some cases, neighboring cells of the same type are also influenced by the released ligand. In embryological development, this process of stimulating a group of neighboring cells may help to direct the differentiation of identical cells into the same cell type, thus ensuring the proper developmental outcome.

Direct Signaling Across Gap Junctions

Gap junctions in animals and plasmodesmata in plants are connections between the plasma membranes of neighboring cells. These water-filled channels allow small signaling molecules, called intracellular mediators, to diffuse between the two cells. Small

molecules, such as calcium ions (Ca^{2+}), are able to move between cells, but large molecules like proteins and DNA cannot fit through the channels. The specificity of the channels ensures that the cells remain independent but can quickly and easily transmit signals. The transfer of signaling molecules communicates the current state of the cell that is directly next to the target cell; this allows a group of cells to coordinate their response to a signal that only one of them may have received. In plants, plasmodesmata are ubiquitous, making the entire plant into a giant, communication network.

Types of Receptors

Receptors are protein molecules in the target cell or on its surface that bind ligand. There are two types of receptors, internal receptors and cell-surface receptors.

Internal receptors

Internal receptors, also known as intracellular or cytoplasmic receptors, are found in the cytoplasm of the cell and respond to hydrophobic ligand molecules that are able to travel across the plasma membrane. Once inside the cell, many of these molecules bind to proteins that act as regulators of mRNA synthesis (transcription) to mediate gene expression. Gene expression is the cellular process of transforming the information in a cell's DNA into a sequence of amino acids, which ultimately forms a protein. When the ligand binds to the internal receptor, a conformational change is triggered that exposes a DNA-binding site on the protein. The ligand-receptor complex moves into the nucleus, then binds to specific regulatory regions of the chromosomal DNA and promotes the initiation of transcription (Figure **44.1.3**). Transcription is the process of copying the information in a cells DNA into a special form of RNA called messenger RNA (mRNA); the cell uses information in the mRNA (which moves out into the cytoplasm and associates with ribosomes) to link specific amino acids in the correct order, producing a protein. Internal receptors can directly influence gene expression without having to pass the signal on to other receptors or messengers.

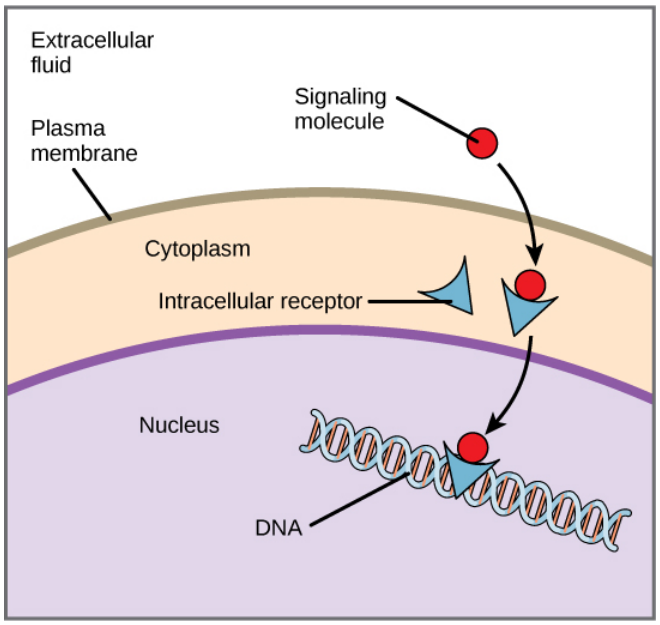


Figure **44.1.3**: Hydrophobic signaling molecules typically diffuse across the plasma membrane and interact with intracellular receptors in the cytoplasm. Many intracellular receptors are transcription factors that interact with DNA in the nucleus and regulate gene expression.

Cell-Surface Receptors

Cell-surface receptors, also known as transmembrane receptors, are cell surface, membrane-anchored (integral) proteins that bind to external ligand molecules. This type of receptor spans the plasma membrane and performs signal transduction, in which an extracellular signal is converted into an intercellular signal. Ligands that interact with cell-surface receptors do not have to enter the cell that they affect. Cell-surface receptors are also called cell-specific proteins or markers because they are specific to individual cell types.

Because cell-surface receptor proteins are fundamental to normal cell functioning, it should come as no surprise that a malfunction in any one of these proteins could have severe consequences. Errors in the protein structures of certain receptor molecules have

been shown to play a role in hypertension (high blood pressure), asthma, heart disease, and cancer.

Each cell-surface receptor has three main components: an external ligand-binding domain, a hydrophobic membrane-spanning region, and an intracellular domain inside the cell. The ligand-binding domain is also called the extracellular domain. The size and extent of each of these domains vary widely, depending on the type of receptor.

Evolution Connection: How Viruses Recognize a Host

Unlike living cells, many viruses do not have a plasma membrane or any of the structures necessary to sustain life. Some viruses are simply composed of an inert protein shell containing DNA or RNA. To reproduce, viruses must invade a living cell, which serves as a host, and then take over the hosts cellular apparatus. But how does a virus recognize its host?

Viruses often bind to cell-surface receptors on the host cell. For example, the virus that causes human influenza (flu) binds specifically to receptors on membranes of cells of the respiratory system. Chemical differences in the cell-surface receptors among hosts mean that a virus that infects a specific species (for example, humans) cannot infect another species (for example, chickens).

However, viruses have very small amounts of DNA or RNA compared to humans, and, as a result, viral reproduction can occur rapidly. Viral reproduction invariably produces errors that can lead to changes in newly produced viruses; these changes mean that the viral proteins that interact with cell-surface receptors may evolve in such a way that they can bind to receptors in a new host. Such changes happen randomly and quite often in the reproductive cycle of a virus, but the changes only matter if a virus with new binding properties comes into contact with a suitable host. In the case of influenza, this situation can occur in settings where animals and people are in close contact, such as poultry and swine farms.[1] Once a virus jumps to a new host, it can spread quickly. Scientists watch newly appearing viruses (called emerging viruses) closely in the hope that such monitoring can reduce the likelihood of global viral epidemics.

Cell-surface receptors are involved in most of the signaling in multicellular organisms. There are three general categories of cell-surface receptors: ion channel-linked receptors, G-protein-linked receptors, and enzyme-linked receptors.

Ion channel-linked receptors bind a ligand and open a channel through the membrane that allows specific ions to pass through. To form a channel, this type of cell-surface receptor has an extensive membrane-spanning region. In order to interact with the phospholipid fatty acid tails that form the center of the plasma membrane, many of the amino acids in the membrane-spanning region are hydrophobic in nature. Conversely, the amino acids that line the inside of the channel are hydrophilic to allow for the passage of water or ions. When a ligand binds to the extracellular region of the channel, there is a conformational change in the proteins structure that allows ions such as sodium, calcium, magnesium, and hydrogen to pass through (Figure **44.1.4**).

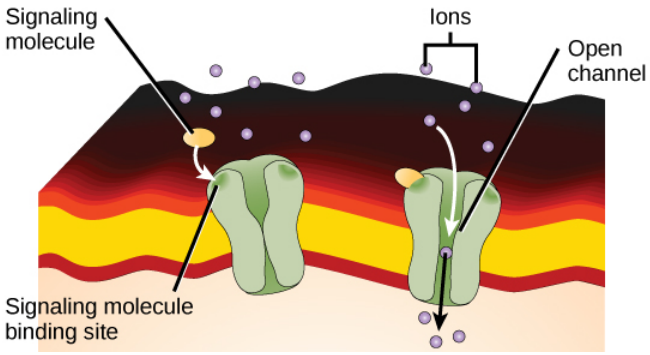


Figure **44.1.4**: Gated ion channels form a pore through the plasma membrane that opens when the signaling molecule binds. The open pore then allows ions to flow into or out of the cell.

G-protein-linked receptors bind a ligand and activate a membrane protein called a G-protein. The activated G-protein then interacts with either an ion channel or an enzyme in the membrane (Figure **44.1.5**). All G-protein-linked receptors have seven transmembrane domains, but each receptor has its own specific extracellular domain and G-protein-binding site.

Cell signaling using G-protein-linked receptors occurs as a cyclic series of events. Before the ligand binds, the inactive G-protein can bind to a newly revealed site on the receptor specific for its binding. Once the G-protein binds to the receptor, the resultant shape change activates the G-protein, which releases GDP and picks up GTP. The subunits of the G-protein then split into the α

subunit and the $\beta\gamma$ subunit. One or both of these G-protein fragments may be able to activate other proteins as a result. After awhile, the GTP on the active α subunit of the G-protein is hydrolyzed to GDP and the $\beta\gamma$ subunit is deactivated. The subunits reassociate to form the inactive G-protein and the cycle begins anew.

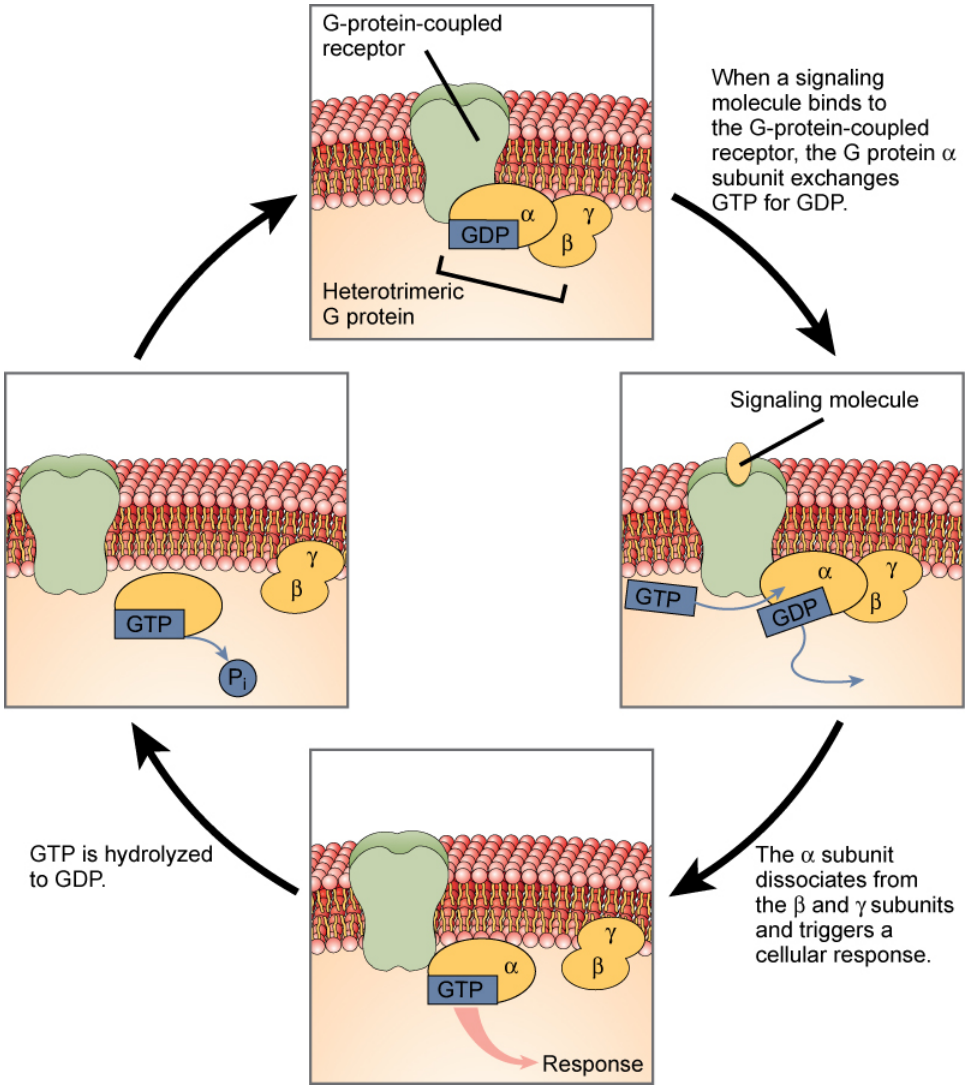
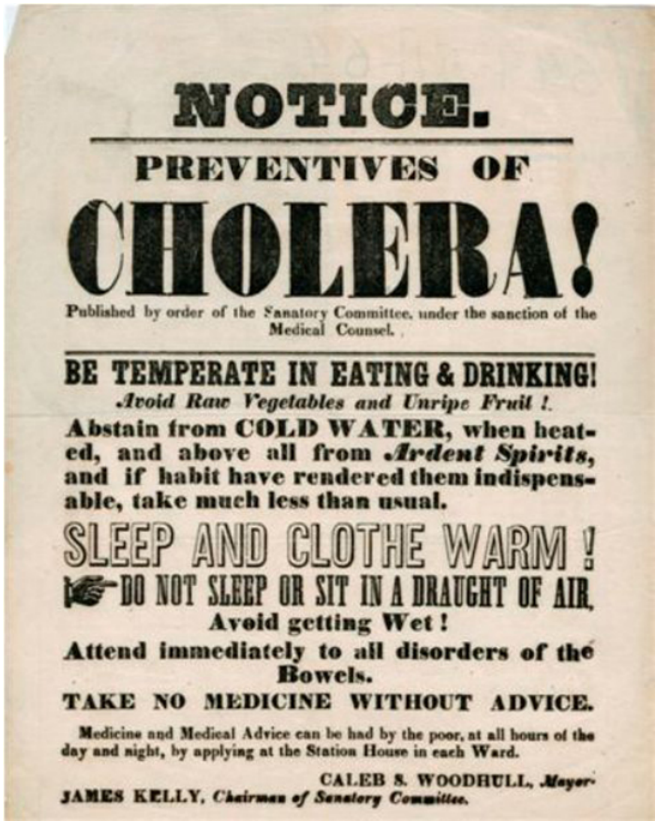


Figure **44.1.5**: Heterotrimeric G proteins have three subunits: α, β, and γ. When a signaling molecule binds to a G-protein-coupled receptor in the plasma membrane, a GDP molecule associated with the α subunit is exchanged for GTP. The β and γ subunits dissociate from the α subunit, and a cellular response is triggered either by the α subunit or the dissociated $\beta\gamma$ pair. Hydrolysis of GTP to GDP terminates the signal.

G-protein-linked receptors have been extensively studied and much has been learned about their roles in maintaining health. Bacteria that are pathogenic to humans can release poisons that interrupt specific G-protein-linked receptor function, leading to illnesses such as pertussis, botulism, and cholera. In cholera (Figure **44.1.6**), for example, the water-borne bacterium *Vibrio cholerae* produces a toxin, choleragen, that binds to cells lining the small intestine. The toxin then enters these intestinal cells, where it modifies a G-protein that controls the opening of a chloride channel and causes it to remain continuously active, resulting in large losses of fluids from the body and potentially fatal dehydration as a result.



NOTICE.

PREVENTIVES OF

CHOLERA!

Published by order of the Sanatory Committee, under the sanction of the Medical Counsel.

BE TEMPERATE IN EATING & DRINKING!

Avoid Raw Vegetables and Unripe Fruit !.

Abstain from COLD WATER, when heated, and above all from *Ardent Spirits*, and if habit have rendered them indispensable, take much less than usual.

SLEEP AND CLOTHE WARM !

DO NOT SLEEP OR SIT IN A DRAUGHT OF AIR.

Avoid getting Wet !

Attend immediately to all disorders of the Bowels.

TAKE NO MEDICINE WITHOUT ADVICE.

Medicine and Medical Advice can be had by the poor, at all hours of the day and night, by applying at the Station House in each Ward.

CALEB S. WOODHULL, *Mayor.*

JAMES KELLY, *Chairman of Sanatory Committee.*

Figure **44.1.6**: Transmitted primarily through contaminated drinking water, cholera is a major cause of death in the developing world and in areas where natural disasters interrupt the availability of clean water. The cholera bacterium, *Vibrio cholerae*, creates a toxin that modifies G-protein-mediated cell signaling pathways in the intestines. Modern sanitation eliminates the threat of cholera outbreaks, such as the one that swept through New York City in 1866. This poster from that era shows how, at that time, the way that the disease was transmitted was not understood. (credit: New York City Sanitary Commission)

Enzyme-linked receptors are cell-surface receptors with intracellular domains that are associated with an enzyme. In some cases, the intracellular domain of the receptor itself is an enzyme. Other enzyme-linked receptors have a small intracellular domain that interacts directly with an enzyme. The enzyme-linked receptors normally have large extracellular and intracellular domains, but the membrane-spanning region consists of a single alpha-helical region of the peptide strand. When a ligand binds to the extracellular domain, a signal is transferred through the membrane, activating the enzyme. Activation of the enzyme sets off a chain of events within the cell that eventually leads to a response. One example of this type of enzyme-linked receptor is the tyrosine kinase receptor (Figure **44.1.7**). A kinase is an enzyme that transfers phosphate groups from ATP to another protein. The tyrosine kinase receptor transfers phosphate groups to tyrosine molecules (tyrosine residues). First, signaling molecules bind to the extracellular domain of two nearby tyrosine kinase receptors. The two neighboring receptors then bond together, or dimerize. Phosphates are then added to tyrosine residues on the intracellular domain of the receptors (phosphorylation). The phosphorylated residues can then transmit the signal to the next messenger within the cytoplasm.

Art Connection

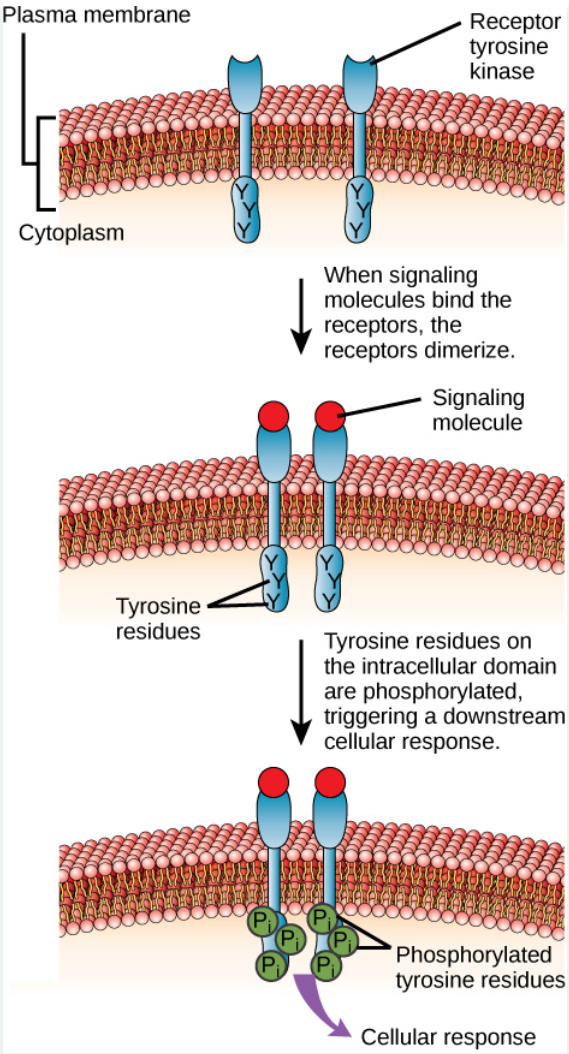


Figure **44.1.7**: A receptor tyrosine kinase is an enzyme-linked receptor with a single transmembrane region, and extracellular and intracellular domains. Binding of a signaling molecule to the extracellular domain causes the receptor to dimerize. Tyrosine residues on the intracellular domain are then autophosphorylated, triggering a downstream cellular response. The signal is terminated by a phosphatase that removes the phosphates from the phosphotyrosine residues.

HER2 is a receptor tyrosine kinase. In 30 percent of human breast cancers, HER2 is permanently activated, resulting in unregulated cell division. Lapatinib, a drug used to treat breast cancer, inhibits HER2 receptor tyrosine kinase autophosphorylation (the process by which the receptor adds phosphates onto itself), thus reducing tumor growth by 50 percent. Besides autophosphorylation, which of the following steps would be inhibited by Lapatinib?

A. Signaling molecule binding, dimerization, and the downstream cellular response
B. Dimerization, and the downstream cellular response
C. The downstream cellular response
D. Phosphatase activity, dimerization, and the downsteam cellular response

Signaling Molecules

Produced by signaling cells and the subsequent binding to receptors in target cells, ligands act as chemical signals that travel to the target cells to coordinate responses. The types of molecules that serve as ligands are incredibly varied and range from small proteins to small ions like calcium (Ca^{2+}).

Small Hydrophobic Ligands

Small hydrophobic ligands can directly diffuse through the plasma membrane and interact with internal receptors. Important members of this class of ligands are the steroid hormones. Steroids are lipids that have a hydrocarbon skeleton with four fused rings; different steroids have different functional groups attached to the carbon skeleton. Steroid hormones include the female sex hormone, estradiol, which is a type of estrogen; the male sex hormone, testosterone; and cholesterol, which is an important structural component of biological membranes and a precursor of steroid hormones (Figure **44.1.8**). Other hydrophobic hormones include thyroid hormones and vitamin D. In order to be soluble in blood, hydrophobic ligands must bind to carrier proteins while they are being transported through the bloodstream.

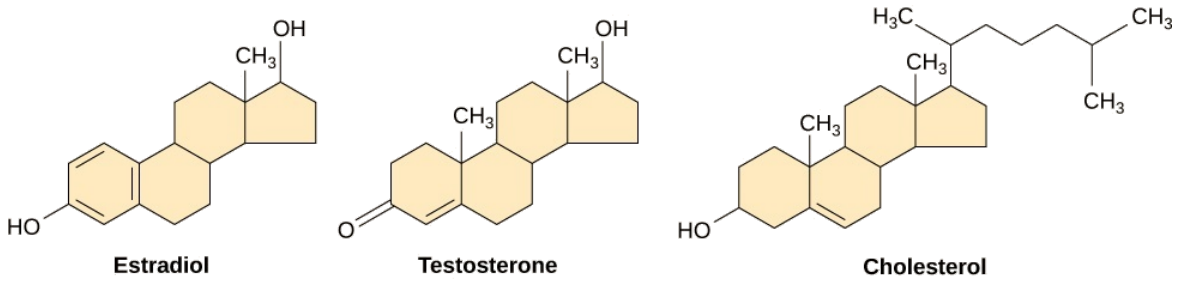


Figure **44.1.8**: Steroid hormones have similar chemical structures to their precursor, cholesterol. Because these molecules are small and hydrophobic, they can diffuse directly across the plasma membrane into the cell, where they interact with internal receptors.

Water-Soluble Ligands

Water-soluble ligands are polar and therefore cannot pass through the plasma membrane unaided; sometimes, they are too large to pass through the membrane at all. Instead, most water-soluble ligands bind to the extracellular domain of cell-surface receptors. This group of ligands is quite diverse and includes small molecules, peptides, and proteins.

Other Ligands

Nitric oxide (NO) is a gas that also acts as a ligand. It is able to diffuse directly across the plasma membrane, and one of its roles is to interact with receptors in smooth muscle and induce relaxation of the tissue. NO has a very short half-life and therefore only functions over short distances. Nitroglycerin, a treatment for heart disease, acts by triggering the release of NO, which causes blood vessels to dilate (expand), thus restoring blood flow to the heart. NO has become better known recently because the pathway that it affects is targeted by prescription medications for erectile dysfunction, such as Viagra (erection involves dilated blood vessels).

Summary

Cells communicate by both inter- and intracellular signaling. Signaling cells secrete ligands that bind to target cells and initiate a chain of events within the target cell. The four categories of signaling in multicellular organisms are paracrine signaling, endocrine signaling, autocrine signaling, and direct signaling across gap junctions. Paracrine signaling takes place over short distances. Endocrine signals are carried long distances through the bloodstream by hormones, and autocrine signals are received by the same cell that sent the signal or other nearby cells of the same kind. Gap junctions allow small molecules, including signaling molecules, to flow between neighboring cells.

Internal receptors are found in the cell cytoplasm. Here, they bind ligand molecules that cross the plasma membrane; these receptor-ligand complexes move to the nucleus and interact directly with cellular DNA. Cell-surface receptors transmit a signal from outside the cell to the cytoplasm. Ion channel-linked receptors, when bound to their ligands, form a pore through the plasma membrane through which certain ions can pass. G-protein-linked receptors interact with a G-protein on the cytoplasmic side of the plasma membrane, promoting the exchange of bound GDP for GTP and interacting with other enzymes or ion channels to transmit a signal. Enzyme-linked receptors transmit a signal from outside the cell to an intracellular domain of a membrane-bound enzyme. Ligand binding causes activation of the enzyme. Small hydrophobic ligands (like steroids) are able to penetrate the plasma membrane and bind to internal receptors. Water-soluble hydrophilic ligands are unable to pass through the membrane; instead, they bind to cell-surface receptors, which transmit the signal to the inside of the cell.

Art Connections

Figure 44.1.7: HER2 is a receptor tyrosine kinase. In 30 percent of human breast cancers, HER2 is permanently activated, resulting in unregulated cell division. Lapatinib, a drug used to treat breast cancer, inhibits HER2 receptor tyrosine kinase autophosphorylation (the process by which the receptor adds phosphates onto itself), thus reducing tumor growth by 50 percent. Besides autophosphorylation, which of the following steps would be inhibited by Lapatinib?

A. Signaling molecule binding, dimerization, and the downstream cellular response.
B. Dimerization, and the downstream cellular response.
C. The downstream cellular response.
D. Phosphatase activity, dimerization, and the downsteam cellular response.

Answer

C. The downstream cellular response would be inhibited.

Footnotes

1. 1 A. B. Sigalov, The School of Nature. IV. Learning from Viruses, *Self/Nonself* 1, no. 4 (2010): 282-298. Y. Cao, X. Koh, L. Dong, X. Du, A. Wu, X. Ding, H. Deng, Y. Shu, J. Chen, T. Jiang, Rapid Estimation of Binding Activity of Influenza Virus Hemagglutinin to Human and Avian Receptors, *PLoS One* 6, no. 4 (2011): e18664.

Glossary

autocrine signal
signal that is sent and received by the same or similar nearby cells

cell-surface receptor
cell-surface protein that transmits a signal from the exterior of the cell to the interior, even though the ligand does not enter the cell

chemical synapse
small space between axon terminals and dendrites of nerve cells where neurotransmitters function

endocrine cell
cell that releases ligands involved in endocrine signaling (hormones)

endocrine signal
long-distance signal that is delivered by ligands (hormones) traveling through an organisms circulatory system from the signaling cell to the target cell

enzyme-linked receptor
cell-surface receptor with intracellular domains that are associated with membrane-bound enzymes

extracellular domain
region of a cell-surface receptor that is located on the cell surface

G-protein-linked receptor
cell-surface receptor that activates membrane-bound G-proteins to transmit a signal from the receptor to nearby membrane components

intercellular signaling
communication between cells

internal receptor

(also, intracellular receptor) receptor protein that is located in the cytosol of a cell and binds to ligands that pass through the plasma membrane

intracellular mediator
(also, second messenger) small molecule that transmits signals within a cell

intracellular signaling
communication within cells

ion channel-linked receptor
cell-surface receptor that forms a plasma membrane channel, which opens when a ligand binds to the extracellular domain (ligand-gated channels)

ligand
molecule produced by a signaling cell that binds with a specific receptor, delivering a signal in the process

neurotransmitter
chemical ligand that carries a signal from one nerve cell to the next

paracrine signal
signal between nearby cells that is delivered by ligands traveling in the liquid medium in the space between the cells

receptor
protein in or on a target cell that bind to ligands

signaling cell
cell that releases signal molecules that allow communication with another cell

synaptic signal
chemical signal (neurotransmitter) that travels between nerve cells

target cell
cell that has a receptor for a signal or ligand from a signaling cell

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44.1.1: Types of Hormones

Skills to Develop

- List the different types of hormones
- Explain their role in maintaining homeostasis

Maintaining homeostasis within the body requires the coordination of many different systems and organs. Communication between neighboring cells, and between cells and tissues in distant parts of the body, occurs through the release of chemicals called hormones. Hormones are released into body fluids (usually blood) that carry these chemicals to their target cells. At the target cells, which are cells that have a receptor for a signal or ligand from a signal cell, the hormones elicit a response. The cells, tissues, and organs that secrete hormones make up the endocrine system. Examples of glands of the endocrine system include the adrenal glands, which produce hormones such as epinephrine and norepinephrine that regulate responses to stress, and the thyroid gland, which produces thyroid hormones that regulate metabolic rates.

Although there are many different hormones in the human body, they can be divided into three classes based on their chemical structure: lipid-derived, amino acid-derived, and peptide (peptide and proteins) hormones. One of the key distinguishing features of lipid-derived hormones is that they can diffuse across plasma membranes whereas the amino acid-derived and peptide hormones cannot.

Lipid-Derived Hormones (or Lipid-soluble Hormones)

Most lipid hormones are derived from cholesterol and thus are structurally similar to it, as illustrated in Figure **44.1.1.1**. The primary class of lipid hormones in humans is the steroid hormones. Chemically, these hormones are usually ketones or alcohols; their chemical names will end in “-ol” for alcohols or “-one” for ketones. Examples of steroid hormones include estradiol, which is an estrogen, or female sex hormone, and testosterone, which is an androgen, or male sex hormone. These two hormones are released by the female and male reproductive organs, respectively. Other steroid hormones include aldosterone and cortisol, which are released by the adrenal glands along with some other types of androgens. Steroid hormones are insoluble in water, and they are transported by transport proteins in blood. As a result, they remain in circulation longer than peptide hormones. For example, cortisol has a half-life of 60 to 90 minutes, while epinephrine, an amino acid derived-hormone, has a half-life of approximately one minute.

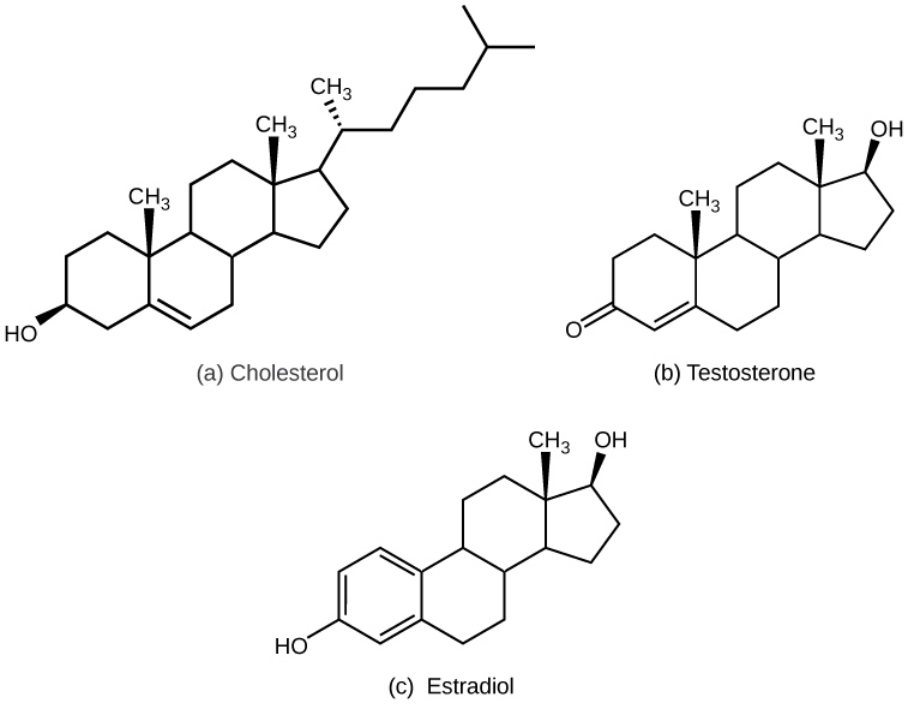


Figure **44.1.1.1**: The structures shown here represent (a) cholesterol, plus the steroid hormones (b) testosterone and (c) estradiol.

Amino Acid-Derived Hormones

The amino acid-derived hormones are relatively small molecules that are derived from the amino acids tyrosine and tryptophan, shown in Figure **44.1.1.2**. If a hormone is amino acid-derived, its chemical name will end in "-ine". Examples of amino acid-derived hormones include epinephrine and norepinephrine, which are synthesized in the medulla of the adrenal glands, and thyroxine, which is produced by the thyroid gland. The pineal gland in the brain makes and secretes melatonin which regulates sleep cycles.

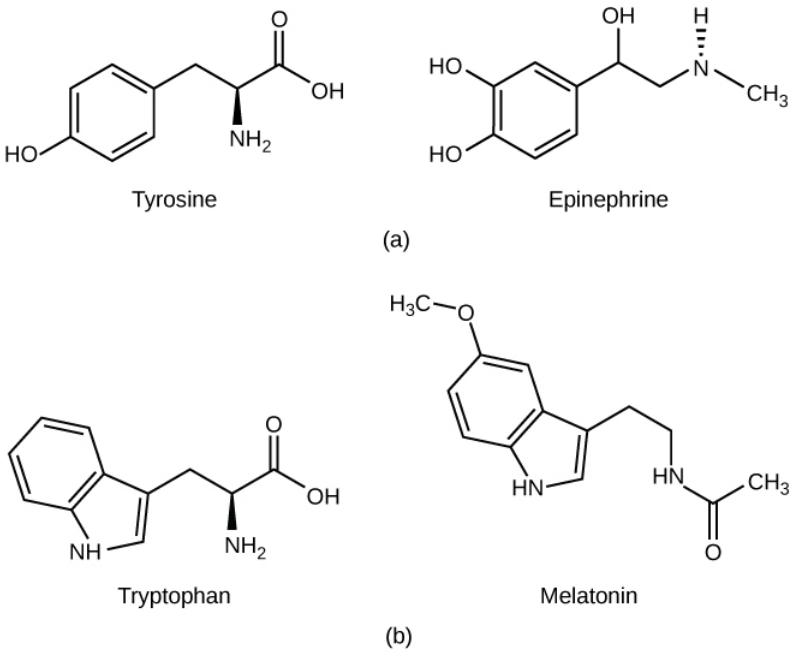


Figure **44.1.1.2**: (a) The hormone epinephrine, which triggers the fight-or-flight response, is derived from the amino acid tyrosine. (b) The hormone melatonin, which regulates circadian rhythms, is derived from the amino acid tryptophan.

Peptide Hormones

The structure of peptide hormones is that of a polypeptide chain (chain of amino acids). The peptide hormones include molecules that are short polypeptide chains, such as antidiuretic hormone and oxytocin produced in the brain and released into the blood in the posterior pituitary gland. This class also includes small proteins, like growth hormones produced by the pituitary, and large glycoproteins such as follicle-stimulating hormone produced by the pituitary. Figure **44.1.1.3** illustrates these peptide hormones.

Secreted peptides like insulin are stored within vesicles in the cells that synthesize them. They are then released in response to stimuli such as high blood glucose levels in the case of insulin. Amino acid-derived and polypeptide hormones are water-soluble and insoluble in lipids. These hormones cannot pass through plasma membranes of cells; therefore, their receptors are found on the surface of the target cells.

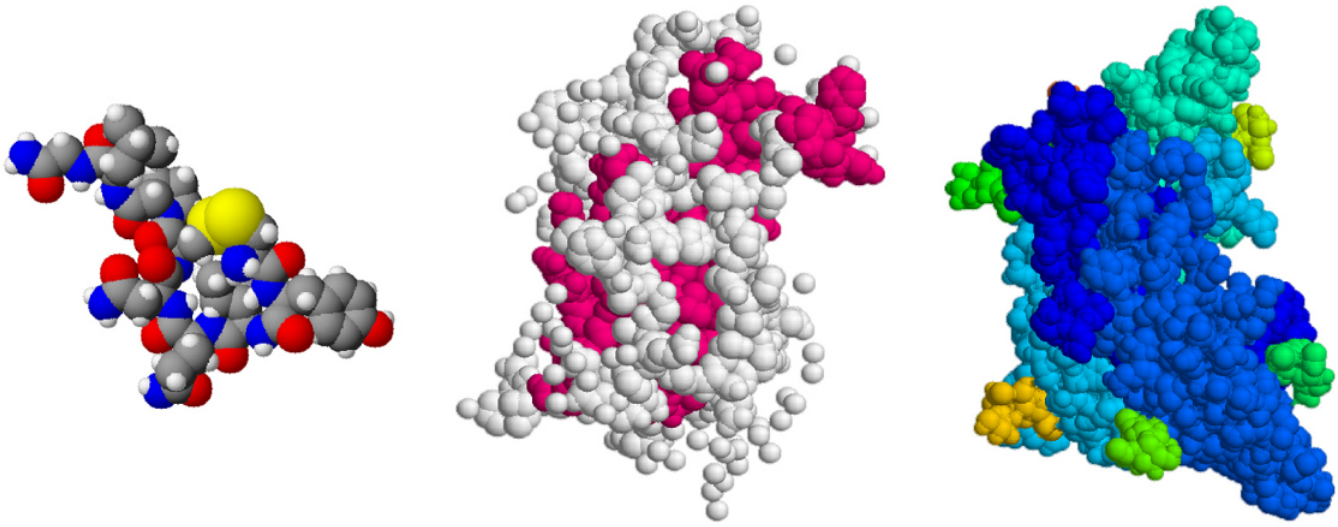


Figure 44.1.1.3: The structures of peptide hormones (a) oxytocin, (b) growth hormone, and (c) follicle-stimulating hormone are shown. These peptide hormones are much larger than those derived from cholesterol or amino acids.

Career Connection: Endocrinologist

An endocrinologist is a medical doctor who specializes in treating disorders of the endocrine glands, hormone systems, and glucose and lipid metabolic pathways. An endocrine surgeon specializes in the surgical treatment of endocrine diseases and glands. Some of the diseases that are managed by endocrinologists: disorders of the pancreas (diabetes mellitus), disorders of the pituitary (gigantism, acromegaly, and pituitary dwarfism), disorders of the thyroid gland (goiter and Graves' disease), and disorders of the adrenal glands (Cushing's disease and Addison's disease).

Endocrinologists are required to assess patients and diagnose endocrine disorders through extensive use of laboratory tests. Many endocrine diseases are diagnosed using tests that stimulate or suppress endocrine organ functioning. Blood samples are then drawn to determine the effect of stimulating or suppressing an endocrine organ on the production of hormones. For example, to diagnose diabetes mellitus, patients are required to fast for 12 to 24 hours. They are then given a sugary drink, which stimulates the pancreas to produce insulin to decrease blood glucose levels. A blood sample is taken one to two hours after the sugar drink is consumed. If the pancreas is functioning properly, the blood glucose level will be within a normal range. Another example is the A1C test, which can be performed during blood screening. The A1C test measures average blood glucose levels over the past two to three months by examining how well the blood glucose is being managed over a long time.

Once a disease has been diagnosed, endocrinologists can prescribe lifestyle changes and/or medications to treat the disease. Some cases of diabetes mellitus can be managed by exercise, weight loss, and a healthy diet; in other cases, medications may be required to enhance insulin release. If the disease cannot be controlled by these means, the endocrinologist may prescribe insulin injections.

In addition to clinical practice, endocrinologists may also be involved in primary research and development activities. For example, ongoing islet transplant research is investigating how healthy pancreas islet cells may be transplanted into diabetic patients. Successful islet transplants may allow patients to stop taking insulin injections.

Summary

There are three basic types of hormones: lipid-derived, amino acid-derived, and peptide. Lipid-derived hormones are structurally similar to cholesterol and include steroid hormones such as estradiol and testosterone. Amino acid-derived hormones are relatively small molecules and include the adrenal hormones epinephrine and norepinephrine. Peptide hormones are polypeptide chains or proteins and include the pituitary hormones, antidiuretic hormone (vasopressin), and oxytocin.

Glossary

amino acid-derived hormone
hormone derived from amino acids

lipid-derived hormone
hormone derived mostly from cholesterol

peptide hormone
hormone composed of a polypeptide chain

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44.1.2: Regulation of Body Processes

Skills to Develop

- Explain how hormones regulate the excretory system
- Discuss the role of hormones in the reproductive system
- Describe how hormones regulate metabolism
- Explain the role of hormones in different diseases

Hormones have a wide range of effects and modulate many different body processes. The key regulatory processes that will be examined here are those affecting the excretory system, the reproductive system, metabolism, blood calcium concentrations, growth, and the stress response.

Hormonal Regulation of the Excretory System

Maintaining a proper water balance in the body is important to avoid dehydration or over-hydration (hyponatremia). The water concentration of the body is monitored by osmoreceptors in the hypothalamus, which detect the concentration of electrolytes in the extracellular fluid. The concentration of electrolytes in the blood rises when there is water loss caused by excessive perspiration, inadequate water intake, or low blood volume due to blood loss. An increase in blood electrolyte levels results in a neuronal signal being sent from the osmoreceptors in hypothalamic nuclei. The pituitary gland has two components: anterior and posterior. The anterior pituitary is composed of glandular cells that secrete protein hormones. The posterior pituitary is an extension of the hypothalamus. It is composed largely of neurons that are continuous with the hypothalamus.

The hypothalamus produces a polypeptide hormone known as antidiuretic hormone (ADH), which is transported to and released from the posterior pituitary gland. The principal action of ADH is to regulate the amount of water excreted by the kidneys. As ADH (which is also known as vasopressin) causes direct water reabsorption from the kidney tubules, salts and wastes are concentrated in what will eventually be excreted as urine. The hypothalamus controls the mechanisms of ADH secretion, either by regulating blood volume or the concentration of water in the blood. Dehydration or physiological stress can cause an increase of osmolarity above 300 mOsm/L, which in turn, raises ADH secretion and water will be retained, causing an increase in blood pressure. ADH travels in the bloodstream to the kidneys. Once at the kidneys, ADH changes the kidneys to become more permeable to water by temporarily inserting water channels, aquaporins, into the kidney tubules. Water moves out of the kidney tubules through the aquaporins, reducing urine volume. The water is reabsorbed into the capillaries lowering blood osmolarity back toward normal. As blood osmolarity decreases, a negative feedback mechanism reduces osmoreceptor activity in the hypothalamus, and ADH secretion is reduced. ADH release can be reduced by certain substances, including alcohol, which can cause increased urine production and dehydration.

Chronic underproduction of ADH or a mutation in the ADH receptor results in diabetes insipidus. If the posterior pituitary does not release enough ADH, water cannot be retained by the kidneys and is lost as urine. This causes increased thirst, but water taken in is lost again and must be continually consumed. If the condition is not severe, dehydration may not occur, but severe cases can lead to electrolyte imbalances due to dehydration.

Another hormone responsible for maintaining electrolyte concentrations in extracellular fluids is aldosterone, a steroid hormone that is produced by the adrenal cortex. In contrast to ADH, which promotes the reabsorption of water to maintain proper water balance, aldosterone maintains proper water balance by enhancing Na^+ reabsorption and K^+ secretion from extracellular fluid of the cells in kidney tubules. Because it is produced in the cortex of the adrenal gland and affects the concentrations of minerals Na^+ and K^+, aldosterone is referred to as a mineralocorticoid, a corticosteroid that affects ion and water balance. Aldosterone release is stimulated by a decrease in blood sodium levels, blood volume, or blood pressure, or an increase in blood potassium levels. It also prevents the loss of Na^+ from sweat, saliva, and gastric juice. The reabsorption of Na^+ also results in the osmotic reabsorption of water, which alters blood volume and blood pressure.

Aldosterone production can be stimulated by low blood pressure, which triggers a sequence of chemical release, as illustrated in Figure **44.1.2.1**. When blood pressure drops, the renin-angiotensin-aldosterone system (RAAS) is activated. Cells in the juxtaglomerular apparatus, which regulates the functions of the nephrons of the kidney, detect this and release renin. Renin, an

enzyme, circulates in the blood and reacts with a plasma protein produced by the liver called angiotensinogen. When angiotensinogen is cleaved by renin, it produces angiotensin I, which is then converted into angiotensin II in the lungs. Angiotensin II functions as a hormone and then causes the release of the hormone aldosterone by the adrenal cortex, resulting in increased Na^+ reabsorption, water retention, and an increase in blood pressure. Angiotensin II in addition to being a potent vasoconstrictor also causes an increase in ADH and increased thirst, both of which help to raise blood pressure.

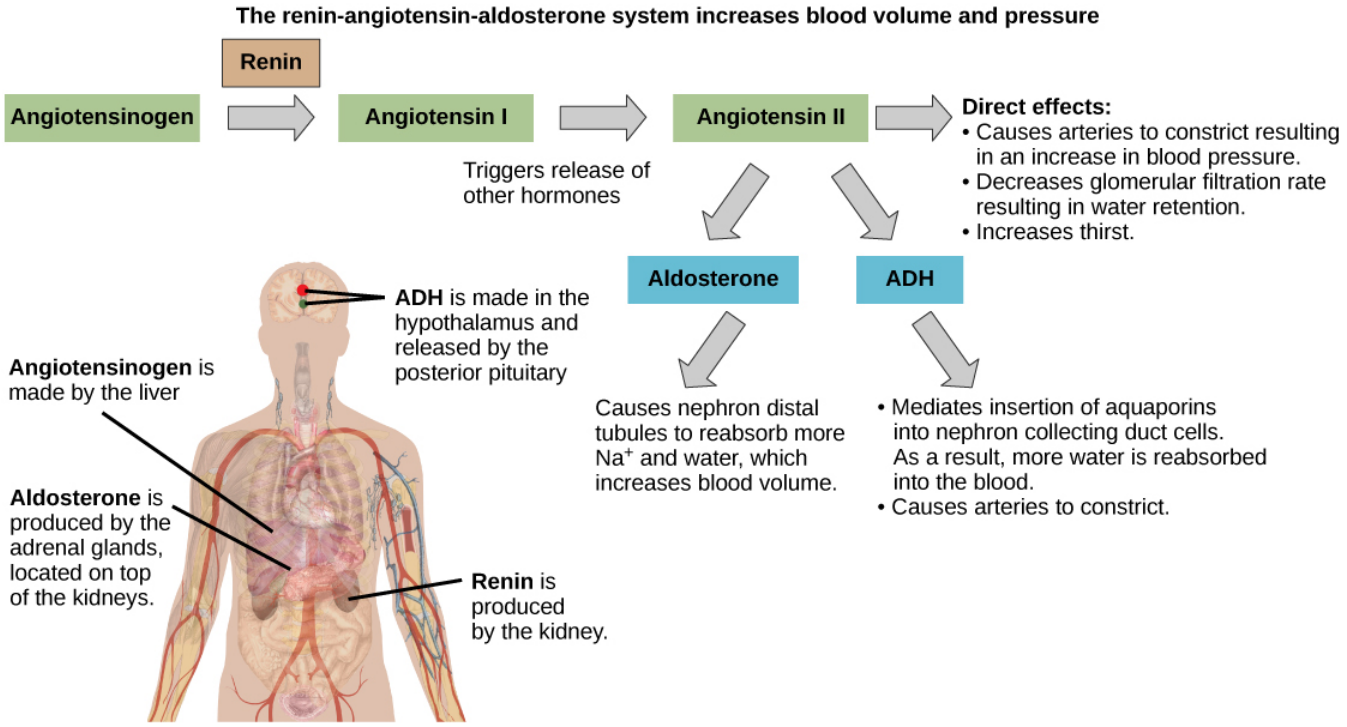


Figure **44.1.2.1**: ADH and aldosterone increase blood pressure and volume. Angiotensin II stimulates release of these hormones. Angiotensin II, in turn, is formed when renin cleaves angiotensinogen. (credit: modification of work by Mikael Häggström).

Hormonal Regulation of the Reproductive System

Regulation of the reproductive system is a process that requires the action of hormones from the pituitary gland, the adrenal cortex, and the gonads. During puberty in both males and females, the hypothalamus produces gonadotropin-releasing hormone (GnRH), which stimulates the production and release of *follicle-stimulating hormone (FSH)* and *luteinizing hormone (LH)* from the anterior pituitary gland. These hormones regulate the gonads (testes in males and ovaries in females) and therefore are called gonadotropins. In both males and females, FSH stimulates gamete production and LH stimulates production of hormones by the gonads. An increase in gonad hormone levels inhibits GnRH production through a negative feedback loop.

Regulation of the Male Reproductive System

In males, FSH stimulates the maturation of sperm cells. FSH production is inhibited by the hormone inhibin, which is released by the testes. LH stimulates production of the sex hormones (androgens) by the interstitial cells of the testes and therefore is also called interstitial cell-stimulating hormone. The most widely known androgen in males is *testosterone*. Testosterone promotes the production of sperm and masculine characteristics. The adrenal cortex also produces small amounts of testosterone precursor, although the role of this additional hormone production is not fully understood.

Everyday Connection: The Dangers of Synthetic Hormones

Some athletes attempt to boost their performance by using artificial hormones that enhance muscle performance. Anabolic steroids, a form of the male sex hormone testosterone, are one of the most widely known performance-enhancing drugs. Steroids are used to help build muscle mass. Other hormones that are used to enhance athletic performance include *erythropoietin*, which triggers the production of red blood cells, and human growth hormone, which can help in building muscle mass. Most performance enhancing drugs are illegal for non-medical purposes. They are also banned by national and

international governing bodies including the International Olympic Committee, the U.S. Olympic Committee, the National Collegiate Athletic Association, the Major League Baseball, and the National Football League.



Figure **44.1.2.2**: Professional baseball player Jason Giambi publically admitted to, and apologized for, his use of anabolic steroids supplied by a trainer. (credit: Bryce Edwards)

The side effects of synthetic hormones are often significant and non-reversible, and in some cases, fatal. Androgens produce several complications such as liver dysfunctions and liver tumors, prostate gland enlargement, difficulty urinating, premature closure of epiphyseal cartilages, testicular atrophy, infertility, and immune system depression. The physiological strain caused by these substances is often greater than what the body can handle, leading to unpredictable and dangerous effects and linking their use to heart attacks, strokes, and impaired cardiac function.

Regulation of the Female Reproductive System

In females, FSH stimulates development of egg cells, called ova, which develop in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production. LH also plays a role in the development of ova, induction of ovulation, and stimulation of estradiol and progesterone production by the ovaries, as illustrated in Figure **44.1.2.3**. Estradiol and progesterone are steroid hormones that prepare the body for pregnancy. Estradiol produces secondary sex characteristics in females, while both estradiol and progesterone regulate the menstrual cycle.

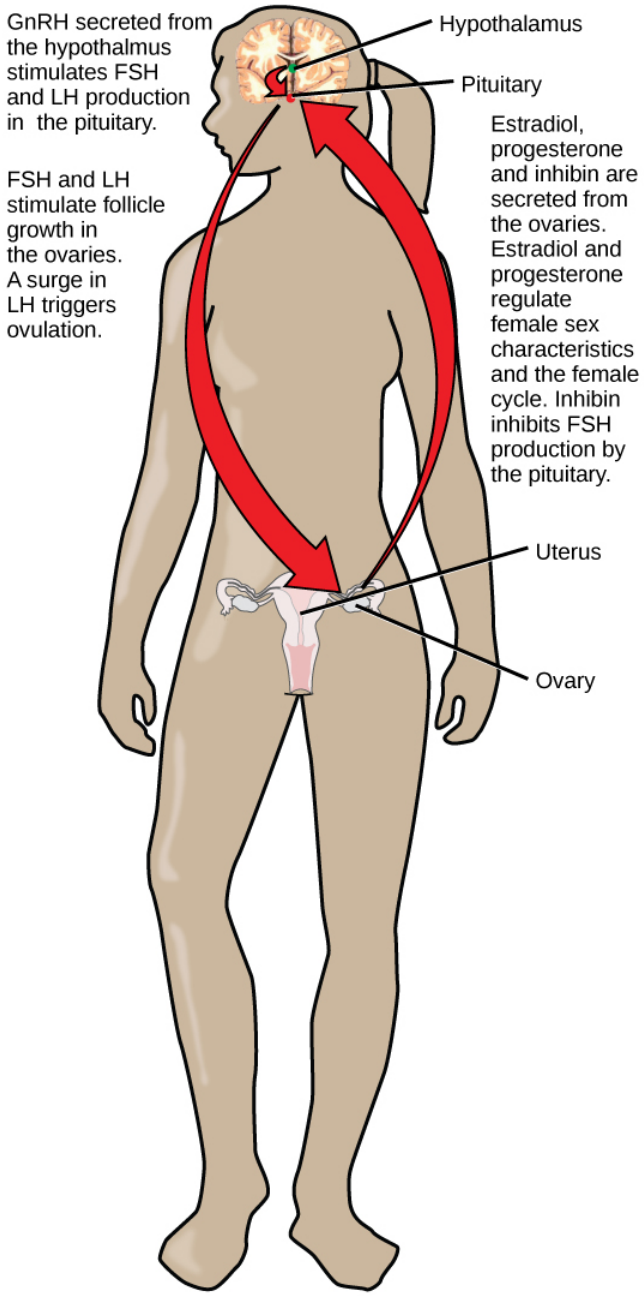


Figure 44.1.2.3: Hormonal regulation of the female reproductive system involves hormones from the hypothalamus, pituitary, and ovaries.

In addition to producing FSH and LH, the anterior portion of the pituitary gland also produces the hormone prolactin (PRL) in females. Prolactin stimulates the production of milk by the mammary glands following childbirth. Prolactin levels are regulated by the hypothalamic hormones prolactin-releasing hormone (PRH) and prolactin-inhibiting hormone (PIH), which is now known to be dopamine. PRH stimulates the release of prolactin and PIH inhibits it.

The posterior pituitary releases the hormone oxytocin, which stimulates uterine contractions during childbirth. The uterine smooth muscles are not very sensitive to oxytocin until late in pregnancy when the number of oxytocin receptors in the uterus peaks. Stretching of tissues in the uterus and cervix stimulates oxytocin release during childbirth. Contractions increase in intensity as blood levels of oxytocin rise via a positive feedback mechanism until the birth is complete. Oxytocin also stimulates the contraction of myoepithelial cells around the milk-producing mammary glands. As these cells contract, milk is forced from the secretory alveoli into milk ducts and is ejected from the breasts in milk ejection (“let-down”) reflex. Oxytocin release is stimulated by the

suckling of an infant, which triggers the synthesis of oxytocin in the hypothalamus and its release into circulation at the posterior pituitary.

Hormonal Regulation of Metabolism

Blood glucose levels vary widely over the course of a day as periods of food consumption alternate with periods of fasting. Insulin and glucagon are the two hormones primarily responsible for maintaining homeostasis of blood glucose levels. Additional regulation is mediated by the thyroid hormones.

Regulation of Blood Glucose Levels by Insulin and Glucagon

Cells of the body require nutrients in order to function, and these nutrients are obtained through feeding. In order to manage nutrient intake, storing excess intake and utilizing reserves when necessary, the body uses hormones to moderate energy stores. Insulin is produced by the beta cells of the pancreas, which are stimulated to release insulin as blood glucose levels rise (for example, after a meal is consumed). Insulin lowers blood glucose levels by enhancing the rate of glucose uptake and utilization by target cells, which use glucose for ATP production. It also stimulates the liver to convert glucose to glycogen, which is then stored by cells for later use. Insulin also increases glucose transport into certain cells, such as muscle cells and the liver. This results from an insulin-mediated increase in the number of glucose transporter proteins in cell membranes, which remove glucose from circulation by facilitated diffusion. As insulin binds to its target cell via insulin receptors and signal transduction, it triggers the cell to incorporate glucose transport proteins into its membrane. This allows glucose to enter the cell, where it can be used as an energy source. However, this does not occur in all cells: some cells, including those in the kidneys and brain, can access glucose without the use of insulin. Insulin also stimulates the conversion of glucose to fat in adipocytes and the synthesis of proteins. These actions mediated by insulin cause blood glucose concentrations to fall, called a hypoglycemic “low sugar” effect, which inhibits further insulin release from beta cells through a negative feedback loop.

Link to Learning



This animation describes the role of insulin and the pancreas in diabetes.

Impaired insulin function can lead to a condition called diabetes mellitus, the main symptoms of which are illustrated in Figure **44.1.2.4**. This can be caused by low levels of insulin production by the beta cells of the pancreas, or by reduced sensitivity of tissue cells to insulin. This prevents glucose from being absorbed by cells, causing high levels of blood glucose, or hyperglycemia (high sugar). High blood glucose levels make it difficult for the kidneys to recover all the glucose from nascent urine, resulting in glucose being lost in urine. High glucose levels also result in less water being reabsorbed by the kidneys, causing high amounts of urine to be produced; this may result in dehydration. Over time, high blood glucose levels can cause nerve damage to the eyes and peripheral body tissues, as well as damage to the kidneys and cardiovascular system. Oversecretion of insulin can cause hypoglycemia, low blood glucose levels. This causes insufficient glucose availability to cells, often leading to muscle weakness, and can sometimes cause unconsciousness or death if left untreated.

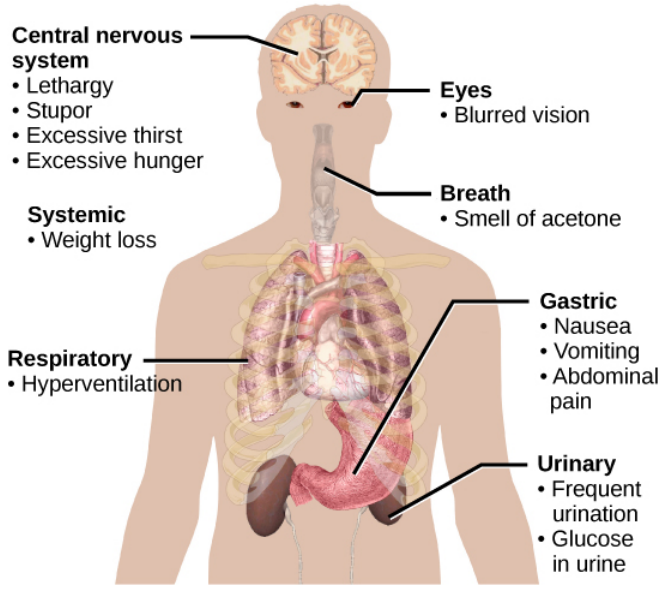


Figure **44.1.2.4**: The main symptoms of diabetes are shown. (credit: modification of work by Mikael Häggström)

When blood glucose levels decline below normal levels, for example between meals or when glucose is utilized rapidly during exercise, the hormone glucagon is released from the alpha cells of the pancreas. Glucagon raises blood glucose levels, eliciting what is called a hyperglycemic effect, by stimulating the breakdown of glycogen to glucose in skeletal muscle cells and liver cells in a process called glycogenolysis. Glucose can then be utilized as energy by muscle cells and released into circulation by the liver cells. Glucagon also stimulates absorption of amino acids from the blood by the liver, which then converts them to glucose. This process of glucose synthesis is called gluconeogenesis. Glucagon also stimulates adipose cells to release fatty acids into the blood. These actions mediated by glucagon result in an increase in blood glucose levels to normal homeostatic levels. Rising blood glucose levels inhibit further glucagon release by the pancreas via a negative feedback mechanism. In this way, insulin and glucagon work together to maintain homeostatic glucose levels, as shown in Figure **44.1.2.5**.

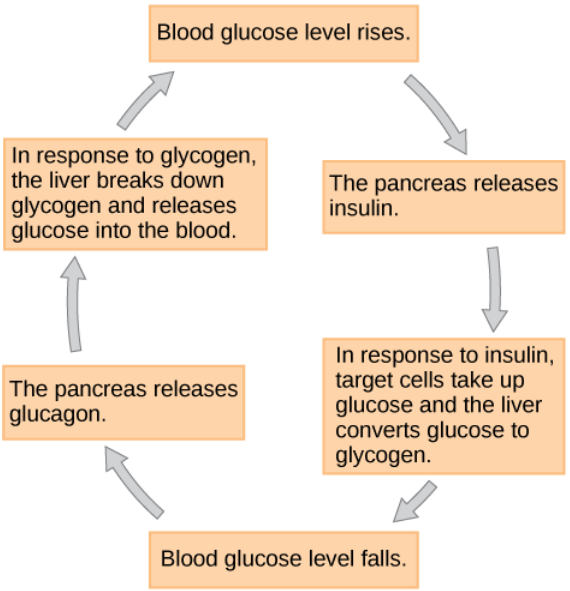


Figure **44.1.2.5**: Insulin and glucagon regulate blood glucose levels.

Exercise

Pancreatic tumors may cause excess secretion of glucagon. Type I diabetes results from the failure of the pancreas to produce insulin. Which of the following statement about these two conditions is true?

A. A pancreatic tumor and type I diabetes will have the opposite effects on blood sugar levels.

B. A pancreatic tumor and type I diabetes will both cause hyperglycemia.
C. A pancreatic tumor and type I diabetes will both cause hypoglycemia.
D. Both pancreatic tumors and type I diabetes result in the inability of cells to take up glucose.

Answer

B

Regulation of Blood Glucose Levels by Thyroid Hormones

The basal metabolic rate, which is the amount of calories required by the body at rest, is determined by two hormones produced by the thyroid gland: thyroxine, also known as tetraiodothyronine or T_4, and triiodothyronine, also known as T_3. These hormones affect nearly every cell in the body except for the adult brain, uterus, testes, blood cells, and spleen. They are transported across the plasma membrane of target cells and bind to receptors on the mitochondria resulting in increased ATP production. In the nucleus, T_3 and T_4 activate genes involved in energy production and glucose oxidation. This results in increased rates of metabolism and body heat production, which is known as the hormone's calorigenic effect.

T_3 and T_4 release from the thyroid gland is stimulated by thyroid-stimulating hormone (TSH), which is produced by the anterior pituitary. TSH binding at the receptors of the follicle of the thyroid triggers the production of T_3 and T_4 from a glycoprotein called thyroglobulin. Thyroglobulin is present in the follicles of the thyroid, and is converted into thyroid hormones with the addition of iodine. Iodine is formed from iodide ions that are actively transported into the thyroid follicle from the bloodstream. A peroxidase enzyme then attaches the iodine to the tyrosine amino acid found in thyroglobulin. T_3 has three iodine ions attached, while T_4 has four iodine ions attached. T_3 and T_4 are then released into the bloodstream, with T_4 being released in much greater amounts than T_3. As T_3 is more active than T_4 and is responsible for most of the effects of thyroid hormones, tissues of the body convert T_4 to T_3 by the removal of an iodine ion. Most of the released T_3 and T_4 becomes attached to transport proteins in the bloodstream and is unable to cross the plasma membrane of cells. These protein-bound molecules are only released when blood levels of the unattached hormone begin to decline. In this way, a week's worth of reserve hormone is maintained in the blood. Increased T_3 and T_4 levels in the blood inhibit the release of TSH, which results in lower T_3 and T_4 release from the thyroid.

The follicular cells of the thyroid require iodides (anions of iodine) in order to synthesize T_3 and T_4. Iodides obtained from the diet are actively transported into follicle cells resulting in a concentration that is approximately 30 times higher than in blood. The typical diet in North America provides more iodine than required due to the addition of iodide to table salt. Inadequate iodine intake, which occurs in many developing countries, results in an inability to synthesize T_3 and T_4 hormones. The thyroid gland enlarges in a condition called goiter, which is caused by overproduction of TSH without the formation of thyroid hormone. Thyroglobulin is contained in a fluid called colloid, and TSH stimulation results in higher levels of colloid accumulation in the thyroid. In the absence of iodine, this is not converted to thyroid hormone, and colloid begins to accumulate more and more in the thyroid gland, leading to goiter.

Disorders can arise from both the underproduction and overproduction of thyroid hormones. Hypothyroidism, underproduction of the thyroid hormones, can cause a low metabolic rate leading to weight gain, sensitivity to cold, and reduced mental activity, among other symptoms. In children, hypothyroidism can cause cretinism, which can lead to mental retardation and growth defects. Hyperthyroidism, the overproduction of thyroid hormones, can lead to an increased metabolic rate and its effects: weight loss, excess heat production, sweating, and an increased heart rate. Graves' disease is one example of a hyperthyroid condition.

Hormonal Control of Blood Calcium Levels

Regulation of blood calcium concentrations is important for generation of muscle contractions and nerve impulses, which are electrically stimulated. If calcium levels get too high, membrane permeability to sodium decreases and membranes become less responsive. If calcium levels get too low, membrane permeability to sodium increases and convulsions or muscle spasms can result.

Blood calcium levels are regulated by parathyroid hormone (PTH), which is produced by the parathyroid glands, as illustrated in Figure **44.1.2.6**. PTH is released in response to low blood Ca^{2+} levels. PTH increases Ca^{2+} levels by targeting the skeleton, the kidneys, and the intestine. In the skeleton, PTH stimulates osteoclasts, which causes bone to be reabsorbed, releasing Ca^{2+} from bone into the blood. PTH also inhibits osteoblasts, reducing Ca^{2+} deposition in bone. In the intestines, PTH increases dietary Ca^{2+} absorption, and in the kidneys, PTH stimulates reabsorption of the CA^{2+}. While PTH acts directly on the kidneys to increase Ca^{2+}

reabsorption, its effects on the intestine are indirect. PTH triggers the formation of calcitriol, an active form of vitamin D, which acts on the intestines to increase absorption of dietary calcium. PTH release is inhibited by rising blood calcium levels.

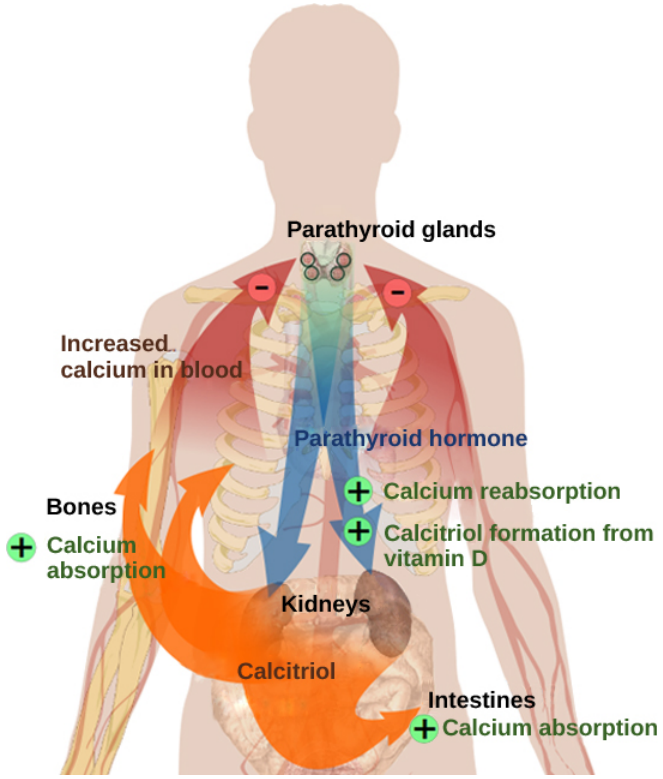


Figure 44.1.2.6: Parathyroid hormone (PTH) is released in response to low blood calcium levels. It increases blood calcium levels by targeting the skeleton, the kidneys, and the intestine. (credit: modification of work by Mikael Häggström)

Hyperparathyroidism results from an overproduction of parathyroid hormone. This results in excessive calcium being removed from bones and introduced into blood circulation, producing structural weakness of the bones, which can lead to deformation and fractures, plus nervous system impairment due to high blood calcium levels. Hypoparathyroidism, the underproduction of PTH, results in extremely low levels of blood calcium, which causes impaired muscle function and may result in tetany (severe sustained muscle contraction).

The hormone calcitonin, which is produced by the parafollicular or C cells of the thyroid, has the opposite effect on blood calcium levels as does PTH. Calcitonin decreases blood calcium levels by inhibiting osteoclasts, stimulating osteoblasts, and stimulating calcium excretion by the kidneys. This results in calcium being added to the bones to promote structural integrity. Calcitonin is most important in children (when it stimulates bone growth), during pregnancy (when it reduces maternal bone loss), and during prolonged starvation (because it reduces bone mass loss). In healthy nonpregnant, unstarved adults, the role of calcitonin is unclear.

Hormonal Regulation of Growth

Hormonal regulation is required for the growth and replication of most cells in the body. Growth hormone (GH), produced by the anterior portion of the pituitary gland, accelerates the rate of protein synthesis, particularly in skeletal muscle and bones. Growth hormone has direct and indirect mechanisms of action. The first direct action of GH is stimulation of triglyceride breakdown (lipolysis) and release into the blood by adipocytes. This results in a switch by most tissues from utilizing glucose as an energy source to utilizing fatty acids. This process is called a glucose-sparing effect. In another direct mechanism, GH stimulates glycogen breakdown in the liver; the glycogen is then released into the blood as glucose. Blood glucose levels increase as most tissues are utilizing fatty acids instead of glucose for their energy needs. The GH mediated increase in blood glucose levels is called a diabetogenic effect because it is similar to the high blood glucose levels seen in diabetes mellitus.

The indirect mechanism of GH action is mediated by insulin-like growth factors (IGFs) or somatomedins, which are a family of growth-promoting proteins produced by the liver, which stimulates tissue growth. IGFs stimulate the uptake of amino acids from the blood, allowing the formation of new proteins, particularly in skeletal muscle cells, cartilage cells, and other target cells, as

shown in Figure **44.1.2.7**. This is especially important after a meal, when glucose and amino acid concentration levels are high in the blood. GH levels are regulated by two hormones produced by the hypothalamus. GH release is stimulated by growth hormone-releasing hormone (GHRH) and is inhibited by growth hormone-inhibiting hormone (GHIH), also called somatostatin.

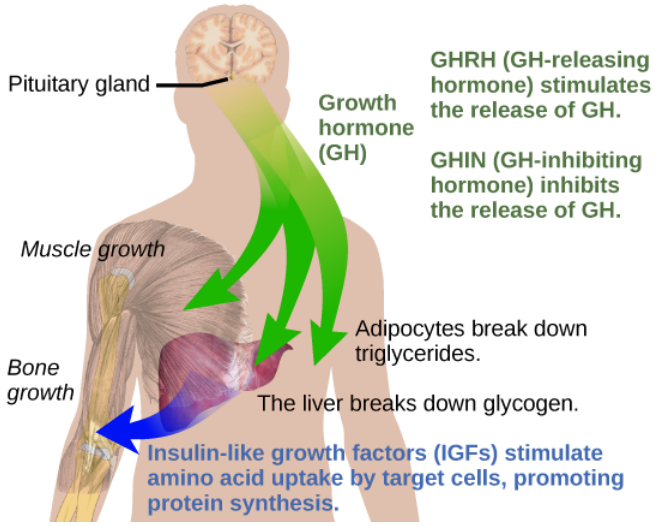


Figure **44.1.2.7**: Growth hormone directly accelerates the rate of protein synthesis in skeletal muscle and bones. Insulin-like growth factor 1 (IGF-1) is activated by growth hormone and also allows formation of new proteins in muscle cells and bone. (credit: modification of work by Mikael Häggström)

A balanced production of growth hormone is critical for proper development. Underproduction of GH in adults does not appear to cause any abnormalities, but in children it can result in pituitary dwarfism, in which growth is reduced. Pituitary dwarfism is characterized by symmetric body formation. In some cases, individuals are under 30 inches in height. Oversecretion of growth hormone can lead to gigantism in children, causing excessive growth. In some documented cases, individuals can reach heights of over eight feet. In adults, excessive GH can lead to acromegaly, a condition in which there is enlargement of bones in the face, hands, and feet that are still capable of growth.

Hormonal Regulation of Stress

When a threat or danger is perceived, the body responds by releasing hormones that will ready it for the “fight-or-flight” response. The effects of this response are familiar to anyone who has been in a stressful situation: increased heart rate, dry mouth, and hair standing up.

Evolution Connection: Fight-or-Flight Response

Interactions of the endocrine hormones have evolved to ensure the body’s internal environment remains stable. Stressors are stimuli that disrupt homeostasis. The sympathetic division of the vertebrate autonomic nervous system has evolved the fight-or-flight response to counter stress-induced disruptions of homeostasis. In the initial alarm phase, the sympathetic nervous system stimulates an increase in energy levels through increased blood glucose levels. This prepares the body for physical activity that may be required to respond to stress: to either fight for survival or to flee from danger.

However, some stresses, such as illness or injury, can last for a long time. Glycogen reserves, which provide energy in the short-term response to stress, are exhausted after several hours and cannot meet long-term energy needs. If glycogen reserves were the only energy source available, neural functioning could not be maintained once the reserves became depleted due to the nervous system’s high requirement for glucose. In this situation, the body has evolved a response to counter long-term stress through the actions of the glucocorticoids, which ensure that long-term energy requirements can be met. The glucocorticoids mobilize lipid and protein reserves, stimulate gluconeogenesis, conserve glucose for use by neural tissue, and stimulate the conservation of salts and water. The mechanisms to maintain homeostasis that are described here are those observed in the human body. However, the fight-or-flight response exists in some form in all vertebrates.

The sympathetic nervous system regulates the stress response via the hypothalamus. Stressful stimuli cause the hypothalamus to signal the adrenal medulla (which mediates short-term stress responses) via nerve impulses, and the adrenal cortex, which

mediates long-term stress responses, via the hormone adrenocorticotropic hormone (ACTH), which is produced by the anterior pituitary.

Short-term Stress Response

When presented with a stressful situation, the body responds by calling for the release of hormones that provide a burst of energy. The hormones epinephrine (also known as adrenaline) and norepinephrine (also known as noradrenaline) are released by the adrenal medulla. How do these hormones provide a burst of energy? Epinephrine and norepinephrine increase blood glucose levels by stimulating the liver and skeletal muscles to break down glycogen and by stimulating glucose release by liver cells. Additionally, these hormones increase oxygen availability to cells by increasing the heart rate and dilating the bronchioles. The hormones also prioritize body function by increasing blood supply to essential organs such as the heart, brain, and skeletal muscles, while restricting blood flow to organs not in immediate need, such as the skin, digestive system, and kidneys. Epinephrine and norepinephrine are collectively called catecholamines.

Link to Learning



Watch this Discovery Channel animation describing the flight-or-flight response.

Long-term Stress Response

Long-term stress response differs from short-term stress response. The body cannot sustain the bursts of energy mediated by epinephrine and norepinephrine for long times. Instead, other hormones come into play. In a long-term stress response, the hypothalamus triggers the release of ACTH from the anterior pituitary gland. The adrenal cortex is stimulated by ACTH to release steroid hormones called corticosteroids. Corticosteroids turn on transcription of certain genes in the nuclei of target cells. They change enzyme concentrations in the cytoplasm and affect cellular metabolism. There are two main corticosteroids: glucocorticoids such as cortisol, and mineralocorticoids such as aldosterone. These hormones target the breakdown of fat into fatty acids in the adipose tissue. The fatty acids are released into the bloodstream for other tissues to use for ATP production. The glucocorticoids primarily affect glucose metabolism by stimulating glucose synthesis. Glucocorticoids also have anti-inflammatory properties through inhibition of the immune system. For example, cortisone is used as an anti-inflammatory medication; however, it cannot be used long term as it increases susceptibility to disease due to its immune-suppressing effects.

Mineralocorticoids function to regulate ion and water balance of the body. The hormone aldosterone stimulates the reabsorption of water and sodium ions in the kidney, which results in increased blood pressure and volume.

Hypersecretion of glucocorticoids can cause a condition known as Cushing's disease, characterized by a shifting of fat storage areas of the body. This can cause the accumulation of adipose tissue in the face and neck, and excessive glucose in the blood.

Hyposecretion of the corticosteroids can cause Addison's disease, which may result in bronzing of the skin, hypoglycemia, and low electrolyte levels in the blood.

Summary

Water levels in the body are controlled by antidiuretic hormone (ADH), which is produced in the hypothalamus and triggers the reabsorption of water by the kidneys. Underproduction of ADH can cause diabetes insipidus. Aldosterone, a hormone produced by the adrenal cortex of the kidneys, enhances Na^+ reabsorption from the extracellular fluids and subsequent water reabsorption by diffusion. The renin-angiotensin-aldosterone system is one way that aldosterone release is controlled.

The reproductive system is controlled by the gonadotropins follicle-stimulating hormone (FSH) and luteinizing hormone (LH), which are produced by the pituitary gland. Gonadotropin release is controlled by the hypothalamic hormone gonadotropin-releasing hormone (GnRH). FSH stimulates the maturation of sperm cells in males and is inhibited by the hormone inhibin, while LH stimulates the production of the androgen testosterone. FSH stimulates egg maturation in females, while LH stimulates the production of estrogens and progesterone. Estrogens are a group of steroid hormones produced by the ovaries that trigger the development of secondary sex characteristics in females as well as control the maturation of the ova. In females, the pituitary also produces prolactin, which stimulates milk production after childbirth, and oxytocin, which stimulates uterine contraction during childbirth and milk let-down during suckling.

Insulin is produced by the pancreas in response to rising blood glucose levels and allows cells to utilize blood glucose and store excess glucose for later use. Diabetes mellitus is caused by reduced insulin activity and causes high blood glucose levels, or hyperglycemia. Glucagon is released by the pancreas in response to low blood glucose levels and stimulates the breakdown of glycogen into glucose, which can be used by the body. The body's basal metabolic rate is controlled by the thyroid hormones thyroxine (T_4) and triiodothyronine (T_3). The anterior pituitary produces thyroid stimulating hormone (TSH), which controls the release of T_3 and T_4 from the thyroid gland. Iodine is necessary in the production of thyroid hormone, and the lack of iodine can lead to a condition called goiter.

Parathyroid hormone (PTH) is produced by the parathyroid glands in response to low blood Ca^{2+} levels. The parafollicular cells of the thyroid produce calcitonin, which reduces blood Ca^{2+} levels. Growth hormone (GH) is produced by the anterior pituitary and controls the growth rate of muscle and bone. GH action is indirectly mediated by insulin-like growth factors (IGFs). Short-term stress causes the hypothalamus to trigger the adrenal medulla to release epinephrine and norepinephrine, which trigger the fight or flight response. Long-term stress causes the hypothalamus to trigger the anterior pituitary to release adrenocorticotropic hormone (ACTH), which causes the release of corticosteroids, glucocorticoids, and mineralocorticoids, from the adrenal cortex.

Glossary

acromegaly
: condition caused by overproduction of GH in adults

Addison's disease
: disorder caused by the hyposecretion of corticosteroids

adrenocorticotropic hormone (ACTH)
: hormone released by the anterior pituitary, which stimulates the adrenal cortex to release corticosteroids during the long-term stress response

aldosterone
: steroid hormone produced by the adrenal cortex that stimulates the reabsorption of Na^+ from extracellular fluids and secretion of K^+.

androgen
: male sex hormone such as testosterone

antidiuretic hormone (ADH)

hormone produced by the hypothalamus and released by the posterior pituitary that increases water reabsorption by the kidneys

calcitonin
hormone produced by the parafollicular cells of the thyroid gland that functions to lower blood Ca^{2+} levels and promote bone growth

corticosteroid
hormone released by the adrenal cortex in response to long-term stress

cortisol
glucocorticoid produced in response to stress

Cushing's disease
disorder caused by the hypersecretion of glucocorticoids

diabetes insipidus
disorder caused by underproduction of ADH

diabetes mellitus
disorder caused by low levels of insulin activity

diabetogenic effect
effect of GH that causes blood glucose levels to rise similar to diabetes mellitus

epinephrine
hormone released by the adrenal medulla in response to a short term stress

estrogens
- a group of steroid hormones, including estradiol and several others, that are produced by the ovaries and elicit secondary sex characteristics in females as well as control the maturation of the ova

follicle-stimulating hormone (FSH)
hormone produced by the anterior pituitary that stimulates gamete production

gigantism
condition caused by overproduction of GH in children

glucagon
hormone produced by the alpha cells of the pancreas in response to low blood sugar; functions to raise blood sugar levels

glucocorticoid
corticosteroid that affects glucose metabolism

gluconeogenesis
synthesis of glucose from amino acids

glucose-sparing effect
effect of GH that causes tissues to use fatty acids instead of glucose as an energy source

glycogenolysis
breakdown of glycogen into glucose

goiter
enlargement of the thyroid gland caused by insufficient dietary iodine levels

gonadotropin
hormone that regulates the gonads, including FSH and LH

growth hormone (GH)
hormone produced by the anterior pituitary that promotes protein synthesis and body growth

growth hormone-inhibiting hormone (GHIH)
hormone produced by the hypothalamus that inhibits growth hormone production, also called somatostatin

growth hormone-releasing hormone (GHRH)
hormone released by the hypothalamus that triggers the release of GH

hyperglycemia
high blood sugar level

hyperthyroidism
overactivity of the thyroid gland

hypoglycemia
low blood sugar level

hypothyroidism
underactivity of the thyroid gland

insulin
hormone produced by the beta cells of the pancreas in response to high blood glucose levels; functions to lower blood glucose levels

insulin-like growth factor (IGF)
growth-promoting protein produced by the liver

mineralocorticoid
corticosteroid that affects ion and water balance

norepinephrine
hormone released by the adrenal medulla in response to a short-term stress hormone production by the gonads

osmoreceptor
receptor in the hypothalamus that monitors the concentration of electrolytes in the blood

oxytocin
hormone released by the posterior pituitary to stimulate uterine contractions during childbirth and milk let-down in the mammary glands

parathyroid hormone (PTH)
hormone produced by the parathyroid glands in response to low blood Ca^{2+} levels; functions to raise blood Ca^{2+} levels

pituitary dwarfism
condition caused by underproduction of GH in children

prolactin (PRL)
hormone produced by the anterior pituitary that stimulates milk production

prolactin-inhibiting hormone

hormone produced by the hypothalamus that inhibits the release of prolactin

prolactin-releasing hormone
hormone produced by the hypothalamus that stimulates the release of prolactin

renin
enzyme produced by the juxtaglomerular apparatus of the kidneys that reacts with angiotensinogen to cause the release of aldosterone

thyroglobulin
glycoprotein found in the thyroid that is converted into thyroid hormone

thyroid-stimulating hormone (TSH)
hormone produced by the anterior pituitary that controls the release of T_3 and T_4 from the thyroid gland

thyroxine (tetraiodothyronine, T_4)
thyroid hormone that controls the basal metabolic rate

triiodothyronine (T_3)
thyroid hormone that controls the basal metabolic rate

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44.1.3: Endocrine Glands

Skills to Develop

- Describe the role of different glands in the endocrine system
- Explain how the different glands work together to maintain homeostasis

Both the endocrine and nervous systems use chemical signals to communicate and regulate the body's physiology. The endocrine system releases hormones that act on target cells to regulate development, growth, energy metabolism, reproduction, and many behaviors. The nervous system releases neurotransmitters or neurohormones that regulate neurons, muscle cells, and endocrine cells. Because the neurons can regulate the release of hormones, the nervous and endocrine systems work in a coordinated manner to regulate the body's physiology.

Hypothalamic-Pituitary Axis

The hypothalamus in vertebrates integrates the endocrine and nervous systems. The hypothalamus is an endocrine organ located in the diencephalon of the brain. It receives input from the body and other brain areas and initiates endocrine responses to environmental changes. The hypothalamus acts as an endocrine organ, synthesizing hormones and transporting them along axons to the posterior pituitary gland. It synthesizes and secretes regulatory hormones that control the endocrine cells in the anterior pituitary gland. The hypothalamus contains autonomic centers that control endocrine cells in the adrenal medulla via neuronal control.

The pituitary gland, sometimes called the hypophysis or “master gland” is located at the base of the brain in the sella turcica, a groove of the sphenoid bone of the skull, illustrated in Figure **44.1.3.1**. It is attached to the hypothalamus via a stalk called the pituitary stalk (or infundibulum). The anterior portion of the pituitary gland is regulated by releasing or release-inhibiting hormones produced by the hypothalamus, and the posterior pituitary receives signals via neurosecretory cells to release hormones produced by the hypothalamus. The pituitary has two distinct regions—the anterior pituitary and the posterior pituitary—which between them secrete nine different peptide or protein hormones. The posterior lobe of the pituitary gland contains axons of the hypothalamic neurons.

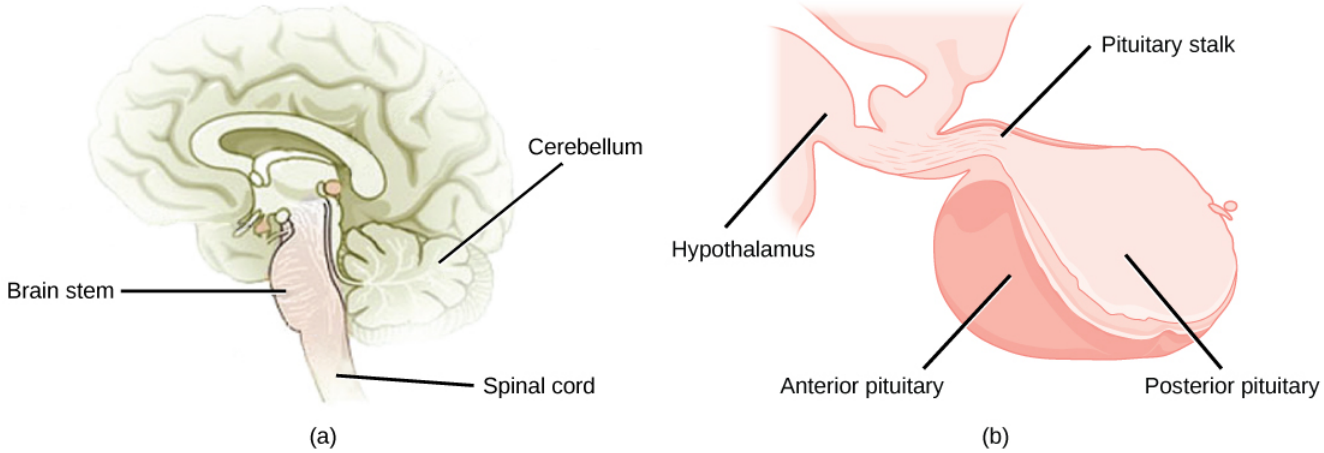


Figure **44.1.3.1**: The pituitary gland is located at (a) the base of the brain and (b) connected to the hypothalamus by the pituitary stalk. (credit a: modification of work by NCI; credit b: modification of work by Gray’s Anatomy)

Anterior Pituitary

The anterior pituitary gland, or adenohypophysis, is surrounded by a capillary network that extends from the hypothalamus, down along the infundibulum, and to the anterior pituitary. This capillary network is a part of the hypophyseal portal system that carries substances from the hypothalamus to the anterior pituitary and hormones from the anterior pituitary into the circulatory system. A portal system carries blood from one capillary network to another; therefore, the hypophyseal portal system allows hormones produced by the hypothalamus to be carried directly to the anterior pituitary without first entering the circulatory system.

The anterior pituitary produces seven hormones: growth hormone (GH), prolactin (PRL), thyroid-stimulating hormone (TSH), melanin-stimulating hormone (MSH), adrenocorticotropic hormone (ACTH), follicle-stimulating hormone (FSH), and luteinizing hormone (LH). Anterior pituitary hormones are sometimes referred to as tropic hormones, because they control the functioning of other organs. While these hormones are produced by the anterior pituitary, their production is controlled by regulatory hormones produced by the hypothalamus. These regulatory hormones can be releasing hormones or inhibiting hormones, causing more or less of the anterior pituitary hormones to be secreted. These travel from the hypothalamus through the hypophyseal portal system to the anterior pituitary where they exert their effect. Negative feedback then regulates how much of these regulatory hormones are released and how much anterior pituitary hormone is secreted.

Posterior Pituitary

The posterior pituitary is significantly different in structure from the anterior pituitary. It is a part of the brain, extending down from the hypothalamus, and contains mostly nerve fibers and neuroglial cells, which support axons that extend from the hypothalamus to the posterior pituitary. The posterior pituitary and the infundibulum together are referred to as the neurohypophysis.

The hormones antidiuretic hormone (ADH), also known as vasopressin, and oxytocin are produced by neurons in the hypothalamus and transported within these axons along the infundibulum to the posterior pituitary. They are released into the circulatory system via neural signaling from the hypothalamus. These hormones are considered to be posterior pituitary hormones, even though they are produced by the hypothalamus, because that is where they are released into the circulatory system. The posterior pituitary itself does not produce hormones, but instead stores hormones produced by the hypothalamus and releases them into the blood stream.

Thyroid Gland

The thyroid gland is located in the neck, just below the larynx and in front of the trachea, as shown in Figure **44.1.3.2**. It is a butterfly-shaped gland with two lobes that are connected by the isthmus. It has a dark red color due to its extensive vascular system. When the thyroid swells due to dysfunction, it can be felt under the skin of the neck.

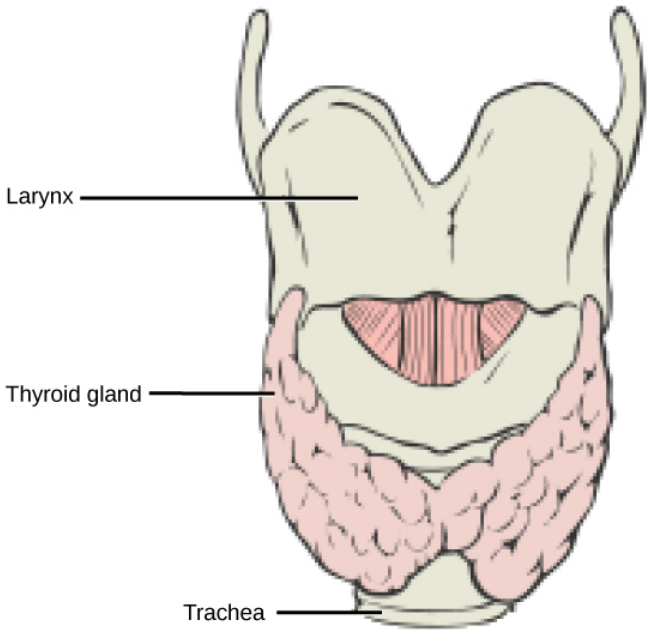


Figure **44.1.3.2**: This illustration shows the location of the thyroid gland.

The thyroid gland is made up of many spherical thyroid follicles, which are lined with a simple cuboidal epithelium. These follicles contain a viscous fluid, called colloid, which stores the glycoprotein thyroglobulin, the precursor to the thyroid hormones. The follicles produce hormones that can be stored in the colloid or released into the surrounding capillary network for transport to the rest of the body via the circulatory system.

Thyroid follicle cells synthesize the hormone thyroxine, which is also known as T_4 because it contains four atoms of iodine, and triiodothyronine, also known as T_3 because it contains three atoms of iodine. Follicle cells are stimulated to release stored T_3 and T_4

by thyroid stimulating hormone (TSH), which is produced by the anterior pituitary. These thyroid hormones increase the rates of mitochondrial ATP production.

A third hormone, calcitonin, is produced by parafollicular cells of the thyroid either releasing hormones or inhibiting hormones. Calcitonin release is not controlled by TSH, but instead is released when calcium ion concentrations in the blood rise. Calcitonin functions to help regulate calcium concentrations in body fluids. It acts in the bones to inhibit osteoclast activity and in the kidneys to stimulate excretion of calcium. The combination of these two events lowers body fluid levels of calcium.

Parathyroid Glands

Most people have four parathyroid glands; however, the number can vary from two to six. These glands are located on the posterior surface of the thyroid gland, as shown in Figure **44.1.3.3**. Normally, there is a superior gland and an inferior gland associated with each of the thyroid's two lobes. Each parathyroid gland is covered by connective tissue and contains many secretory cells that are associated with a capillary network.

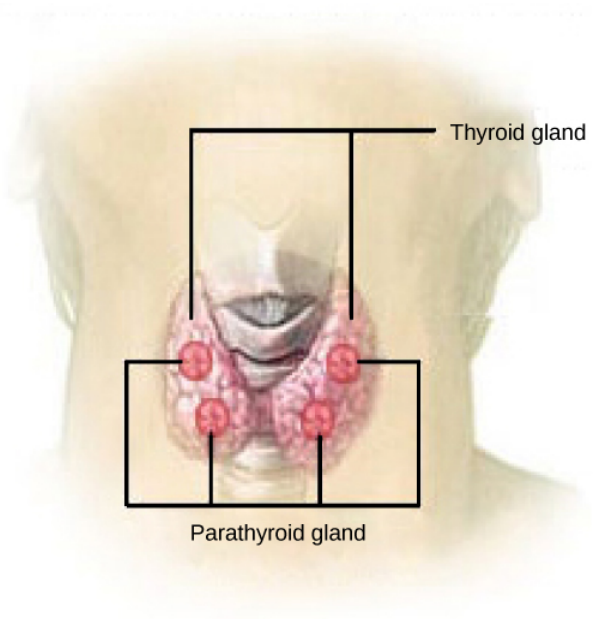


Figure **44.1.3.3**: The parathyroid glands are located on the posterior of the thyroid gland. (credit: modification of work by NCI)

The parathyroid glands produce parathyroid hormone (PTH). PTH increases blood calcium concentrations when calcium ion levels fall below normal. PTH (1) enhances reabsorption of Ca^{2+} by the kidneys, (2) stimulates osteoclast activity and inhibits osteoblast activity, and (3) it stimulates synthesis and secretion of calcitriol by the kidneys, which enhances Ca^{2+} absorption by the digestive system. PTH is produced by chief cells of the parathyroid. PTH and calcitonin work in opposition to one another to maintain homeostatic Ca^{2+} levels in body fluids. Another type of cells, oxyphil cells, exist in the parathyroid but their function is not known. These hormones encourage bone growth, muscle mass, and blood cell formation in children and women.

Adrenal Glands

The adrenal glands are associated with the kidneys; one gland is located on top of each kidney as illustrated in Figure **44.1.3.4**. The adrenal glands consist of an outer adrenal cortex and an inner adrenal medulla. These regions secrete different hormones.

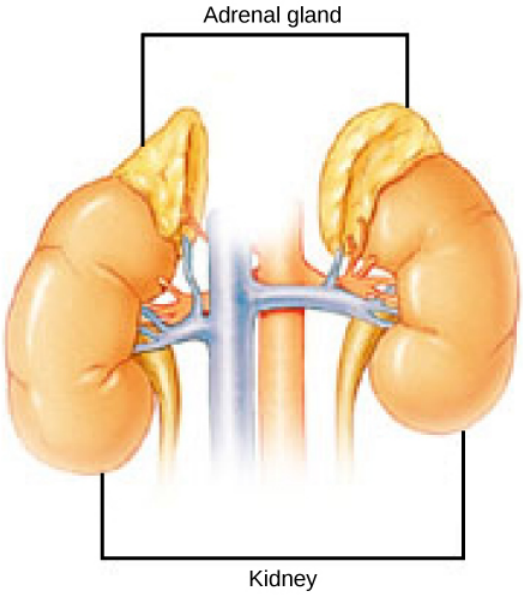


Figure **44.1.3.4**: The location of the adrenal glands on top of the kidneys is shown. (credit: modification of work by NCI)

Adrenal Cortex

The adrenal cortex is made up of layers of epithelial cells and associated capillary networks. These layers form three distinct regions: an outer zona glomerulosa that produces mineralocorticoids, a middle zona fasciculata that produces glucocorticoids, and an inner zona reticularis that produces androgens.

The main mineralocorticoid is aldosterone, which regulates the concentration of Na^+ ions in urine, sweat, pancreas, and saliva. Aldosterone release from the adrenal cortex is stimulated by a decrease in blood concentrations of sodium ions, blood volume, or blood pressure, or by an increase in blood potassium levels.

The three main glucocorticoids are cortisol, corticosterone, and cortisone. The glucocorticoids stimulate the synthesis of glucose and gluconeogenesis (converting a non-carbohydrate to glucose) by liver cells and they promote the release of fatty acids from adipose tissue. These hormones increase blood glucose levels to maintain levels within a normal range between meals. These hormones are secreted in response to ACTH and levels are regulated by negative feedback.

Androgens are sex hormones that promote masculinity. They are produced in small amounts by the adrenal cortex in both males and females. They do not affect sexual characteristics and may supplement sex hormones released from the gonads.

Adrenal Medulla

The adrenal medulla contains large, irregularly shaped cells that are closely associated with blood vessels. These cells are innervated by preganglionic autonomic nerve fibers from the central nervous system.

The adrenal medulla contains two types of secretory cells: one that produces epinephrine (adrenaline) and another that produces norepinephrine (noradrenaline). Epinephrine is the primary adrenal medulla hormone accounting for 75 to 80 percent of its secretions. Epinephrine and norepinephrine increase heart rate, breathing rate, cardiac muscle contractions, blood pressure, and blood glucose levels. They also accelerate the breakdown of glucose in skeletal muscles and stored fats in adipose tissue.

The release of epinephrine and norepinephrine is stimulated by neural impulses from the sympathetic nervous system. Secretion of these hormones is stimulated by acetylcholine release from preganglionic sympathetic fibers innervating the adrenal medulla. These neural impulses originate from the hypothalamus in response to stress to prepare the body for the fight-or-flight response.

Pancreas

The pancreas, illustrated in Figure **44.1.3.5**, is an elongated organ that is located between the stomach and the proximal portion of the small intestine. It contains both exocrine cells that excrete digestive enzymes and endocrine cells that release hormones. It is sometimes referred to as a heterocrine gland because it has both endocrine and exocrine functions.

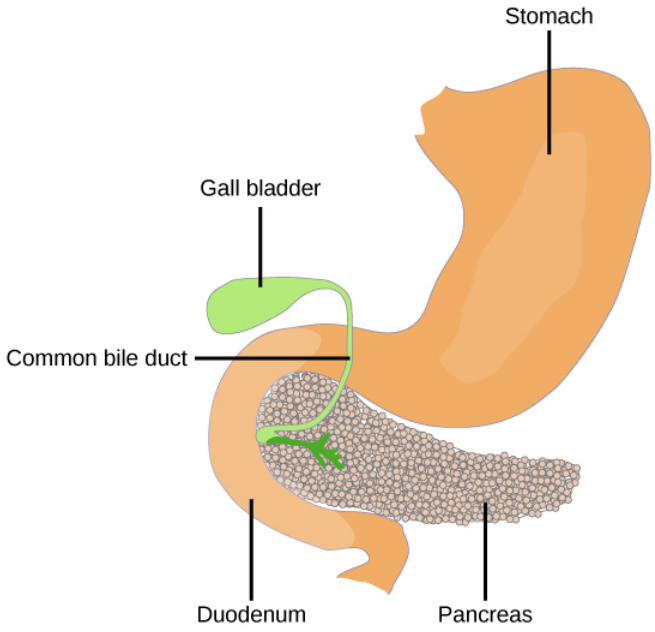


Figure **44.1.3.5**: The pancreas is found underneath the stomach and points toward the spleen. (credit: modification of work by NCI)

The endocrine cells of the pancreas form clusters called pancreatic islets or the islets of Langerhans, as visible in the micrograph shown in Figure **44.1.3.6**. The pancreatic islets contain two primary cell types: alpha cells, which produce the hormone glucagon, and beta cells, which produce the hormone insulin. These hormones regulate blood glucose levels. As blood glucose levels decline, alpha cells release glucagon to raise the blood glucose levels by increasing rates of glycogen breakdown and glucose release by the liver. When blood glucose levels rise, such as after a meal, beta cells release insulin to lower blood glucose levels by increasing the rate of glucose uptake in most body cells, and by increasing glycogen synthesis in skeletal muscles and the liver. Together, glucagon and insulin regulate blood glucose levels.

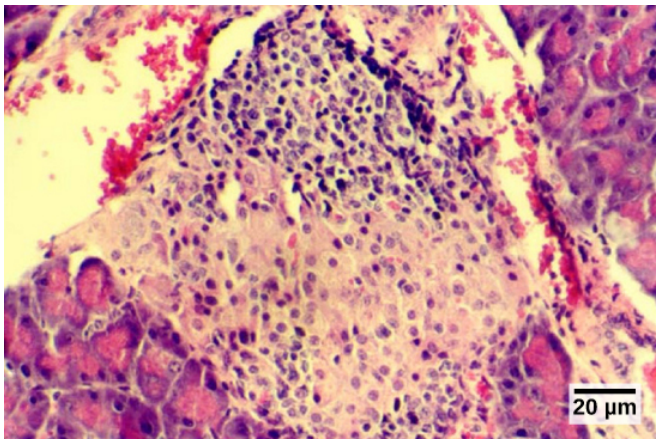


Figure **44.1.3.6**: The islets of Langerhans are clusters of endocrine cells found in the pancreas; they stain lighter than surrounding cells. (credit: modification of work by Muhammad T. Tabiin, Christopher P. White, Grant Morahan, and Bernard E. Tuch; scale-bar data from Matt Russell)

Pineal Gland

The pineal gland produces melatonin. The rate of melatonin production is affected by the photoperiod. Collaterals from the visual pathways innervate the pineal gland. During the day photoperiod, little melatonin is produced; however, melatonin production increases during the dark photoperiod (night). In some mammals, melatonin has an inhibitory affect on reproductive functions by decreasing production and maturation of sperm, oocytes, and reproductive organs. Melatonin is an effective antioxidant, protecting the CNS from free radicals such as nitric oxide and hydrogen peroxide. Lastly, melatonin is involved in biological rhythms, particularly circadian rhythms such as the sleep-wake cycle and eating habits.

Gonads

The gonads—the male testes and female ovaries—produce steroid hormones. The testes produce androgens, testosterone being the most prominent, which allow for the development of secondary sex characteristics and the production of sperm cells. The ovaries produce estradiol and progesterone, which cause secondary sex characteristics and prepare the body for childbirth.

Table 44.1.3.1: Endocrine Glands and their Associated Hormones

Endocrine Gland	Associated Hormones	Effect
Hypothalamus	releasing and inhibiting hormones	regulate hormone release from pituitary gland; produce oxytocin; produce uterine contractions and milk secretion in females
	antidiuretic hormone (ADH)	water reabsorption from kidneys; vasoconstriction to increase blood pressure
Pituitary (Anterior)	growth hormone (GH)	promotes growth of body tissues, protein synthesis; metabolic functions
	prolactin (PRL)	promotes milk production
	thyroid stimulating hormone (TSH)	stimulates thyroid hormone release
	adrenocorticotropic hormone (ACTH)	stimulates hormone release by adrenal cortex, glucocorticoids
	follicle-stimulating hormone (FSH)	stimulates gamete production (both ova and sperm); secretion of estradiol
	luteinizing hormone (LH)	stimulates androgen production by gonads; ovulation, secretion of progesterone
	melanocyte-stimulating hormone (MSH)	stimulates melanocytes of the skin increasing melanin pigment production.
Pituitary (Posterior)	antidiuretic hormone (ADH)	stimulates water reabsorption by kidneys
	oxytocin	stimulates uterine contractions during childbirth; milk ejection; stimulates ductus deferens and prostate gland contraction during emission
Thyroid	thyroxine, triiodothyronine	stimulate and maintain metabolism; growth and development
	calcitonin	reduces blood Ca^{2+} levels
Parathyroid	parathyroid hormone (PTH)	increases blood Ca^{2+} levels
Adrenal (Cortex)	aldosterone	increases blood Na^{+} levels; increase K^{+} secretion
	cortisol, corticosterone, cortisone	increase blood glucose levels; anti-inflammatory effects
Adrenal (Medulla)	epinephrine, norepinephrine	stimulate fight-or-flight response; increase blood gluclose levels; increase metabolic activities
Pancreas	insulin	reduces blood glucose levels
	glucagon	increases blood glucose levels
Pineal gland	melatonin	regulates some biological rhythms and protects CNS from free radicals
Testes	androgens	regulate, promote, increase or maintain sperm production; male secondary sexual characteristics
Ovaries	estrogen	promotes uterine lining growth; female

Endocrine Gland	Associated Hormones	Effect
		secondary sexual characteristics
	progestins	promote and maintain uterine lining growth

Organs with Secondary Endocrine Functions

There are several organs whose primary functions are non-endocrine but that also possess endocrine functions. These include the heart, kidneys, intestines, thymus, gonads, and adipose tissue.

The heart possesses endocrine cells in the walls of the atria that are specialized cardiac muscle cells. These cells release the hormone atrial natriuretic peptide (ANP) in response to increased blood volume. High blood volume causes the cells to be stretched, resulting in hormone release. ANP acts on the kidneys to reduce the reabsorption of Na^+, causing Na^+ and water to be excreted in the urine. ANP also reduces the amounts of renin released by the kidneys and aldosterone released by the adrenal cortex, further preventing the retention of water. In this way, ANP causes a reduction in blood volume and blood pressure, and reduces the concentration of Na^+ in the blood.

The gastrointestinal tract produces several hormones that aid in digestion. The endocrine cells are located in the mucosa of the GI tract throughout the stomach and small intestine. Some of the hormones produced include gastrin, secretin, and cholecystokinin, which are secreted in the presence of food, and some of which act on other organs such as the pancreas, gallbladder, and liver. They trigger the release of gastric juices, which help to break down and digest food in the GI tract.

While the adrenal glands associated with the kidneys are major endocrine glands, the kidneys themselves also possess endocrine function. Renin is released in response to decreased blood volume or pressure and is part of the renin-angiotensin-aldosterone system that leads to the release of aldosterone. Aldosterone then causes the retention of Na^+ and water, raising blood volume. The kidneys also release calcitriol, which aids in the absorption of Ca^{2+} and phosphate ions. Erythropoietin (EPO) is a protein hormone that triggers the formation of red blood cells in the bone marrow. EPO is released in response to low oxygen levels. Because red blood cells are oxygen carriers, increased production results in greater oxygen delivery throughout the body. EPO has been used by athletes to improve performance, as greater oxygen delivery to muscle cells allows for greater endurance. Because red blood cells increase the viscosity of blood, artificially high levels of EPO can cause severe health risks.

The thymus is found behind the sternum; it is most prominent in infants, becoming smaller in size through adulthood. The thymus produces hormones referred to as thymosins, which contribute to the development of the immune response.

Adipose tissue is a connective tissue found throughout the body. It produces the hormone leptin in response to food intake. Leptin increases the activity of anorexigenic neurons and decreases that of orexigenic neurons, producing a feeling of satiety after eating, thus affecting appetite and reducing the urge for further eating. Leptin is also associated with reproduction. It must be present for GnRH and gonadotropin synthesis to occur. Extremely thin females may enter puberty late; however, if adipose levels increase, more leptin will be produced, improving fertility.

Summary

The pituitary gland is located at the base of the brain and is attached to the hypothalamus by the infundibulum. The anterior pituitary receives products from the hypothalamus by the hypophyseal portal system and produces six hormones. The posterior pituitary is an extension of the brain and releases hormones (antidiuretic hormone and oxytocin) produced by the hypothalamus.

The thyroid gland is located in the neck and is composed of two lobes connected by the isthmus. The thyroid is made up of follicle cells that produce the hormones thyroxine and triiodothyronine. Parafollicular cells of the thyroid produce calcitonin. The parathyroid glands lie on the posterior surface of the thyroid gland and produce parathyroid hormone.

The adrenal glands are located on top of the kidneys and consist of the renal cortex and renal medulla. The adrenal cortex is the outer part of the adrenal gland and produces the corticosteroids, glucocorticoids, and mineralocorticoids. The adrenal medulla is the inner part of the adrenal gland and produces the catecholamines epinephrine and norepinephrine.

The pancreas lies in the abdomen between the stomach and the small intestine. Clusters of endocrine cells in the pancreas form the islets of Langerhans, which are composed of alpha cells that release glucagon and beta cells that release insulin.

Some organs possess endocrine activity as a secondary function but have another primary function. The heart produces the hormone atrial natriuretic peptide, which functions to reduce blood volume, pressure, and Na^+ concentration. The gastrointestinal tract produces various hormones that aid in digestion. The kidneys produce renin, calcitriol, and erythropoietin. Adipose tissue produces leptin, which promotes satiety signals in the brain.

Glossary

adrenal cortex
outer portion of adrenal glands that produces corticosteroids

adrenal gland
endocrine glands associated with the kidneys

adrenal medulla
inner portion of adrenal glands that produces epinephrine and norepinephrine

alpha cell
endocrine cell of the pancreatic islets that produces the hormone glucagon

anterior pituitary
portion of the pituitary gland that produces six hormones; also called adenohypophysis

atrial natriuretic peptide (ANP)
hormone produced by the heart to reduce blood volume, pressure, and Na^+ concentration

beta cell
endocrine cell of the pancreatic islets that produces the hormone insulin

colloid
fluid inside the thyroid gland that contains the glycoprotein thyroglobulin

endocrine gland
gland that secretes hormones into the surrounding interstitial fluid, which then diffuse into blood and are carried to various organs and tissues within the body

erythropoietin (EPO)
hormone produced by the kidneys to stimulate red blood cell production in the bone marrow

hypophyseal portal system
system of blood vessels that carries hormones from the hypothalamus to the anterior pituitary

islets of Langerhans (pancreatic islets)
endocrine cells of the pancreas

isthmus
tissue mass that connects the two lobes of the thyroid gland

leptin
hormone produced by adipose tissue that promotes feelings of satiety and reduces hunger

pancreas
organ located between the stomach and the small intestine that contains exocrine and endocrine cells

parafollicular cell

thyroid cell that produces the hormone calcitonin

parathyroid gland
gland located on the surface of the thyroid that produces parathyroid hormone

pituitary gland
endocrine gland located at the base of the brain composed of an anterior and posterior region; also called hypophysis

pituitary stalk
(also, infundibulum) stalk that connects the pituitary gland to the hypothalamus

posterior pituitary
extension of the brain that releases hormones produced by the hypothalamus; along with the infundibulum, it is also referred to as the neurohypophysis

thymus
gland located behind the sternum that produces thymosin hormones that contribute to the development of the immune system

thyroid gland
endocrine gland located in the neck that produces thyroid hormones thyroxine and triiodothyronine

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44.2: Overview of Hormone Action

Skills to Develop

- Explain how hormones work
- Discuss the role of different types of hormone receptors

Hormones mediate changes in target cells by binding to specific hormone receptors. In this way, even though hormones circulate throughout the body and come into contact with many different cell types, they only affect cells that possess the necessary receptors. Receptors for a specific hormone may be found on many different cells or may be limited to a small number of specialized cells. For example, thyroid hormones act on many different tissue types, stimulating metabolic activity throughout the body. Cells can have many receptors for the same hormone but often also possess receptors for different types of hormones. The number of receptors that respond to a hormone determines the cell's sensitivity to that hormone, and the resulting cellular response. Additionally, the number of receptors that respond to a hormone can change over time, resulting in increased or decreased cell sensitivity. In up-regulation, the number of receptors increases in response to rising hormone levels, making the cell more sensitive to the hormone and allowing for more cellular activity. When the number of receptors decreases in response to rising hormone levels, called down-regulation, cellular activity is reduced.

Receptor binding alters cellular activity and results in an increase or decrease in normal body processes. Depending on the location of the protein receptor on the target cell and the chemical structure of the hormone, hormones can mediate changes directly by binding to intracellular hormone receptors and modulating gene transcription, or indirectly by binding to cell surface receptors and stimulating signaling pathways.

Intracellular Hormone Receptors

Lipid-derived (soluble) hormones such as steroid hormones diffuse across the membranes of the endocrine cell. Once outside the cell, they bind to transport proteins that keep them soluble in the bloodstream. At the target cell, the hormones are released from the carrier protein and diffuse across the lipid bilayer of the plasma membrane of cells. The steroid hormones pass through the plasma membrane of a target cell and adhere to intracellular receptors residing in the cytoplasm or in the nucleus. The cell signaling pathways induced by the steroid hormones regulate specific genes on the cell's DNA. The hormones and receptor complex act as transcription regulators by increasing or decreasing the synthesis of mRNA molecules of specific genes. This, in turn, determines the amount of corresponding protein that is synthesized by altering gene expression. This protein can be used either to change the structure of the cell or to produce enzymes that catalyze chemical reactions. In this way, the steroid hormone regulates specific cell processes as illustrated in Figure **44.2.1**.

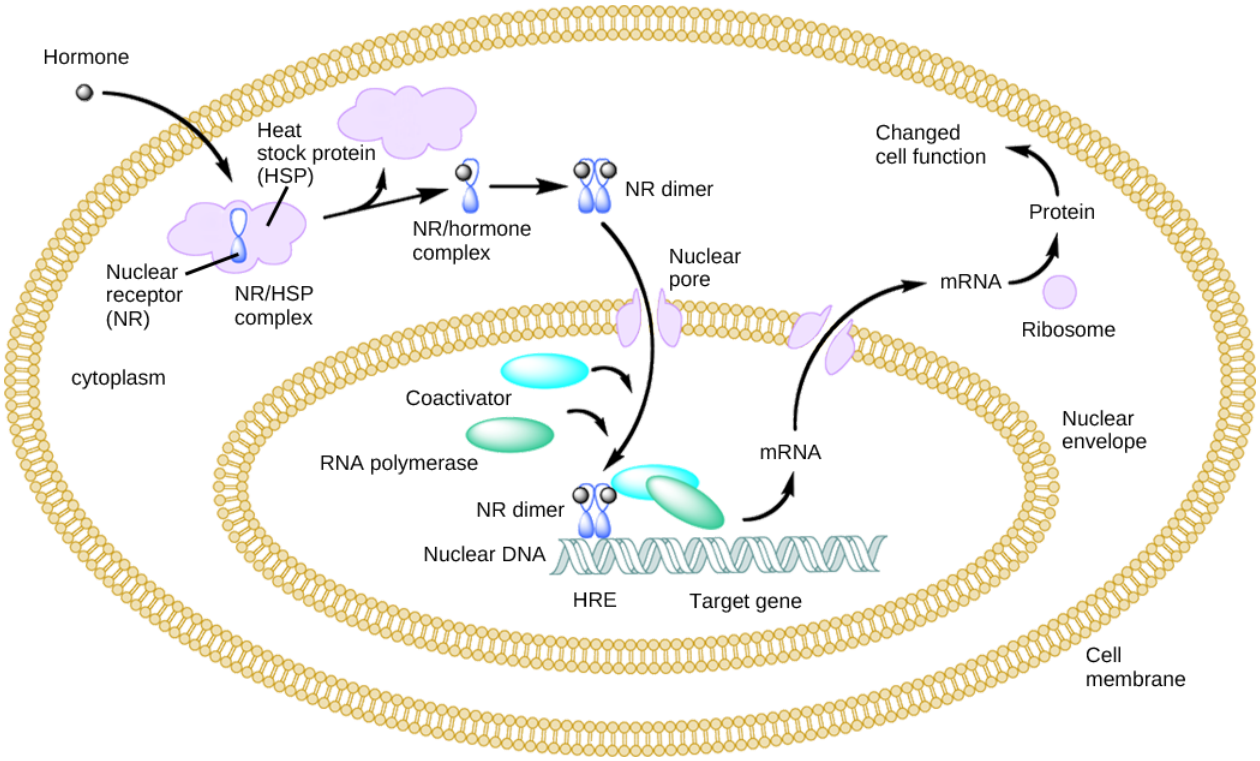


Figure **44.2.1**: An intracellular nuclear receptor (NR) is located in the cytoplasm bound to a heat shock protein (HSP). Upon hormone binding, the receptor dissociates from the heat shock protein and translocates to the nucleus. In the nucleus, the hormone-receptor complex binds to a DNA sequence called a hormone response element (HRE), which triggers gene transcription and translation. The corresponding protein product can then mediate changes in cell function.

Exercise 44.2.1

Heat shock proteins (HSP) are so named because they help refold misfolded proteins. In response to increased temperature (a "heat shock"), heat shock proteins are activated by release from the NR/HSP complex. At the same time, transcription of HSP genes is activated. Why do you think the cell responds to a heat shock by increasing the activity of proteins that help refold misfolded proteins?

Answer

Proteins unfold, or denature, at higher temperatures.

Other lipid-soluble hormones that are not steroid hormones, such as vitamin D and thyroxine, have receptors located in the nucleus. The hormones diffuse across both the plasma membrane and the nuclear envelope, then bind to receptors in the nucleus. The hormone-receptor complex stimulates transcription of specific genes.

Plasma Membrane Hormone Receptors

Amino acid derived hormones and polypeptide hormones are not lipid-derived (lipid-soluble) and therefore cannot diffuse through the plasma membrane of cells. Lipid insoluble hormones bind to receptors on the outer surface of the plasma membrane, via plasma membrane hormone receptors. Unlike steroid hormones, lipid insoluble hormones do not directly affect the target cell because they cannot enter the cell and act directly on DNA. Binding of these hormones to a cell surface receptor results in activation of a signaling pathway; this triggers intracellular activity and carries out the specific effects associated with the hormone. In this way, nothing passes through the cell membrane; the hormone that binds at the surface remains at the surface of the cell while the intracellular product remains inside the cell. The hormone that initiates the signaling pathway is called a first messenger, which activates a second messenger in the cytoplasm, as illustrated in Figure **44.2.2**.

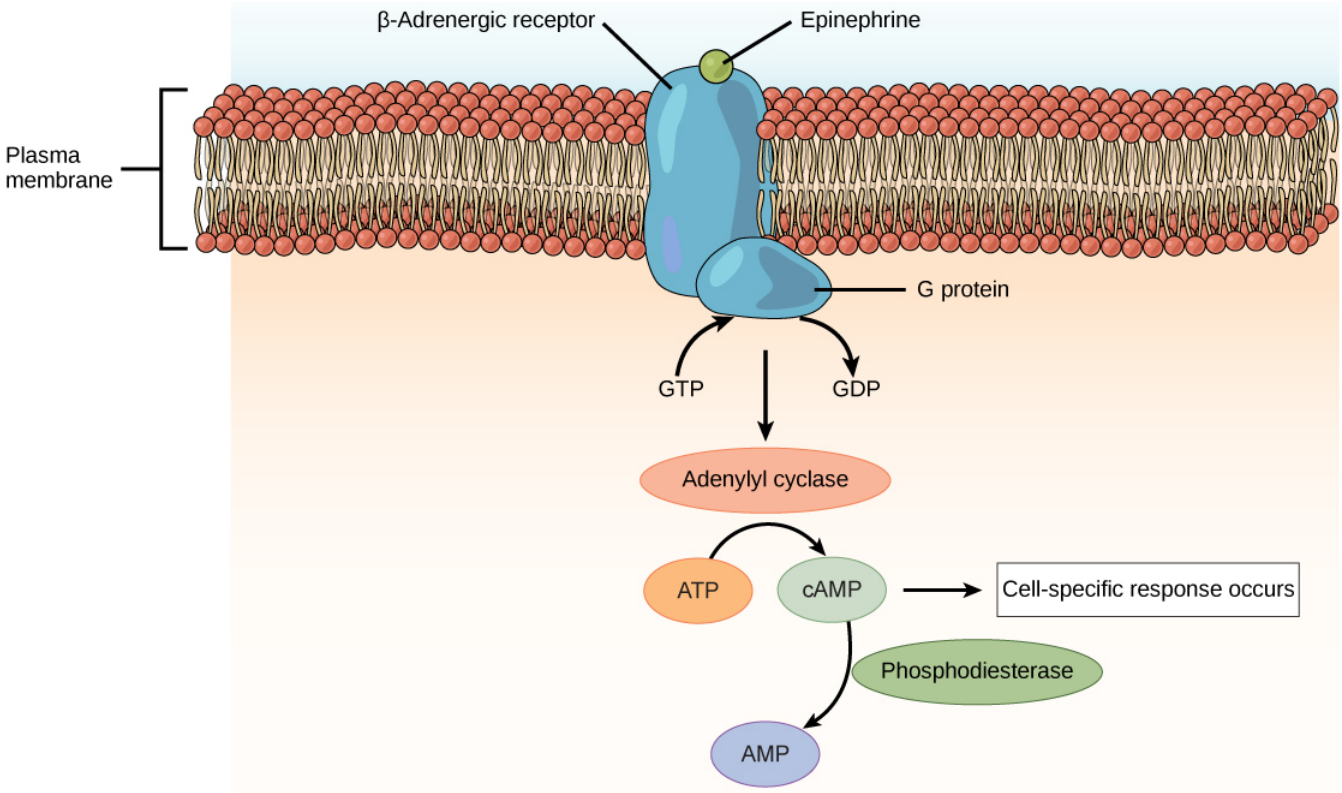


Figure **44.2.2**: The amino acid-derived hormones epinephrine and norepinephrine bind to beta-adrenergic receptors on the plasma membrane of cells. Hormone binding to receptor activates a G-protein, which in turn activates adenylyl cyclase, converting ATP to cAMP. cAMP is a second messenger that mediates a cell-specific response. An enzyme called phosphodiesterase breaks down cAMP, terminating the signal.

One very important second messenger is cyclic AMP (cAMP). When a hormone binds to its membrane receptor, a G-protein that is associated with the receptor is activated; G-proteins are proteins separate from receptors that are found in the cell membrane. When a hormone is not bound to the receptor, the G-protein is inactive and is bound to guanosine diphosphate, or GDP. When a hormone binds to the receptor, the G-protein is activated by binding guanosine triphosphate, or GTP, in place of GDP. After binding, GTP is hydrolysed by the G-protein into GDP and becomes inactive.

The activated G-protein in turn activates a membrane-bound enzyme called adenylyl cyclase. Adenylyl cyclase catalyzes the conversion of ATP to cAMP. cAMP, in turn, activates a group of proteins called protein kinases, which transfer a phosphate group from ATP to a substrate molecule in a process called phosphorylation. The phosphorylation of a substrate molecule changes its structural orientation, thereby activating it. These activated molecules can then mediate changes in cellular processes.

The effect of a hormone is amplified as the signaling pathway progresses. The binding of a hormone at a single receptor causes the activation of many G-proteins, which activates adenylyl cyclase. Each molecule of adenylyl cyclase then triggers the formation of many molecules of cAMP. Further amplification occurs as protein kinases, once activated by cAMP, can catalyze many reactions. In this way, a small amount of hormone can trigger the formation of a large amount of cellular product. To stop hormone activity, cAMP is deactivated by the cytoplasmic enzyme phosphodiesterase, or PDE. PDE is always present in the cell and breaks down cAMP to control hormone activity, preventing overproduction of cellular products.

The specific response of a cell to a lipid insoluble hormone depends on the type of receptors that are present on the cell membrane and the substrate molecules present in the cell cytoplasm. Cellular responses to hormone binding of a receptor include altering membrane permeability and metabolic pathways, stimulating synthesis of proteins and enzymes, and activating hormone release.

Summary

Hormones cause cellular changes by binding to receptors on target cells. The number of receptors on a target cell can increase or decrease in response to hormone activity. Hormones can affect cells directly through intracellular hormone receptors or indirectly

through plasma membrane hormone receptors.

Lipid-derived (soluble) hormones can enter the cell by diffusing across the plasma membrane and binding to DNA to regulate gene transcription and to change the cell's activities by inducing production of proteins that affect, in general, the long-term structure and function of the cell. Lipid insoluble hormones bind to receptors on the plasma membrane surface and trigger a signaling pathway to change the cell's activities by inducing production of various cell products that affect the cell in the short-term. The hormone is called a first messenger and the cellular component is called a second messenger. G-proteins activate the second messenger (cyclic AMP), triggering the cellular response. Response to hormone binding is amplified as the signaling pathway progresses. Cellular responses to hormones include the production of proteins and enzymes and altered membrane permeability.

Glossary

adenylate cyclase
an enzyme that catalyzes the conversion of ATP to cyclic AMP

down-regulation
a decrease in the number of hormone receptors in response to increased hormone levels

first messenger
the hormone that binds to a plasma membrane hormone receptor to trigger a signal transduction pathway

G-protein
a membrane protein activated by the hormone first messenger to activate formation of cyclic AMP

hormone receptor
the cellular protein that binds to a hormone

intracellular hormone receptor
a hormone receptor in the cytoplasm or nucleus of a cell

phosphodiesterase (PDE)
enzyme that deactivates cAMP, stopping hormone activity

plasma membrane hormone receptor
a hormone receptor on the surface of the plasma membrane of a cell

up-regulation
an increase in the number of hormone receptors in response to increased hormone levels

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44.3: The Pituitary and Hypothalamus- The Body's Control Centers

Skills to Develop

- List the different types of hormones
- Explain their role in maintaining homeostasis

Maintaining homeostasis within the body requires the coordination of many different systems and organs. Communication between neighboring cells, and between cells and tissues in distant parts of the body, occurs through the release of chemicals called hormones. Hormones are released into body fluids (usually blood) that carry these chemicals to their target cells. At the target cells, which are cells that have a receptor for a signal or ligand from a signal cell, the hormones elicit a response. The cells, tissues, and organs that secrete hormones make up the endocrine system. Examples of glands of the endocrine system include the adrenal glands, which produce hormones such as epinephrine and norepinephrine that regulate responses to stress, and the thyroid gland, which produces thyroid hormones that regulate metabolic rates.

Although there are many different hormones in the human body, they can be divided into three classes based on their chemical structure: lipid-derived, amino acid-derived, and peptide (peptide and proteins) hormones. One of the key distinguishing features of lipid-derived hormones is that they can diffuse across plasma membranes whereas the amino acid-derived and peptide hormones cannot.

Lipid-Derived Hormones (or Lipid-soluble Hormones)

Most lipid hormones are derived from cholesterol and thus are structurally similar to it, as illustrated in Figure **44.3.1**. The primary class of lipid hormones in humans is the steroid hormones. Chemically, these hormones are usually ketones or alcohols; their chemical names will end in “-ol” for alcohols or “-one” for ketones. Examples of steroid hormones include estradiol, which is an estrogen, or female sex hormone, and testosterone, which is an androgen, or male sex hormone. These two hormones are released by the female and male reproductive organs, respectively. Other steroid hormones include aldosterone and cortisol, which are released by the adrenal glands along with some other types of androgens. Steroid hormones are insoluble in water, and they are transported by transport proteins in blood. As a result, they remain in circulation longer than peptide hormones. For example, cortisol has a half-life of 60 to 90 minutes, while epinephrine, an amino acid derived-hormone, has a half-life of approximately one minute.

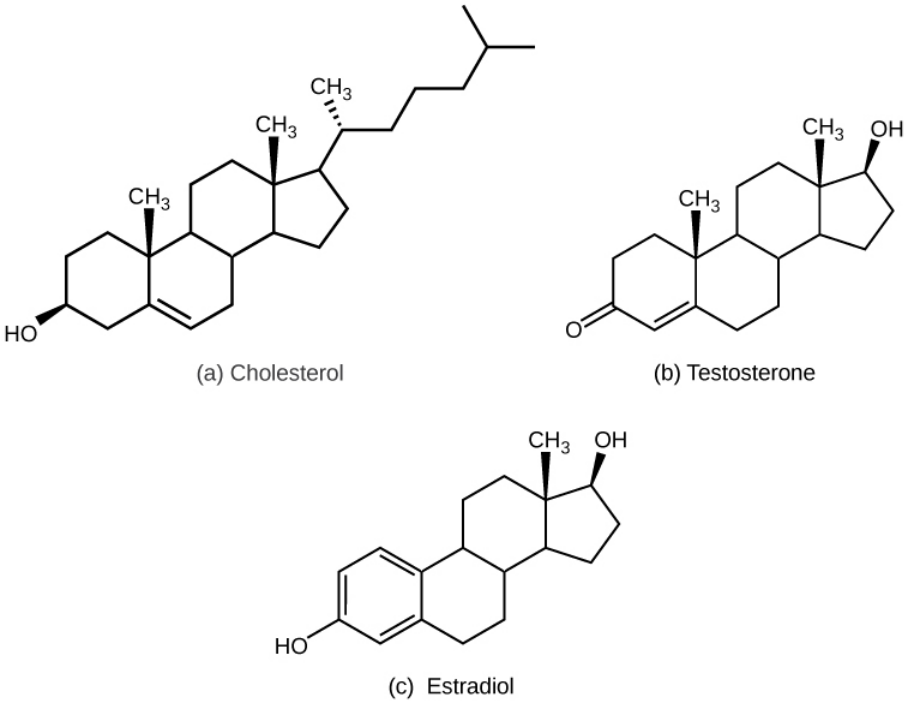


Figure **44.3.1**: The structures shown here represent (a) cholesterol, plus the steroid hormones (b) testosterone and (c) estradiol.

Amino Acid-Derived Hormones

The amino acid-derived hormones are relatively small molecules that are derived from the amino acids tyrosine and tryptophan, shown in Figure **44.3.2**. If a hormone is amino acid-derived, its chemical name will end in "-ine". Examples of amino acid-derived hormones include epinephrine and norepinephrine, which are synthesized in the medulla of the adrenal glands, and thyroxine, which is produced by the thyroid gland. The pineal gland in the brain makes and secretes melatonin which regulates sleep cycles.

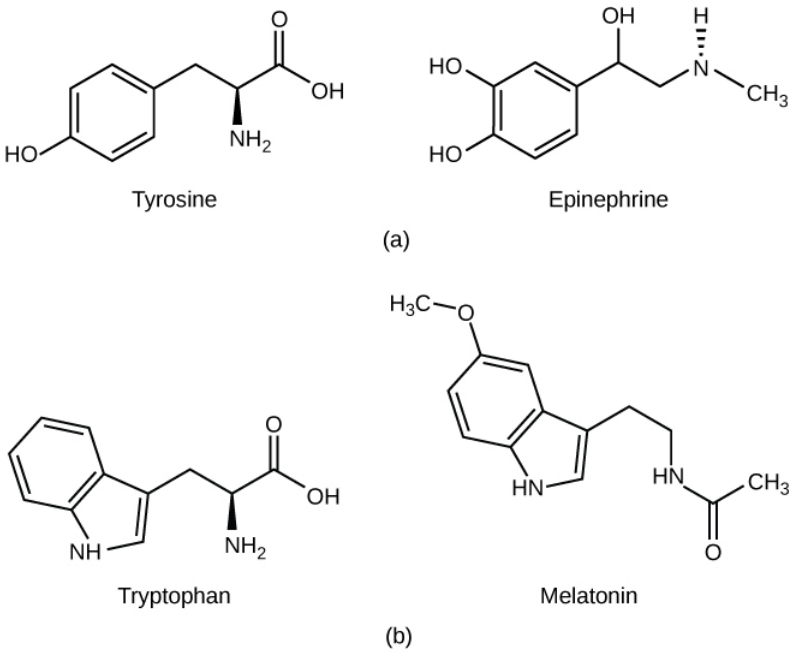


Figure **44.3.2**: (a) The hormone epinephrine, which triggers the fight-or-flight response, is derived from the amino acid tyrosine. (b) The hormone melatonin, which regulates circadian rhythms, is derived from the amino acid tryptophan.

Peptide Hormones

The structure of peptide hormones is that of a polypeptide chain (chain of amino acids). The peptide hormones include molecules that are short polypeptide chains, such as antidiuretic hormone and oxytocin produced in the brain and released into the blood in the posterior pituitary gland. This class also includes small proteins, like growth hormones produced by the pituitary, and large glycoproteins such as follicle-stimulating hormone produced by the pituitary. Figure **44.3.3** illustrates these peptide hormones.

Secreted peptides like insulin are stored within vesicles in the cells that synthesize them. They are then released in response to stimuli such as high blood glucose levels in the case of insulin. Amino acid-derived and polypeptide hormones are water-soluble and insoluble in lipids. These hormones cannot pass through plasma membranes of cells; therefore, their receptors are found on the surface of the target cells.

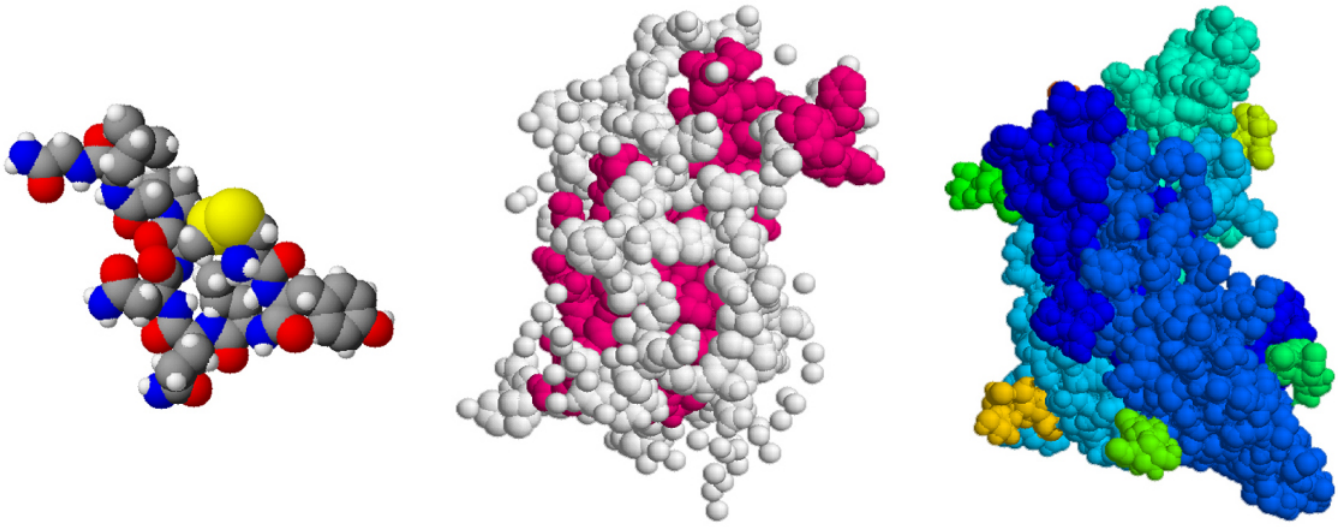


Figure 44.3.3: The structures of peptide hormones (a) oxytocin, (b) growth hormone, and (c) follicle-stimulating hormone are shown. These peptide hormones are much larger than those derived from cholesterol or amino acids.

Career Connection: Endocrinologist

An endocrinologist is a medical doctor who specializes in treating disorders of the endocrine glands, hormone systems, and glucose and lipid metabolic pathways. An endocrine surgeon specializes in the surgical treatment of endocrine diseases and glands. Some of the diseases that are managed by endocrinologists: disorders of the pancreas (diabetes mellitus), disorders of the pituitary (gigantism, acromegaly, and pituitary dwarfism), disorders of the thyroid gland (goiter and Graves' disease), and disorders of the adrenal glands (Cushing's disease and Addison's disease).

Endocrinologists are required to assess patients and diagnose endocrine disorders through extensive use of laboratory tests. Many endocrine diseases are diagnosed using tests that stimulate or suppress endocrine organ functioning. Blood samples are then drawn to determine the effect of stimulating or suppressing an endocrine organ on the production of hormones. For example, to diagnose diabetes mellitus, patients are required to fast for 12 to 24 hours. They are then given a sugary drink, which stimulates the pancreas to produce insulin to decrease blood glucose levels. A blood sample is taken one to two hours after the sugar drink is consumed. If the pancreas is functioning properly, the blood glucose level will be within a normal range. Another example is the A1C test, which can be performed during blood screening. The A1C test measures average blood glucose levels over the past two to three months by examining how well the blood glucose is being managed over a long time.

Once a disease has been diagnosed, endocrinologists can prescribe lifestyle changes and/or medications to treat the disease. Some cases of diabetes mellitus can be managed by exercise, weight loss, and a healthy diet; in other cases, medications may be required to enhance insulin release. If the disease cannot be controlled by these means, the endocrinologist may prescribe insulin injections.

In addition to clinical practice, endocrinologists may also be involved in primary research and development activities. For example, ongoing islet transplant research is investigating how healthy pancreas islet cells may be transplanted into diabetic patients. Successful islet transplants may allow patients to stop taking insulin injections.

Summary

There are three basic types of hormones: lipid-derived, amino acid-derived, and peptide. Lipid-derived hormones are structurally similar to cholesterol and include steroid hormones such as estradiol and testosterone. Amino acid-derived hormones are relatively small molecules and include the adrenal hormones epinephrine and norepinephrine. Peptide hormones are polypeptide chains or proteins and include the pituitary hormones, antidiuretic hormone (vasopressin), and oxytocin.

Glossary

amino acid-derived hormone
hormone derived from amino acids

lipid-derived hormone
hormone derived mostly from cholesterol

peptide hormone
hormone composed of a polypeptide chain

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44.3.1: Regulation of Body Processes

Skills to Develop

- Explain how hormones regulate the excretory system
- Discuss the role of hormones in the reproductive system
- Describe how hormones regulate metabolism
- Explain the role of hormones in different diseases

Hormones have a wide range of effects and modulate many different body processes. The key regulatory processes that will be examined here are those affecting the excretory system, the reproductive system, metabolism, blood calcium concentrations, growth, and the stress response.

Hormonal Regulation of the Excretory System

Maintaining a proper water balance in the body is important to avoid dehydration or over-hydration (hyponatremia). The water concentration of the body is monitored by osmoreceptors in the hypothalamus, which detect the concentration of electrolytes in the extracellular fluid. The concentration of electrolytes in the blood rises when there is water loss caused by excessive perspiration, inadequate water intake, or low blood volume due to blood loss. An increase in blood electrolyte levels results in a neuronal signal being sent from the osmoreceptors in hypothalamic nuclei. The pituitary gland has two components: anterior and posterior. The anterior pituitary is composed of glandular cells that secrete protein hormones. The posterior pituitary is an extension of the hypothalamus. It is composed largely of neurons that are continuous with the hypothalamus.

The hypothalamus produces a polypeptide hormone known as antidiuretic hormone (ADH), which is transported to and released from the posterior pituitary gland. The principal action of ADH is to regulate the amount of water excreted by the kidneys. As ADH (which is also known as vasopressin) causes direct water reabsorption from the kidney tubules, salts and wastes are concentrated in what will eventually be excreted as urine. The hypothalamus controls the mechanisms of ADH secretion, either by regulating blood volume or the concentration of water in the blood. Dehydration or physiological stress can cause an increase of osmolarity above 300 mOsm/L, which in turn, raises ADH secretion and water will be retained, causing an increase in blood pressure. ADH travels in the bloodstream to the kidneys. Once at the kidneys, ADH changes the kidneys to become more permeable to water by temporarily inserting water channels, aquaporins, into the kidney tubules. Water moves out of the kidney tubules through the aquaporins, reducing urine volume. The water is reabsorbed into the capillaries lowering blood osmolarity back toward normal. As blood osmolarity decreases, a negative feedback mechanism reduces osmoreceptor activity in the hypothalamus, and ADH secretion is reduced. ADH release can be reduced by certain substances, including alcohol, which can cause increased urine production and dehydration.

Chronic underproduction of ADH or a mutation in the ADH receptor results in diabetes insipidus. If the posterior pituitary does not release enough ADH, water cannot be retained by the kidneys and is lost as urine. This causes increased thirst, but water taken in is lost again and must be continually consumed. If the condition is not severe, dehydration may not occur, but severe cases can lead to electrolyte imbalances due to dehydration.

Another hormone responsible for maintaining electrolyte concentrations in extracellular fluids is aldosterone, a steroid hormone that is produced by the adrenal cortex. In contrast to ADH, which promotes the reabsorption of water to maintain proper water balance, aldosterone maintains proper water balance by enhancing Na^+ reabsorption and K^+ secretion from extracellular fluid of the cells in kidney tubules. Because it is produced in the cortex of the adrenal gland and affects the concentrations of minerals Na^+ and K^+, aldosterone is referred to as a mineralocorticoid, a corticosteroid that affects ion and water balance. Aldosterone release is stimulated by a decrease in blood sodium levels, blood volume, or blood pressure, or an increase in blood potassium levels. It also prevents the loss of Na^+ from sweat, saliva, and gastric juice. The reabsorption of Na^+ also results in the osmotic reabsorption of water, which alters blood volume and blood pressure.

Aldosterone production can be stimulated by low blood pressure, which triggers a sequence of chemical release, as illustrated in Figure **44.3.1.1**. When blood pressure drops, the renin-angiotensin-aldosterone system (RAAS) is activated. Cells in the juxtaglomerular apparatus, which regulates the functions of the nephrons of the kidney, detect this and release renin. Renin, an

enzyme, circulates in the blood and reacts with a plasma protein produced by the liver called angiotensinogen. When angiotensinogen is cleaved by renin, it produces angiotensin I, which is then converted into angiotensin II in the lungs. Angiotensin II functions as a hormone and then causes the release of the hormone aldosterone by the adrenal cortex, resulting in increased Na^+ reabsorption, water retention, and an increase in blood pressure. Angiotensin II in addition to being a potent vasoconstrictor also causes an increase in ADH and increased thirst, both of which help to raise blood pressure.

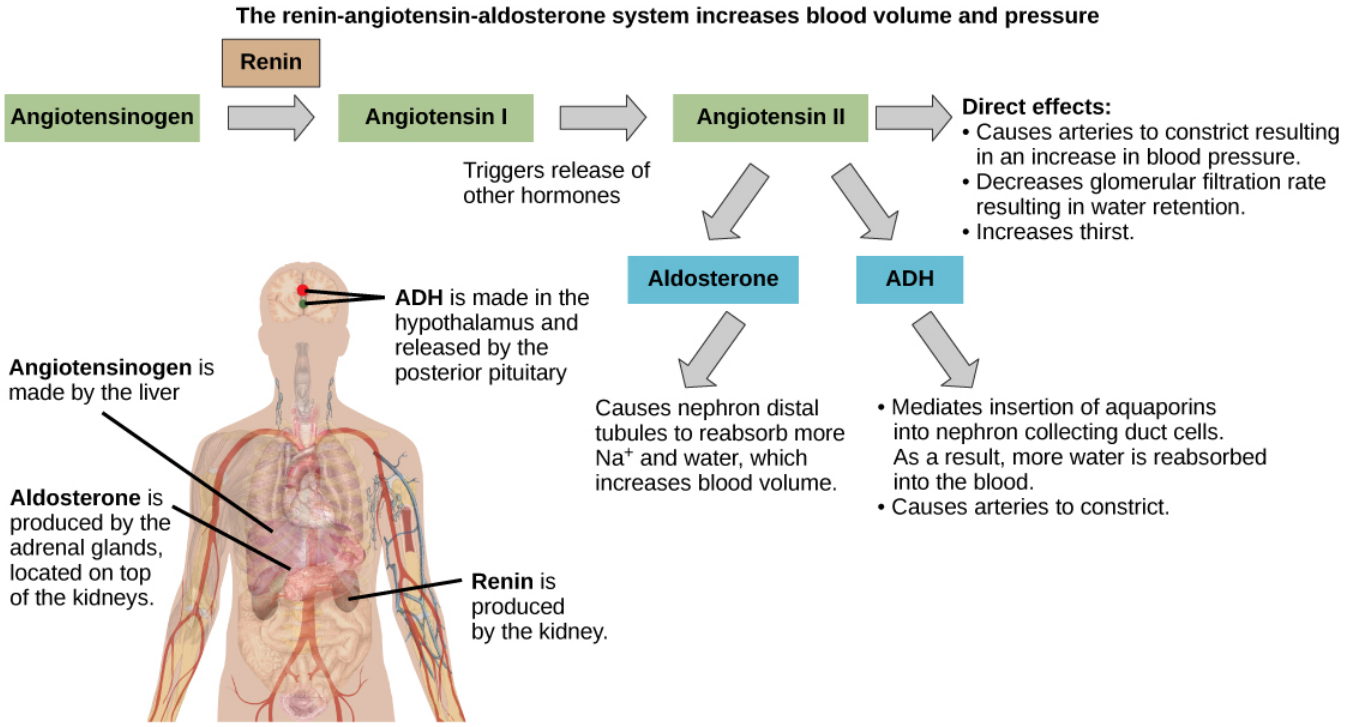


Figure **44.3.1.1**: ADH and aldosterone increase blood pressure and volume. Angiotensin II stimulates release of these hormones. Angiotensin II, in turn, is formed when renin cleaves angiotensinogen. (credit: modification of work by Mikael Häggström).

Hormonal Regulation of the Reproductive System

Regulation of the reproductive system is a process that requires the action of hormones from the pituitary gland, the adrenal cortex, and the gonads. During puberty in both males and females, the hypothalamus produces gonadotropin-releasing hormone (GnRH), which stimulates the production and release of *follicle-stimulating hormone (FSH)* and *luteinizing hormone (LH)* from the anterior pituitary gland. These hormones regulate the gonads (testes in males and ovaries in females) and therefore are called gonadotropins. In both males and females, FSH stimulates gamete production and LH stimulates production of hormones by the gonads. An increase in gonad hormone levels inhibits GnRH production through a negative feedback loop.

Regulation of the Male Reproductive System

In males, FSH stimulates the maturation of sperm cells. FSH production is inhibited by the hormone inhibin, which is released by the testes. LH stimulates production of the sex hormones (androgens) by the interstitial cells of the testes and therefore is also called interstitial cell-stimulating hormone. The most widely known androgen in males is *testosterone*. Testosterone promotes the production of sperm and masculine characteristics. The adrenal cortex also produces small amounts of testosterone precursor, although the role of this additional hormone production is not fully understood.

Everyday Connection: The Dangers of Synthetic Hormones

Some athletes attempt to boost their performance by using artificial hormones that enhance muscle performance. Anabolic steroids, a form of the male sex hormone testosterone, are one of the most widely known performance-enhancing drugs. Steroids are used to help build muscle mass. Other hormones that are used to enhance athletic performance include *erythropoietin*, which triggers the production of red blood cells, and human growth hormone, which can help in building muscle mass. Most performance enhancing drugs are illegal for non-medical purposes. They are also banned by national and

international governing bodies including the International Olympic Committee, the U.S. Olympic Committee, the National Collegiate Athletic Association, the Major League Baseball, and the National Football League.



Figure **44.3.1.2**: Professional baseball player Jason Giambi publically admitted to, and apologized for, his use of anabolic steroids supplied by a trainer. (credit: Bryce Edwards)

The side effects of synthetic hormones are often significant and non-reversible, and in some cases, fatal. Androgens produce several complications such as liver dysfunctions and liver tumors, prostate gland enlargement, difficulty urinating, premature closure of epiphyseal cartilages, testicular atrophy, infertility, and immune system depression. The physiological strain caused by these substances is often greater than what the body can handle, leading to unpredictable and dangerous effects and linking their use to heart attacks, strokes, and impaired cardiac function.

Regulation of the Female Reproductive System

In females, FSH stimulates development of egg cells, called ova, which develop in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production. LH also plays a role in the development of ova, induction of ovulation, and stimulation of estradiol and progesterone production by the ovaries, as illustrated in Figure **44.3.1.3**. Estradiol and progesterone are steroid hormones that prepare the body for pregnancy. Estradiol produces secondary sex characteristics in females, while both estradiol and progesterone regulate the menstrual cycle.

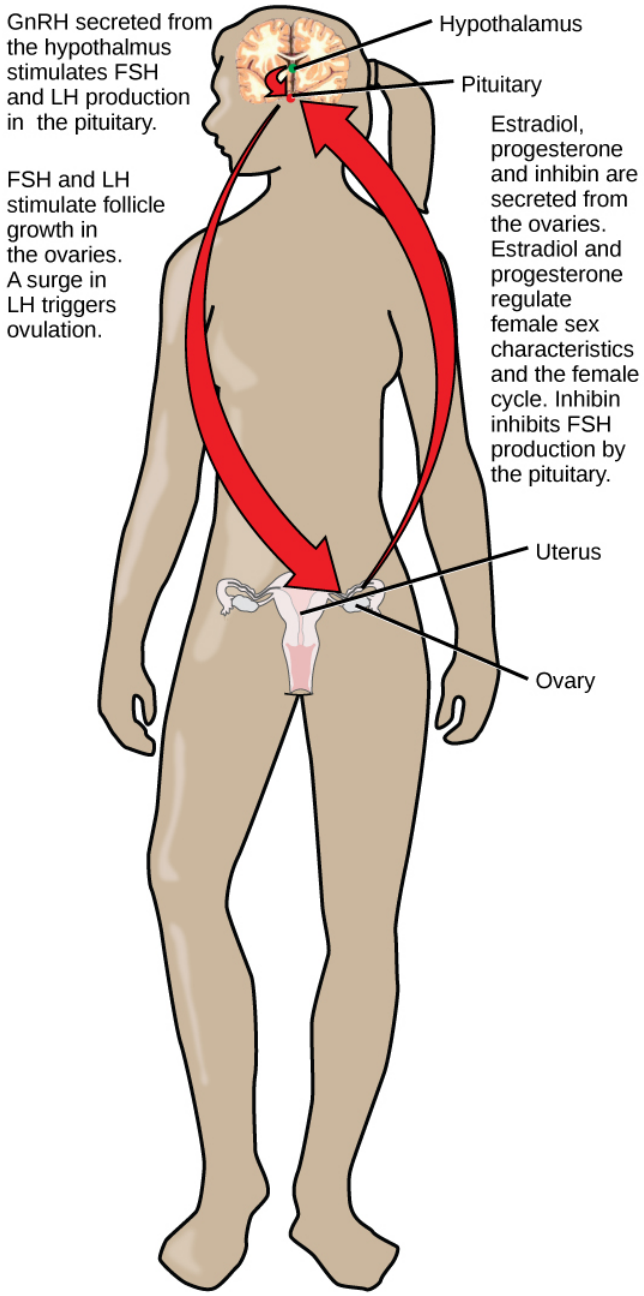


Figure **44.3.1.3**: Hormonal regulation of the female reproductive system involves hormones from the hypothalamus, pituitary, and ovaries.

In addition to producing FSH and LH, the anterior portion of the pituitary gland also produces the hormone prolactin (PRL) in females. Prolactin stimulates the production of milk by the mammary glands following childbirth. Prolactin levels are regulated by the hypothalamic hormones prolactin-releasing hormone (PRH) and prolactin-inhibiting hormone (PIH), which is now known to be dopamine. PRH stimulates the release of prolactin and PIH inhibits it.

The posterior pituitary releases the hormone oxytocin, which stimulates uterine contractions during childbirth. The uterine smooth muscles are not very sensitive to oxytocin until late in pregnancy when the number of oxytocin receptors in the uterus peaks. Stretching of tissues in the uterus and cervix stimulates oxytocin release during childbirth. Contractions increase in intensity as blood levels of oxytocin rise via a positive feedback mechanism until the birth is complete. Oxytocin also stimulates the contraction of myoepithelial cells around the milk-producing mammary glands. As these cells contract, milk is forced from the secretory alveoli into milk ducts and is ejected from the breasts in milk ejection (“let-down”) reflex. Oxytocin release is stimulated by the

suckling of an infant, which triggers the synthesis of oxytocin in the hypothalamus and its release into circulation at the posterior pituitary.

Hormonal Regulation of Metabolism

Blood glucose levels vary widely over the course of a day as periods of food consumption alternate with periods of fasting. Insulin and glucagon are the two hormones primarily responsible for maintaining homeostasis of blood glucose levels. Additional regulation is mediated by the thyroid hormones.

Regulation of Blood Glucose Levels by Insulin and Glucagon

Cells of the body require nutrients in order to function, and these nutrients are obtained through feeding. In order to manage nutrient intake, storing excess intake and utilizing reserves when necessary, the body uses hormones to moderate energy stores. Insulin is produced by the beta cells of the pancreas, which are stimulated to release insulin as blood glucose levels rise (for example, after a meal is consumed). Insulin lowers blood glucose levels by enhancing the rate of glucose uptake and utilization by target cells, which use glucose for ATP production. It also stimulates the liver to convert glucose to glycogen, which is then stored by cells for later use. Insulin also increases glucose transport into certain cells, such as muscle cells and the liver. This results from an insulin-mediated increase in the number of glucose transporter proteins in cell membranes, which remove glucose from circulation by facilitated diffusion. As insulin binds to its target cell via insulin receptors and signal transduction, it triggers the cell to incorporate glucose transport proteins into its membrane. This allows glucose to enter the cell, where it can be used as an energy source. However, this does not occur in all cells: some cells, including those in the kidneys and brain, can access glucose without the use of insulin. Insulin also stimulates the conversion of glucose to fat in adipocytes and the synthesis of proteins. These actions mediated by insulin cause blood glucose concentrations to fall, called a hypoglycemic “low sugar” effect, which inhibits further insulin release from beta cells through a negative feedback loop.

Link to Learning



This animation describes the role of insulin and the pancreas in diabetes.

Impaired insulin function can lead to a condition called diabetes mellitus, the main symptoms of which are illustrated in Figure **44.3.1.4**. This can be caused by low levels of insulin production by the beta cells of the pancreas, or by reduced sensitivity of tissue cells to insulin. This prevents glucose from being absorbed by cells, causing high levels of blood glucose, or hyperglycemia (high sugar). High blood glucose levels make it difficult for the kidneys to recover all the glucose from nascent urine, resulting in glucose being lost in urine. High glucose levels also result in less water being reabsorbed by the kidneys, causing high amounts of urine to be produced; this may result in dehydration. Over time, high blood glucose levels can cause nerve damage to the eyes and peripheral body tissues, as well as damage to the kidneys and cardiovascular system. Oversecretion of insulin can cause hypoglycemia, low blood glucose levels. This causes insufficient glucose availability to cells, often leading to muscle weakness, and can sometimes cause unconsciousness or death if left untreated.

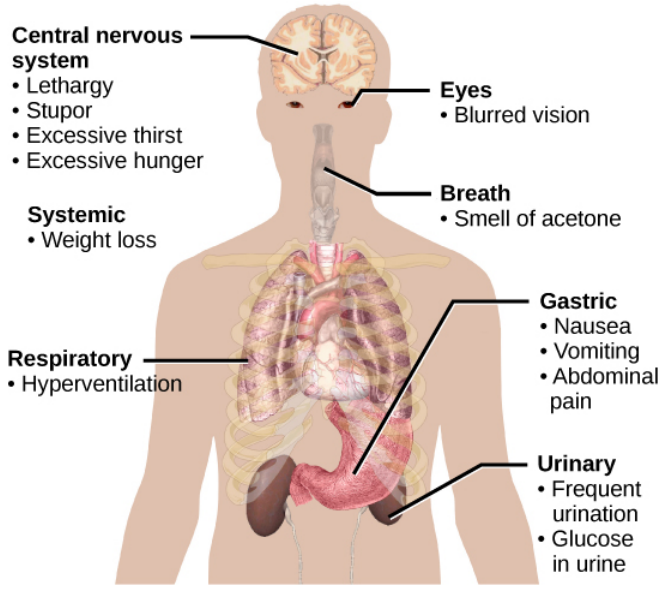


Figure **44.3.1.4**: The main symptoms of diabetes are shown. (credit: modification of work by Mikael Häggström)

When blood glucose levels decline below normal levels, for example between meals or when glucose is utilized rapidly during exercise, the hormone glucagon is released from the alpha cells of the pancreas. Glucagon raises blood glucose levels, eliciting what is called a hyperglycemic effect, by stimulating the breakdown of glycogen to glucose in skeletal muscle cells and liver cells in a process called glycogenolysis. Glucose can then be utilized as energy by muscle cells and released into circulation by the liver cells. Glucagon also stimulates absorption of amino acids from the blood by the liver, which then converts them to glucose. This process of glucose synthesis is called gluconeogenesis. Glucagon also stimulates adipose cells to release fatty acids into the blood. These actions mediated by glucagon result in an increase in blood glucose levels to normal homeostatic levels. Rising blood glucose levels inhibit further glucagon release by the pancreas via a negative feedback mechanism. In this way, insulin and glucagon work together to maintain homeostatic glucose levels, as shown in Figure **44.3.1.5**.

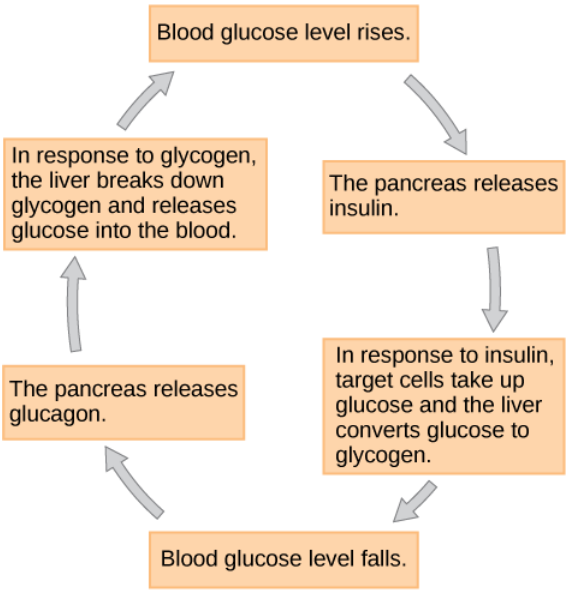


Figure **44.3.1.5**: Insulin and glucagon regulate blood glucose levels.

Exercise

Pancreatic tumors may cause excess secretion of glucagon. Type I diabetes results from the failure of the pancreas to produce insulin. Which of the following statement about these two conditions is true?

A. A pancreatic tumor and type I diabetes will have the opposite effects on blood sugar levels.

B. A pancreatic tumor and type I diabetes will both cause hyperglycemia.
C. A pancreatic tumor and type I diabetes will both cause hypoglycemia.
D. Both pancreatic tumors and type I diabetes result in the inability of cells to take up glucose.

Answer

B

Regulation of Blood Glucose Levels by Thyroid Hormones

The basal metabolic rate, which is the amount of calories required by the body at rest, is determined by two hormones produced by the thyroid gland: thyroxine, also known as tetraiodothyronine or T_4, and triiodothyronine, also known as T_3. These hormones affect nearly every cell in the body except for the adult brain, uterus, testes, blood cells, and spleen. They are transported across the plasma membrane of target cells and bind to receptors on the mitochondria resulting in increased ATP production. In the nucleus, T_3 and T_4 activate genes involved in energy production and glucose oxidation. This results in increased rates of metabolism and body heat production, which is known as the hormone's calorigenic effect.

T_3 and T_4 release from the thyroid gland is stimulated by thyroid-stimulating hormone (TSH), which is produced by the anterior pituitary. TSH binding at the receptors of the follicle of the thyroid triggers the production of T_3 and T_4 from a glycoprotein called thyroglobulin. Thyroglobulin is present in the follicles of the thyroid, and is converted into thyroid hormones with the addition of iodine. Iodine is formed from iodide ions that are actively transported into the thyroid follicle from the bloodstream. A peroxidase enzyme then attaches the iodine to the tyrosine amino acid found in thyroglobulin. T_3 has three iodine ions attached, while T_4 has four iodine ions attached. T_3 and T_4 are then released into the bloodstream, with T_4 being released in much greater amounts than T_3. As T_3 is more active than T_4 and is responsible for most of the effects of thyroid hormones, tissues of the body convert T_4 to T_3 by the removal of an iodine ion. Most of the released T_3 and T_4 becomes attached to transport proteins in the bloodstream and is unable to cross the plasma membrane of cells. These protein-bound molecules are only released when blood levels of the unattached hormone begin to decline. In this way, a week's worth of reserve hormone is maintained in the blood. Increased T_3 and T_4 levels in the blood inhibit the release of TSH, which results in lower T_3 and T_4 release from the thyroid.

The follicular cells of the thyroid require iodides (anions of iodine) in order to synthesize T_3 and T_4. Iodides obtained from the diet are actively transported into follicle cells resulting in a concentration that is approximately 30 times higher than in blood. The typical diet in North America provides more iodine than required due to the addition of iodide to table salt. Inadequate iodine intake, which occurs in many developing countries, results in an inability to synthesize T_3 and T_4 hormones. The thyroid gland enlarges in a condition called goiter, which is caused by overproduction of TSH without the formation of thyroid hormone. Thyroglobulin is contained in a fluid called colloid, and TSH stimulation results in higher levels of colloid accumulation in the thyroid. In the absence of iodine, this is not converted to thyroid hormone, and colloid begins to accumulate more and more in the thyroid gland, leading to goiter.

Disorders can arise from both the underproduction and overproduction of thyroid hormones. Hypothyroidism, underproduction of the thyroid hormones, can cause a low metabolic rate leading to weight gain, sensitivity to cold, and reduced mental activity, among other symptoms. In children, hypothyroidism can cause cretinism, which can lead to mental retardation and growth defects. Hyperthyroidism, the overproduction of thyroid hormones, can lead to an increased metabolic rate and its effects: weight loss, excess heat production, sweating, and an increased heart rate. Graves' disease is one example of a hyperthyroid condition.

Hormonal Control of Blood Calcium Levels

Regulation of blood calcium concentrations is important for generation of muscle contractions and nerve impulses, which are electrically stimulated. If calcium levels get too high, membrane permeability to sodium decreases and membranes become less responsive. If calcium levels get too low, membrane permeability to sodium increases and convulsions or muscle spasms can result.

Blood calcium levels are regulated by parathyroid hormone (PTH), which is produced by the parathyroid glands, as illustrated in Figure **44.3.1.6**. PTH is released in response to low blood Ca^{2+} levels. PTH increases Ca^{2+} levels by targeting the skeleton, the kidneys, and the intestine. In the skeleton, PTH stimulates osteoclasts, which causes bone to be reabsorbed, releasing Ca^{2+} from bone into the blood. PTH also inhibits osteoblasts, reducing Ca^{2+} deposition in bone. In the intestines, PTH increases dietary Ca^{2+} absorption, and in the kidneys, PTH stimulates reabsorption of the CA^{2+}. While PTH acts directly on the kidneys to increase Ca^{2+}

reabsorption, its effects on the intestine are indirect. PTH triggers the formation of calcitriol, an active form of vitamin D, which acts on the intestines to increase absorption of dietary calcium. PTH release is inhibited by rising blood calcium levels.

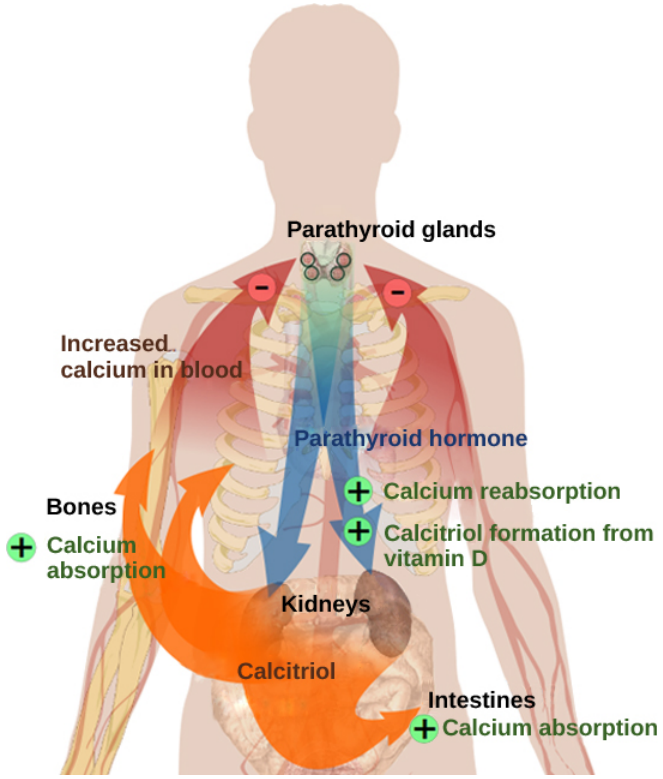


Figure 44.3.1.6: Parathyroid hormone (PTH) is released in response to low blood calcium levels. It increases blood calcium levels by targeting the skeleton, the kidneys, and the intestine. (credit: modification of work by Mikael Häggström)

Hyperparathyroidism results from an overproduction of parathyroid hormone. This results in excessive calcium being removed from bones and introduced into blood circulation, producing structural weakness of the bones, which can lead to deformation and fractures, plus nervous system impairment due to high blood calcium levels. Hypoparathyroidism, the underproduction of PTH, results in extremely low levels of blood calcium, which causes impaired muscle function and may result in tetany (severe sustained muscle contraction).

The hormone calcitonin, which is produced by the parafollicular or C cells of the thyroid, has the opposite effect on blood calcium levels as does PTH. Calcitonin decreases blood calcium levels by inhibiting osteoclasts, stimulating osteoblasts, and stimulating calcium excretion by the kidneys. This results in calcium being added to the bones to promote structural integrity. Calcitonin is most important in children (when it stimulates bone growth), during pregnancy (when it reduces maternal bone loss), and during prolonged starvation (because it reduces bone mass loss). In healthy nonpregnant, unstarved adults, the role of calcitonin is unclear.

Hormonal Regulation of Growth

Hormonal regulation is required for the growth and replication of most cells in the body. Growth hormone (GH), produced by the anterior portion of the pituitary gland, accelerates the rate of protein synthesis, particularly in skeletal muscle and bones. Growth hormone has direct and indirect mechanisms of action. The first direct action of GH is stimulation of triglyceride breakdown (lipolysis) and release into the blood by adipocytes. This results in a switch by most tissues from utilizing glucose as an energy source to utilizing fatty acids. This process is called a glucose-sparing effect. In another direct mechanism, GH stimulates glycogen breakdown in the liver; the glycogen is then released into the blood as glucose. Blood glucose levels increase as most tissues are utilizing fatty acids instead of glucose for their energy needs. The GH mediated increase in blood glucose levels is called a diabetogenic effect because it is similar to the high blood glucose levels seen in diabetes mellitus.

The indirect mechanism of GH action is mediated by insulin-like growth factors (IGFs) or somatomedins, which are a family of growth-promoting proteins produced by the liver, which stimulates tissue growth. IGFs stimulate the uptake of amino acids from the blood, allowing the formation of new proteins, particularly in skeletal muscle cells, cartilage cells, and other target cells, as

shown in Figure **44.3.1.7**. This is especially important after a meal, when glucose and amino acid concentration levels are high in the blood. GH levels are regulated by two hormones produced by the hypothalamus. GH release is stimulated by growth hormone-releasing hormone (GHRH) and is inhibited by growth hormone-inhibiting hormone (GHIH), also called somatostatin.

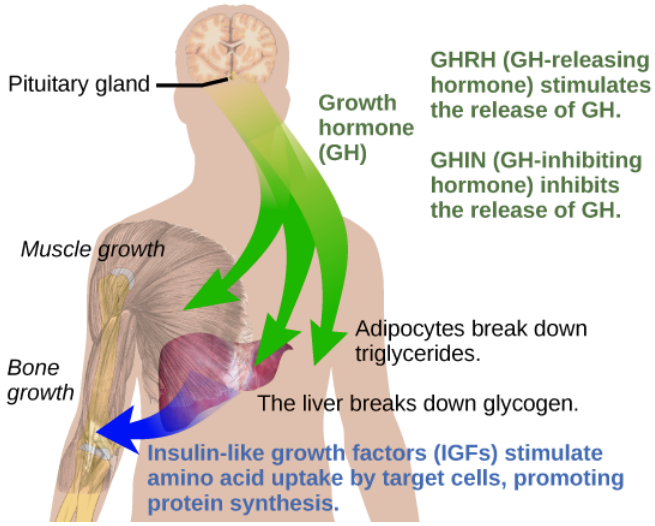


Figure **44.3.1.7**: Growth hormone directly accelerates the rate of protein synthesis in skeletal muscle and bones. Insulin-like growth factor 1 (IGF-1) is activated by growth hormone and also allows formation of new proteins in muscle cells and bone. (credit: modification of work by Mikael Häggström)

A balanced production of growth hormone is critical for proper development. Underproduction of GH in adults does not appear to cause any abnormalities, but in children it can result in pituitary dwarfism, in which growth is reduced. Pituitary dwarfism is characterized by symmetric body formation. In some cases, individuals are under 30 inches in height. Oversecretion of growth hormone can lead to gigantism in children, causing excessive growth. In some documented cases, individuals can reach heights of over eight feet. In adults, excessive GH can lead to acromegaly, a condition in which there is enlargement of bones in the face, hands, and feet that are still capable of growth.

Hormonal Regulation of Stress

When a threat or danger is perceived, the body responds by releasing hormones that will ready it for the “fight-or-flight” response. The effects of this response are familiar to anyone who has been in a stressful situation: increased heart rate, dry mouth, and hair standing up.

Evolution Connection: Fight-or-Flight Response

Interactions of the endocrine hormones have evolved to ensure the body’s internal environment remains stable. Stressors are stimuli that disrupt homeostasis. The sympathetic division of the vertebrate autonomic nervous system has evolved the fight-or-flight response to counter stress-induced disruptions of homeostasis. In the initial alarm phase, the sympathetic nervous system stimulates an increase in energy levels through increased blood glucose levels. This prepares the body for physical activity that may be required to respond to stress: to either fight for survival or to flee from danger.

However, some stresses, such as illness or injury, can last for a long time. Glycogen reserves, which provide energy in the short-term response to stress, are exhausted after several hours and cannot meet long-term energy needs. If glycogen reserves were the only energy source available, neural functioning could not be maintained once the reserves became depleted due to the nervous system’s high requirement for glucose. In this situation, the body has evolved a response to counter long-term stress through the actions of the glucocorticoids, which ensure that long-term energy requirements can be met. The glucocorticoids mobilize lipid and protein reserves, stimulate gluconeogenesis, conserve glucose for use by neural tissue, and stimulate the conservation of salts and water. The mechanisms to maintain homeostasis that are described here are those observed in the human body. However, the fight-or-flight response exists in some form in all vertebrates.

The sympathetic nervous system regulates the stress response via the hypothalamus. Stressful stimuli cause the hypothalamus to signal the adrenal medulla (which mediates short-term stress responses) via nerve impulses, and the adrenal cortex, which

mediates long-term stress responses, via the hormone adrenocorticotropic hormone (ACTH), which is produced by the anterior pituitary.

Short-term Stress Response

When presented with a stressful situation, the body responds by calling for the release of hormones that provide a burst of energy. The hormones epinephrine (also known as adrenaline) and norepinephrine (also known as noradrenaline) are released by the adrenal medulla. How do these hormones provide a burst of energy? Epinephrine and norepinephrine increase blood glucose levels by stimulating the liver and skeletal muscles to break down glycogen and by stimulating glucose release by liver cells. Additionally, these hormones increase oxygen availability to cells by increasing the heart rate and dilating the bronchioles. The hormones also prioritize body function by increasing blood supply to essential organs such as the heart, brain, and skeletal muscles, while restricting blood flow to organs not in immediate need, such as the skin, digestive system, and kidneys. Epinephrine and norepinephrine are collectively called catecholamines.

Link to Learning



Watch this Discovery Channel animation describing the flight-or-flight response.

Long-term Stress Response

Long-term stress response differs from short-term stress response. The body cannot sustain the bursts of energy mediated by epinephrine and norepinephrine for long times. Instead, other hormones come into play. In a long-term stress response, the hypothalamus triggers the release of ACTH from the anterior pituitary gland. The adrenal cortex is stimulated by ACTH to release steroid hormones called corticosteroids. Corticosteroids turn on transcription of certain genes in the nuclei of target cells. They change enzyme concentrations in the cytoplasm and affect cellular metabolism. There are two main corticosteroids: glucocorticoids such as cortisol, and mineralocorticoids such as aldosterone. These hormones target the breakdown of fat into fatty acids in the adipose tissue. The fatty acids are released into the bloodstream for other tissues to use for ATP production. The glucocorticoids primarily affect glucose metabolism by stimulating glucose synthesis. Glucocorticoids also have anti-inflammatory properties through inhibition of the immune system. For example, cortisone is used as an anti-inflammatory medication; however, it cannot be used long term as it increases susceptibility to disease due to its immune-suppressing effects.

Mineralocorticoids function to regulate ion and water balance of the body. The hormone aldosterone stimulates the reabsorption of water and sodium ions in the kidney, which results in increased blood pressure and volume.

Hypersecretion of glucocorticoids can cause a condition known as Cushing's disease, characterized by a shifting of fat storage areas of the body. This can cause the accumulation of adipose tissue in the face and neck, and excessive glucose in the blood.

Hyposecretion of the corticosteroids can cause Addison's disease, which may result in bronzing of the skin, hypoglycemia, and low electrolyte levels in the blood.

Summary

Water levels in the body are controlled by antidiuretic hormone (ADH), which is produced in the hypothalamus and triggers the reabsorption of water by the kidneys. Underproduction of ADH can cause diabetes insipidus. Aldosterone, a hormone produced by the adrenal cortex of the kidneys, enhances Na^+ reabsorption from the extracellular fluids and subsequent water reabsorption by diffusion. The renin-angiotensin-aldosterone system is one way that aldosterone release is controlled.

The reproductive system is controlled by the gonadotropins follicle-stimulating hormone (FSH) and luteinizing hormone (LH), which are produced by the pituitary gland. Gonadotropin release is controlled by the hypothalamic hormone gonadotropin-releasing hormone (GnRH). FSH stimulates the maturation of sperm cells in males and is inhibited by the hormone inhibin, while LH stimulates the production of the androgen testosterone. FSH stimulates egg maturation in females, while LH stimulates the production of estrogens and progesterone. Estrogens are a group of steroid hormones produced by the ovaries that trigger the development of secondary sex characteristics in females as well as control the maturation of the ova. In females, the pituitary also produces prolactin, which stimulates milk production after childbirth, and oxytocin, which stimulates uterine contraction during childbirth and milk let-down during suckling.

Insulin is produced by the pancreas in response to rising blood glucose levels and allows cells to utilize blood glucose and store excess glucose for later use. Diabetes mellitus is caused by reduced insulin activity and causes high blood glucose levels, or hyperglycemia. Glucagon is released by the pancreas in response to low blood glucose levels and stimulates the breakdown of glycogen into glucose, which can be used by the body. The body's basal metabolic rate is controlled by the thyroid hormones thyroxine (T_4) and triiodothyronine (T_3). The anterior pituitary produces thyroid stimulating hormone (TSH), which controls the release of T_3 and T_4 from the thyroid gland. Iodine is necessary in the production of thyroid hormone, and the lack of iodine can lead to a condition called goiter.

Parathyroid hormone (PTH) is produced by the parathyroid glands in response to low blood Ca^{2+} levels. The parafollicular cells of the thyroid produce calcitonin, which reduces blood Ca^{2+} levels. Growth hormone (GH) is produced by the anterior pituitary and controls the growth rate of muscle and bone. GH action is indirectly mediated by insulin-like growth factors (IGFs). Short-term stress causes the hypothalamus to trigger the adrenal medulla to release epinephrine and norepinephrine, which trigger the fight or flight response. Long-term stress causes the hypothalamus to trigger the anterior pituitary to release adrenocorticotropic hormone (ACTH), which causes the release of corticosteroids, glucocorticoids, and mineralocorticoids, from the adrenal cortex.

Glossary

acromegaly
: condition caused by overproduction of GH in adults

Addison's disease
: disorder caused by the hyposecretion of corticosteroids

adrenocorticotropic hormone (ACTH)
: hormone released by the anterior pituitary, which stimulates the adrenal cortex to release corticosteroids during the long-term stress response

aldosterone
: steroid hormone produced by the adrenal cortex that stimulates the reabsorption of Na^+ from extracellular fluids and secretion of K^+.

androgen
: male sex hormone such as testosterone

antidiuretic hormone (ADH)

hormone produced by the hypothalamus and released by the posterior pituitary that increases water reabsorption by the kidneys

calcitonin
hormone produced by the parafollicular cells of the thyroid gland that functions to lower blood Ca^{2+} levels and promote bone growth

corticosteroid
hormone released by the adrenal cortex in response to long-term stress

cortisol
glucocorticoid produced in response to stress

Cushing's disease
disorder caused by the hypersecretion of glucocorticoids

diabetes insipidus
disorder caused by underproduction of ADH

diabetes mellitus
disorder caused by low levels of insulin activity

diabetogenic effect
effect of GH that causes blood glucose levels to rise similar to diabetes mellitus

epinephrine
hormone released by the adrenal medulla in response to a short term stress

estrogens
- a group of steroid hormones, including estradiol and several others, that are produced by the ovaries and elicit secondary sex characteristics in females as well as control the maturation of the ova

follicle-stimulating hormone (FSH)
hormone produced by the anterior pituitary that stimulates gamete production

gigantism
condition caused by overproduction of GH in children

glucagon
hormone produced by the alpha cells of the pancreas in response to low blood sugar; functions to raise blood sugar levels

glucocorticoid
corticosteroid that affects glucose metabolism

gluconeogenesis
synthesis of glucose from amino acids

glucose-sparing effect
effect of GH that causes tissues to use fatty acids instead of glucose as an energy source

glycogenolysis
breakdown of glycogen into glucose

goiter
enlargement of the thyroid gland caused by insufficient dietary iodine levels

gonadotropin
hormone that regulates the gonads, including FSH and LH

growth hormone (GH)
hormone produced by the anterior pituitary that promotes protein synthesis and body growth

growth hormone-inhibiting hormone (GHIH)
hormone produced by the hypothalamus that inhibits growth hormone production, also called somatostatin

growth hormone-releasing hormone (GHRH)
hormone released by the hypothalamus that triggers the release of GH

hyperglycemia
high blood sugar level

hyperthyroidism
overactivity of the thyroid gland

hypoglycemia
low blood sugar level

hypothyroidism
underactivity of the thyroid gland

insulin
hormone produced by the beta cells of the pancreas in response to high blood glucose levels; functions to lower blood glucose levels

insulin-like growth factor (IGF)
growth-promoting protein produced by the liver

mineralocorticoid
corticosteroid that affects ion and water balance

norepinephrine
hormone released by the adrenal medulla in response to a short-term stress hormone production by the gonads

osmoreceptor
receptor in the hypothalamus that monitors the concentration of electrolytes in the blood

oxytocin
hormone released by the posterior pituitary to stimulate uterine contractions during childbirth and milk let-down in the mammary glands

parathyroid hormone (PTH)
hormone produced by the parathyroid glands in response to low blood Ca^{2+} levels; functions to raise blood Ca^{2+} levels

pituitary dwarfism
condition caused by underproduction of GH in children

prolactin (PRL)
hormone produced by the anterior pituitary that stimulates milk production

prolactin-inhibiting hormone

hormone produced by the hypothalamus that inhibits the release of prolactin

prolactin-releasing hormone
hormone produced by the hypothalamus that stimulates the release of prolactin

renin
enzyme produced by the juxtaglomerular apparatus of the kidneys that reacts with angiotensinogen to cause the release of aldosterone

thyroglobulin
glycoprotein found in the thyroid that is converted into thyroid hormone

thyroid-stimulating hormone (TSH)
hormone produced by the anterior pituitary that controls the release of T_3 and T_4 from the thyroid gland

thyroxine (tetraiodothyronine, T_4)
thyroid hormone that controls the basal metabolic rate

triiodothyronine (T_3)
thyroid hormone that controls the basal metabolic rate

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44.3.2: Endocrine Glands

Skills to Develop

- Describe the role of different glands in the endocrine system
- Explain how the different glands work together to maintain homeostasis

Both the endocrine and nervous systems use chemical signals to communicate and regulate the body's physiology. The endocrine system releases hormones that act on target cells to regulate development, growth, energy metabolism, reproduction, and many behaviors. The nervous system releases neurotransmitters or neurohormones that regulate neurons, muscle cells, and endocrine cells. Because the neurons can regulate the release of hormones, the nervous and endocrine systems work in a coordinated manner to regulate the body's physiology.

Hypothalamic-Pituitary Axis

The hypothalamus in vertebrates integrates the endocrine and nervous systems. The hypothalamus is an endocrine organ located in the diencephalon of the brain. It receives input from the body and other brain areas and initiates endocrine responses to environmental changes. The hypothalamus acts as an endocrine organ, synthesizing hormones and transporting them along axons to the posterior pituitary gland. It synthesizes and secretes regulatory hormones that control the endocrine cells in the anterior pituitary gland. The hypothalamus contains autonomic centers that control endocrine cells in the adrenal medulla via neuronal control.

The pituitary gland, sometimes called the hypophysis or “master gland” is located at the base of the brain in the sella turcica, a groove of the sphenoid bone of the skull, illustrated in Figure **44.3.2.1**. It is attached to the hypothalamus via a stalk called the pituitary stalk (or infundibulum). The anterior portion of the pituitary gland is regulated by releasing or release-inhibiting hormones produced by the hypothalamus, and the posterior pituitary receives signals via neurosecretory cells to release hormones produced by the hypothalamus. The pituitary has two distinct regions—the anterior pituitary and the posterior pituitary—which between them secrete nine different peptide or protein hormones. The posterior lobe of the pituitary gland contains axons of the hypothalamic neurons.

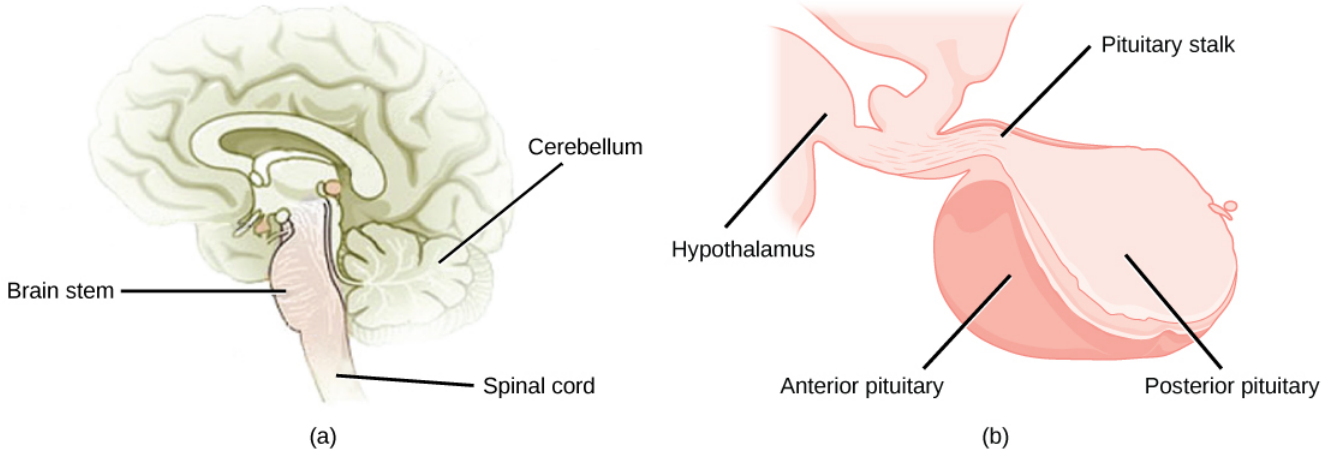


Figure **44.3.2.1**: The pituitary gland is located at (a) the base of the brain and (b) connected to the hypothalamus by the pituitary stalk. (credit a: modification of work by NCI; credit b: modification of work by Gray’s Anatomy)

Anterior Pituitary

The anterior pituitary gland, or adenohypophysis, is surrounded by a capillary network that extends from the hypothalamus, down along the infundibulum, and to the anterior pituitary. This capillary network is a part of the hypophyseal portal system that carries substances from the hypothalamus to the anterior pituitary and hormones from the anterior pituitary into the circulatory system. A portal system carries blood from one capillary network to another; therefore, the hypophyseal portal system allows hormones produced by the hypothalamus to be carried directly to the anterior pituitary without first entering the circulatory system.

The anterior pituitary produces seven hormones: growth hormone (GH), prolactin (PRL), thyroid-stimulating hormone (TSH), melanin-stimulating hormone (MSH), adrenocorticotropic hormone (ACTH), follicle-stimulating hormone (FSH), and luteinizing hormone (LH). Anterior pituitary hormones are sometimes referred to as tropic hormones, because they control the functioning of other organs. While these hormones are produced by the anterior pituitary, their production is controlled by regulatory hormones produced by the hypothalamus. These regulatory hormones can be releasing hormones or inhibiting hormones, causing more or less of the anterior pituitary hormones to be secreted. These travel from the hypothalamus through the hypophyseal portal system to the anterior pituitary where they exert their effect. Negative feedback then regulates how much of these regulatory hormones are released and how much anterior pituitary hormone is secreted.

Posterior Pituitary

The posterior pituitary is significantly different in structure from the anterior pituitary. It is a part of the brain, extending down from the hypothalamus, and contains mostly nerve fibers and neuroglial cells, which support axons that extend from the hypothalamus to the posterior pituitary. The posterior pituitary and the infundibulum together are referred to as the neurohypophysis.

The hormones antidiuretic hormone (ADH), also known as vasopressin, and oxytocin are produced by neurons in the hypothalamus and transported within these axons along the infundibulum to the posterior pituitary. They are released into the circulatory system via neural signaling from the hypothalamus. These hormones are considered to be posterior pituitary hormones, even though they are produced by the hypothalamus, because that is where they are released into the circulatory system. The posterior pituitary itself does not produce hormones, but instead stores hormones produced by the hypothalamus and releases them into the blood stream.

Thyroid Gland

The thyroid gland is located in the neck, just below the larynx and in front of the trachea, as shown in Figure **44.3.2.2**. It is a butterfly-shaped gland with two lobes that are connected by the isthmus. It has a dark red color due to its extensive vascular system. When the thyroid swells due to dysfunction, it can be felt under the skin of the neck.

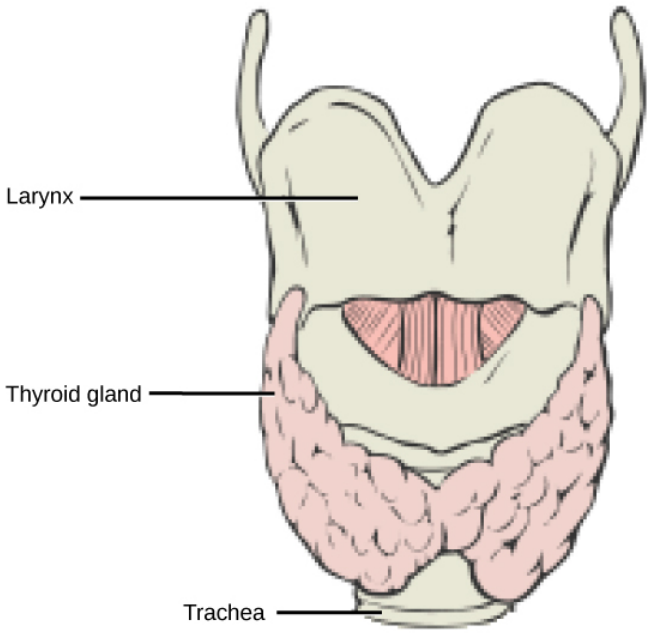


Figure **44.3.2.2**: This illustration shows the location of the thyroid gland.

The thyroid gland is made up of many spherical thyroid follicles, which are lined with a simple cuboidal epithelium. These follicles contain a viscous fluid, called colloid, which stores the glycoprotein thyroglobulin, the precursor to the thyroid hormones. The follicles produce hormones that can be stored in the colloid or released into the surrounding capillary network for transport to the rest of the body via the circulatory system.

Thyroid follicle cells synthesize the hormone thyroxine, which is also known as T_4 because it contains four atoms of iodine, and triiodothyronine, also known as T_3 because it contains three atoms of iodine. Follicle cells are stimulated to release stored T_3 and T_4

by thyroid stimulating hormone (TSH), which is produced by the anterior pituitary. These thyroid hormones increase the rates of mitochondrial ATP production.

A third hormone, calcitonin, is produced by parafollicular cells of the thyroid either releasing hormones or inhibiting hormones. Calcitonin release is not controlled by TSH, but instead is released when calcium ion concentrations in the blood rise. Calcitonin functions to help regulate calcium concentrations in body fluids. It acts in the bones to inhibit osteoclast activity and in the kidneys to stimulate excretion of calcium. The combination of these two events lowers body fluid levels of calcium.

Parathyroid Glands

Most people have four parathyroid glands; however, the number can vary from two to six. These glands are located on the posterior surface of the thyroid gland, as shown in Figure **44.3.2.3**. Normally, there is a superior gland and an inferior gland associated with each of the thyroid's two lobes. Each parathyroid gland is covered by connective tissue and contains many secretory cells that are associated with a capillary network.

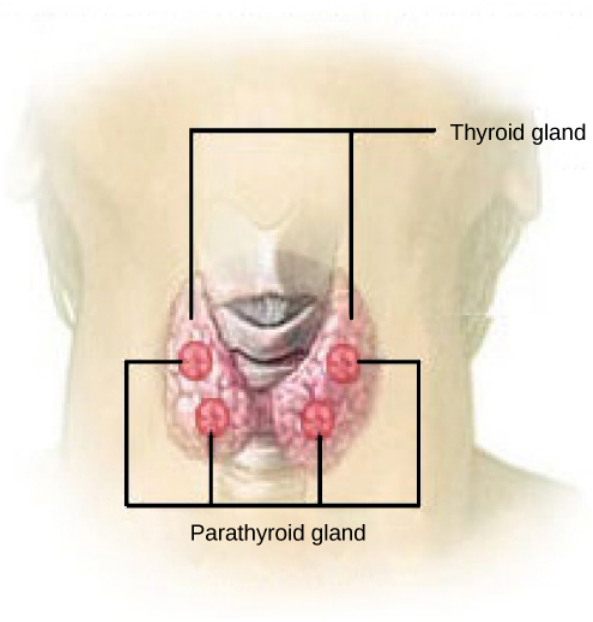


Figure **44.3.2.3**: The parathyroid glands are located on the posterior of the thyroid gland. (credit: modification of work by NCI)

The parathyroid glands produce parathyroid hormone (PTH). PTH increases blood calcium concentrations when calcium ion levels fall below normal. PTH (1) enhances reabsorption of Ca^{2+} by the kidneys, (2) stimulates osteoclast activity and inhibits osteoblast activity, and (3) it stimulates synthesis and secretion of calcitriol by the kidneys, which enhances Ca^{2+} absorption by the digestive system. PTH is produced by chief cells of the parathyroid. PTH and calcitonin work in opposition to one another to maintain homeostatic Ca^{2+} levels in body fluids. Another type of cells, oxyphil cells, exist in the parathyroid but their function is not known. These hormones encourage bone growth, muscle mass, and blood cell formation in children and women.

Adrenal Glands

The adrenal glands are associated with the kidneys; one gland is located on top of each kidney as illustrated in Figure **44.3.2.4**. The adrenal glands consist of an outer adrenal cortex and an inner adrenal medulla. These regions secrete different hormones.

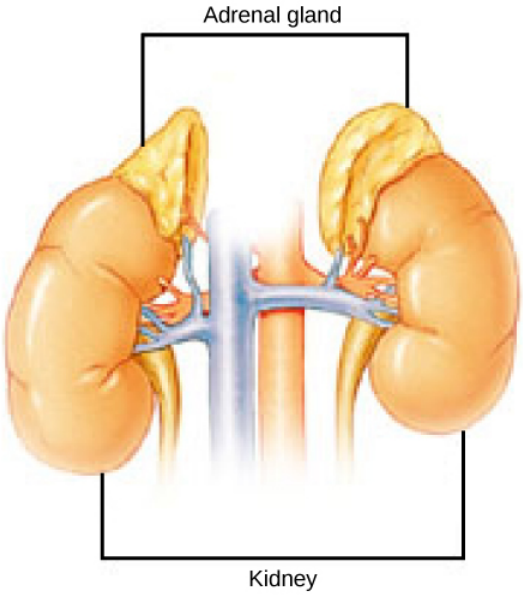


Figure **44.3.2.4**: The location of the adrenal glands on top of the kidneys is shown. (credit: modification of work by NCI)

Adrenal Cortex

The adrenal cortex is made up of layers of epithelial cells and associated capillary networks. These layers form three distinct regions: an outer zona glomerulosa that produces mineralocorticoids, a middle zona fasciculata that produces glucocorticoids, and an inner zona reticularis that produces androgens.

The main mineralocorticoid is aldosterone, which regulates the concentration of Na^+ ions in urine, sweat, pancreas, and saliva. Aldosterone release from the adrenal cortex is stimulated by a decrease in blood concentrations of sodium ions, blood volume, or blood pressure, or by an increase in blood potassium levels.

The three main glucocorticoids are cortisol, corticosterone, and cortisone. The glucocorticoids stimulate the synthesis of glucose and gluconeogenesis (converting a non-carbohydrate to glucose) by liver cells and they promote the release of fatty acids from adipose tissue. These hormones increase blood glucose levels to maintain levels within a normal range between meals. These hormones are secreted in response to ACTH and levels are regulated by negative feedback.

Androgens are sex hormones that promote masculinity. They are produced in small amounts by the adrenal cortex in both males and females. They do not affect sexual characteristics and may supplement sex hormones released from the gonads.

Adrenal Medulla

The adrenal medulla contains large, irregularly shaped cells that are closely associated with blood vessels. These cells are innervated by preganglionic autonomic nerve fibers from the central nervous system.

The adrenal medulla contains two types of secretory cells: one that produces epinephrine (adrenaline) and another that produces norepinephrine (noradrenaline). Epinephrine is the primary adrenal medulla hormone accounting for 75 to 80 percent of its secretions. Epinephrine and norepinephrine increase heart rate, breathing rate, cardiac muscle contractions, blood pressure, and blood glucose levels. They also accelerate the breakdown of glucose in skeletal muscles and stored fats in adipose tissue.

The release of epinephrine and norepinephrine is stimulated by neural impulses from the sympathetic nervous system. Secretion of these hormones is stimulated by acetylcholine release from preganglionic sympathetic fibers innervating the adrenal medulla. These neural impulses originate from the hypothalamus in response to stress to prepare the body for the fight-or-flight response.

Pancreas

The pancreas, illustrated in Figure **44.3.2.5**, is an elongated organ that is located between the stomach and the proximal portion of the small intestine. It contains both exocrine cells that excrete digestive enzymes and endocrine cells that release hormones. It is sometimes referred to as a heterocrine gland because it has both endocrine and exocrine functions.

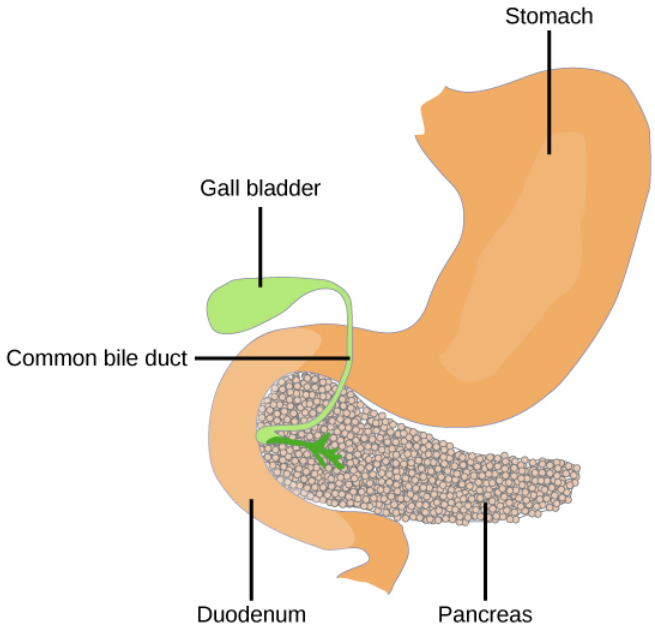


Figure **44.3.2.5**: The pancreas is found underneath the stomach and points toward the spleen. (credit: modification of work by NCI)

The endocrine cells of the pancreas form clusters called pancreatic islets or the islets of Langerhans, as visible in the micrograph shown in Figure **44.3.2.6**. The pancreatic islets contain two primary cell types: alpha cells, which produce the hormone glucagon, and beta cells, which produce the hormone insulin. These hormones regulate blood glucose levels. As blood glucose levels decline, alpha cells release glucagon to raise the blood glucose levels by increasing rates of glycogen breakdown and glucose release by the liver. When blood glucose levels rise, such as after a meal, beta cells release insulin to lower blood glucose levels by increasing the rate of glucose uptake in most body cells, and by increasing glycogen synthesis in skeletal muscles and the liver. Together, glucagon and insulin regulate blood glucose levels.

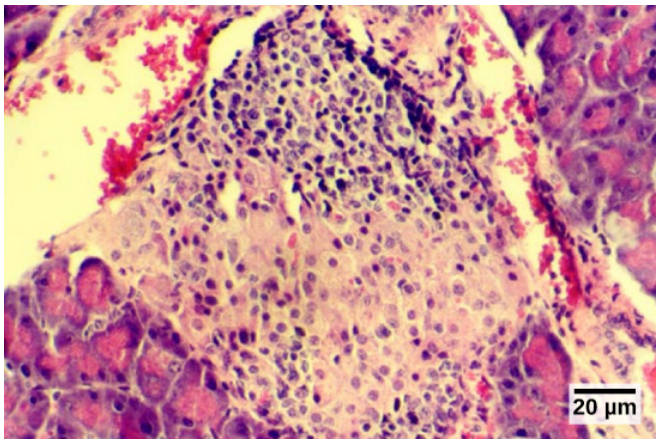


Figure **44.3.2.6**: The islets of Langerhans are clusters of endocrine cells found in the pancreas; they stain lighter than surrounding cells. (credit: modification of work by Muhammad T. Tabiin, Christopher P. White, Grant Morahan, and Bernard E. Tuch; scale-bar data from Matt Russell)

Pineal Gland

The pineal gland produces melatonin. The rate of melatonin production is affected by the photoperiod. Collaterals from the visual pathways innervate the pineal gland. During the day photoperiod, little melatonin is produced; however, melatonin production increases during the dark photoperiod (night). In some mammals, melatonin has an inhibitory affect on reproductive functions by decreasing production and maturation of sperm, oocytes, and reproductive organs. Melatonin is an effective antioxidant, protecting the CNS from free radicals such as nitric oxide and hydrogen peroxide. Lastly, melatonin is involved in biological rhythms, particularly circadian rhythms such as the sleep-wake cycle and eating habits.

Gonads

The gonads—the male testes and female ovaries—produce steroid hormones. The testes produce androgens, testosterone being the most prominent, which allow for the development of secondary sex characteristics and the production of sperm cells. The ovaries produce estradiol and progesterone, which cause secondary sex characteristics and prepare the body for childbirth.

Table 44.3.2.1: Endocrine Glands and their Associated Hormones

Endocrine Gland	Associated Hormones	Effect
Hypothalamus	releasing and inhibiting hormones	regulate hormone release from pituitary gland; produce oxytocin; produce uterine contractions and milk secretion in females
	antidiuretic hormone (ADH)	water reabsorption from kidneys; vasoconstriction to increase blood pressure
Pituitary (Anterior)	growth hormone (GH)	promotes growth of body tissues, protein synthesis; metabolic functions
	prolactin (PRL)	promotes milk production
	thyroid stimulating hormone (TSH)	stimulates thyroid hormone release
	adrenocorticotropic hormone (ACTH)	stimulates hormone release by adrenal cortex, glucocorticoids
	follicle-stimulating hormone (FSH)	stimulates gamete production (both ova and sperm); secretion of estradiol
	luteinizing hormone (LH)	stimulates androgen production by gonads; ovulation, secretion of progesterone
	melanocyte-stimulating hormone (MSH)	stimulates melanocytes of the skin increasing melanin pigment production.
Pituitary (Posterior)	antidiuretic hormone (ADH)	stimulates water reabsorption by kidneys
	oxytocin	stimulates uterine contractions during childbirth; milk ejection; stimulates ductus deferens and prostate gland contraction during emission
Thyroid	thyroxine, triiodothyronine	stimulate and maintain metabolism; growth and development
	calcitonin	reduces blood Ca^{2+} levels
Parathyroid	parathyroid hormone (PTH)	increases blood Ca^{2+} levels
Adrenal (Cortex)	aldosterone	increases blood Na^{+} levels; increase K^{+} secretion
	cortisol, corticosterone, cortisone	increase blood glucose levels; anti-inflammatory effects
Adrenal (Medulla)	epinephrine, norepinephrine	stimulate fight-or-flight response; increase blood gluclose levels; increase metabolic activities
Pancreas	insulin	reduces blood glucose levels
	glucagon	increases blood glucose levels
Pineal gland	melatonin	regulates some biological rhythms and protects CNS from free radicals
Testes	androgens	regulate, promote, increase or maintain sperm production; male secondary sexual characteristics
Ovaries	estrogen	promotes uterine lining growth; female

Endocrine Gland	Associated Hormones	Effect
		secondary sexual characteristics
	progestins	promote and maintain uterine lining growth

Organs with Secondary Endocrine Functions

There are several organs whose primary functions are non-endocrine but that also possess endocrine functions. These include the heart, kidneys, intestines, thymus, gonads, and adipose tissue.

The heart possesses endocrine cells in the walls of the atria that are specialized cardiac muscle cells. These cells release the hormone atrial natriuretic peptide (ANP) in response to increased blood volume. High blood volume causes the cells to be stretched, resulting in hormone release. ANP acts on the kidneys to reduce the reabsorption of Na^+, causing Na^+ and water to be excreted in the urine. ANP also reduces the amounts of renin released by the kidneys and aldosterone released by the adrenal cortex, further preventing the retention of water. In this way, ANP causes a reduction in blood volume and blood pressure, and reduces the concentration of Na^+ in the blood.

The gastrointestinal tract produces several hormones that aid in digestion. The endocrine cells are located in the mucosa of the GI tract throughout the stomach and small intestine. Some of the hormones produced include gastrin, secretin, and cholecystokinin, which are secreted in the presence of food, and some of which act on other organs such as the pancreas, gallbladder, and liver. They trigger the release of gastric juices, which help to break down and digest food in the GI tract.

While the adrenal glands associated with the kidneys are major endocrine glands, the kidneys themselves also possess endocrine function. Renin is released in response to decreased blood volume or pressure and is part of the renin-angiotensin-aldosterone system that leads to the release of aldosterone. Aldosterone then causes the retention of Na^+ and water, raising blood volume. The kidneys also release calcitriol, which aids in the absorption of Ca^{2+} and phosphate ions. Erythropoietin (EPO) is a protein hormone that triggers the formation of red blood cells in the bone marrow. EPO is released in response to low oxygen levels. Because red blood cells are oxygen carriers, increased production results in greater oxygen delivery throughout the body. EPO has been used by athletes to improve performance, as greater oxygen delivery to muscle cells allows for greater endurance. Because red blood cells increase the viscosity of blood, artificially high levels of EPO can cause severe health risks.

The thymus is found behind the sternum; it is most prominent in infants, becoming smaller in size through adulthood. The thymus produces hormones referred to as thymosins, which contribute to the development of the immune response.

Adipose tissue is a connective tissue found throughout the body. It produces the hormone leptin in response to food intake. Leptin increases the activity of anorexigenic neurons and decreases that of orexigenic neurons, producing a feeling of satiety after eating, thus affecting appetite and reducing the urge for further eating. Leptin is also associated with reproduction. It must be present for GnRH and gonadotropin synthesis to occur. Extremely thin females may enter puberty late; however, if adipose levels increase, more leptin will be produced, improving fertility.

Summary

The pituitary gland is located at the base of the brain and is attached to the hypothalamus by the infundibulum. The anterior pituitary receives products from the hypothalamus by the hypophyseal portal system and produces six hormones. The posterior pituitary is an extension of the brain and releases hormones (antidiuretic hormone and oxytocin) produced by the hypothalamus.

The thyroid gland is located in the neck and is composed of two lobes connected by the isthmus. The thyroid is made up of follicle cells that produce the hormones thyroxine and triiodothyronine. Parafollicular cells of the thyroid produce calcitonin. The parathyroid glands lie on the posterior surface of the thyroid gland and produce parathyroid hormone.

The adrenal glands are located on top of the kidneys and consist of the renal cortex and renal medulla. The adrenal cortex is the outer part of the adrenal gland and produces the corticosteroids, glucocorticoids, and mineralocorticoids. The adrenal medulla is the inner part of the adrenal gland and produces the catecholamines epinephrine and norepinephrine.

The pancreas lies in the abdomen between the stomach and the small intestine. Clusters of endocrine cells in the pancreas form the islets of Langerhans, which are composed of alpha cells that release glucagon and beta cells that release insulin.

Some organs possess endocrine activity as a secondary function but have another primary function. The heart produces the hormone atrial natriuretic peptide, which functions to reduce blood volume, pressure, and Na^+ concentration. The gastrointestinal tract produces various hormones that aid in digestion. The kidneys produce renin, calcitriol, and erythropoietin. Adipose tissue produces leptin, which promotes satiety signals in the brain.

Glossary

adrenal cortex
outer portion of adrenal glands that produces corticosteroids

adrenal gland
endocrine glands associated with the kidneys

adrenal medulla
inner portion of adrenal glands that produces epinephrine and norepinephrine

alpha cell
endocrine cell of the pancreatic islets that produces the hormone glucagon

anterior pituitary
portion of the pituitary gland that produces six hormones; also called adenohypophysis

atrial natriuretic peptide (ANP)
hormone produced by the heart to reduce blood volume, pressure, and Na^+ concentration

beta cell
endocrine cell of the pancreatic islets that produces the hormone insulin

colloid
fluid inside the thyroid gland that contains the glycoprotein thyroglobulin

endocrine gland
gland that secretes hormones into the surrounding interstitial fluid, which then diffuse into blood and are carried to various organs and tissues within the body

erythropoietin (EPO)
hormone produced by the kidneys to stimulate red blood cell production in the bone marrow

hypophyseal portal system
system of blood vessels that carries hormones from the hypothalamus to the anterior pituitary

islets of Langerhans (pancreatic islets)
endocrine cells of the pancreas

isthmus
tissue mass that connects the two lobes of the thyroid gland

leptin
hormone produced by adipose tissue that promotes feelings of satiety and reduces hunger

pancreas
organ located between the stomach and the small intestine that contains exocrine and endocrine cells

parafollicular cell

thyroid cell that produces the hormone calcitonin

parathyroid gland
gland located on the surface of the thyroid that produces parathyroid hormone

pituitary gland
endocrine gland located at the base of the brain composed of an anterior and posterior region; also called hypophysis

pituitary stalk
(also, infundibulum) stalk that connects the pituitary gland to the hypothalamus

posterior pituitary
extension of the brain that releases hormones produced by the hypothalamus; along with the infundibulum, it is also referred to as the neurohypophysis

thymus
gland located behind the sternum that produces thymosin hormones that contribute to the development of the immune system

thyroid gland
endocrine gland located in the neck that produces thyroid hormones thyroxine and triiodothyronine

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44.4: The Major Peripheral Endocrine Glands

Skills to Develop

- Explain how hormones regulate the excretory system
- Discuss the role of hormones in the reproductive system
- Describe how hormones regulate metabolism
- Explain the role of hormones in different diseases

Hormones have a wide range of effects and modulate many different body processes. The key regulatory processes that will be examined here are those affecting the excretory system, the reproductive system, metabolism, blood calcium concentrations, growth, and the stress response.

Hormonal Regulation of the Excretory System

Maintaining a proper water balance in the body is important to avoid dehydration or over-hydration (hyponatremia). The water concentration of the body is monitored by osmoreceptors in the hypothalamus, which detect the concentration of electrolytes in the extracellular fluid. The concentration of electrolytes in the blood rises when there is water loss caused by excessive perspiration, inadequate water intake, or low blood volume due to blood loss. An increase in blood electrolyte levels results in a neuronal signal being sent from the osmoreceptors in hypothalamic nuclei. The pituitary gland has two components: anterior and posterior. The anterior pituitary is composed of glandular cells that secrete protein hormones. The posterior pituitary is an extension of the hypothalamus. It is composed largely of neurons that are continuous with the hypothalamus.

The hypothalamus produces a polypeptide hormone known as antidiuretic hormone (ADH), which is transported to and released from the posterior pituitary gland. The principal action of ADH is to regulate the amount of water excreted by the kidneys. As ADH (which is also known as vasopressin) causes direct water reabsorption from the kidney tubules, salts and wastes are concentrated in what will eventually be excreted as urine. The hypothalamus controls the mechanisms of ADH secretion, either by regulating blood volume or the concentration of water in the blood. Dehydration or physiological stress can cause an increase of osmolarity above 300 mOsm/L, which in turn, raises ADH secretion and water will be retained, causing an increase in blood pressure. ADH travels in the bloodstream to the kidneys. Once at the kidneys, ADH changes the kidneys to become more permeable to water by temporarily inserting water channels, aquaporins, into the kidney tubules. Water moves out of the kidney tubules through the aquaporins, reducing urine volume. The water is reabsorbed into the capillaries lowering blood osmolarity back toward normal. As blood osmolarity decreases, a negative feedback mechanism reduces osmoreceptor activity in the hypothalamus, and ADH secretion is reduced. ADH release can be reduced by certain substances, including alcohol, which can cause increased urine production and dehydration.

Chronic underproduction of ADH or a mutation in the ADH receptor results in diabetes insipidus. If the posterior pituitary does not release enough ADH, water cannot be retained by the kidneys and is lost as urine. This causes increased thirst, but water taken in is lost again and must be continually consumed. If the condition is not severe, dehydration may not occur, but severe cases can lead to electrolyte imbalances due to dehydration.

Another hormone responsible for maintaining electrolyte concentrations in extracellular fluids is aldosterone, a steroid hormone that is produced by the adrenal cortex. In contrast to ADH, which promotes the reabsorption of water to maintain proper water balance, aldosterone maintains proper water balance by enhancing Na^+ reabsorption and K^+ secretion from extracellular fluid of the cells in kidney tubules. Because it is produced in the cortex of the adrenal gland and affects the concentrations of minerals Na^+ and K^+, aldosterone is referred to as a mineralocorticoid, a corticosteroid that affects ion and water balance. Aldosterone release is stimulated by a decrease in blood sodium levels, blood volume, or blood pressure, or an increase in blood potassium levels. It also prevents the loss of Na^+ from sweat, saliva, and gastric juice. The reabsorption of Na^+ also results in the osmotic reabsorption of water, which alters blood volume and blood pressure.

Aldosterone production can be stimulated by low blood pressure, which triggers a sequence of chemical release, as illustrated in Figure **44.4.1**. When blood pressure drops, the renin-angiotensin-aldosterone system (RAAS) is activated. Cells in the juxtaglomerular apparatus, which regulates the functions of the nephrons of the kidney, detect this and release renin. Renin, an

enzyme, circulates in the blood and reacts with a plasma protein produced by the liver called angiotensinogen. When angiotensinogen is cleaved by renin, it produces angiotensin I, which is then converted into angiotensin II in the lungs. Angiotensin II functions as a hormone and then causes the release of the hormone aldosterone by the adrenal cortex, resulting in increased Na^+ reabsorption, water retention, and an increase in blood pressure. Angiotensin II in addition to being a potent vasoconstrictor also causes an increase in ADH and increased thirst, both of which help to raise blood pressure.

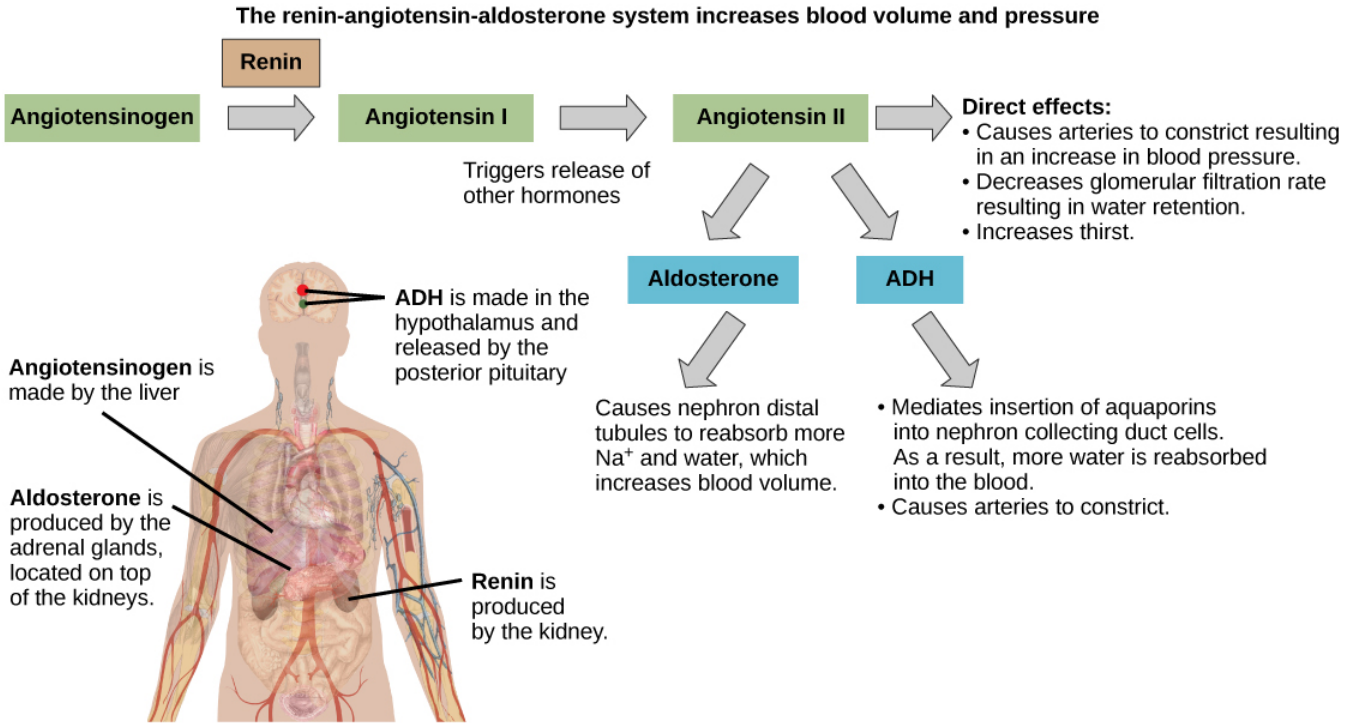


Figure **44.4.1**: ADH and aldosterone increase blood pressure and volume. Angiotensin II stimulates release of these hormones. Angiotensin II, in turn, is formed when renin cleaves angiotensinogen. (credit: modification of work by Mikael Häggström).

Hormonal Regulation of the Reproductive System

Regulation of the reproductive system is a process that requires the action of hormones from the pituitary gland, the adrenal cortex, and the gonads. During puberty in both males and females, the hypothalamus produces gonadotropin-releasing hormone (GnRH), which stimulates the production and release of *follicle-stimulating hormone (FSH)* and *luteinizing hormone (LH)* from the anterior pituitary gland. These hormones regulate the gonads (testes in males and ovaries in females) and therefore are called gonadotropins. In both males and females, FSH stimulates gamete production and LH stimulates production of hormones by the gonads. An increase in gonad hormone levels inhibits GnRH production through a negative feedback loop.

Regulation of the Male Reproductive System

In males, FSH stimulates the maturation of sperm cells. FSH production is inhibited by the hormone inhibin, which is released by the testes. LH stimulates production of the sex hormones (androgens) by the interstitial cells of the testes and therefore is also called interstitial cell-stimulating hormone. The most widely known androgen in males is *testosterone*. Testosterone promotes the production of sperm and masculine characteristics. The adrenal cortex also produces small amounts of testosterone precursor, although the role of this additional hormone production is not fully understood.

Everyday Connection: The Dangers of Synthetic Hormones

Some athletes attempt to boost their performance by using artificial hormones that enhance muscle performance. Anabolic steroids, a form of the male sex hormone testosterone, are one of the most widely known performance-enhancing drugs. Steroids are used to help build muscle mass. Other hormones that are used to enhance athletic performance include *erythropoietin*, which triggers the production of red blood cells, and human growth hormone, which can help in building muscle mass. Most performance enhancing drugs are illegal for non-medical purposes. They are also banned by national and

international governing bodies including the International Olympic Committee, the U.S. Olympic Committee, the National Collegiate Athletic Association, the Major League Baseball, and the National Football League.



Figure **44.4.2**: Professional baseball player Jason Giambi publically admitted to, and apologized for, his use of anabolic steroids supplied by a trainer. (credit: Bryce Edwards)

The side effects of synthetic hormones are often significant and non-reversible, and in some cases, fatal. Androgens produce several complications such as liver dysfunctions and liver tumors, prostate gland enlargement, difficulty urinating, premature closure of epiphyseal cartilages, testicular atrophy, infertility, and immune system depression. The physiological strain caused by these substances is often greater than what the body can handle, leading to unpredictable and dangerous effects and linking their use to heart attacks, strokes, and impaired cardiac function.

Regulation of the Female Reproductive System

In females, FSH stimulates development of egg cells, called ova, which develop in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production. LH also plays a role in the development of ova, induction of ovulation, and stimulation of estradiol and progesterone production by the ovaries, as illustrated in Figure **44.4.3**. Estradiol and progesterone are steroid hormones that prepare the body for pregnancy. Estradiol produces secondary sex characteristics in females, while both estradiol and progesterone regulate the menstrual cycle.

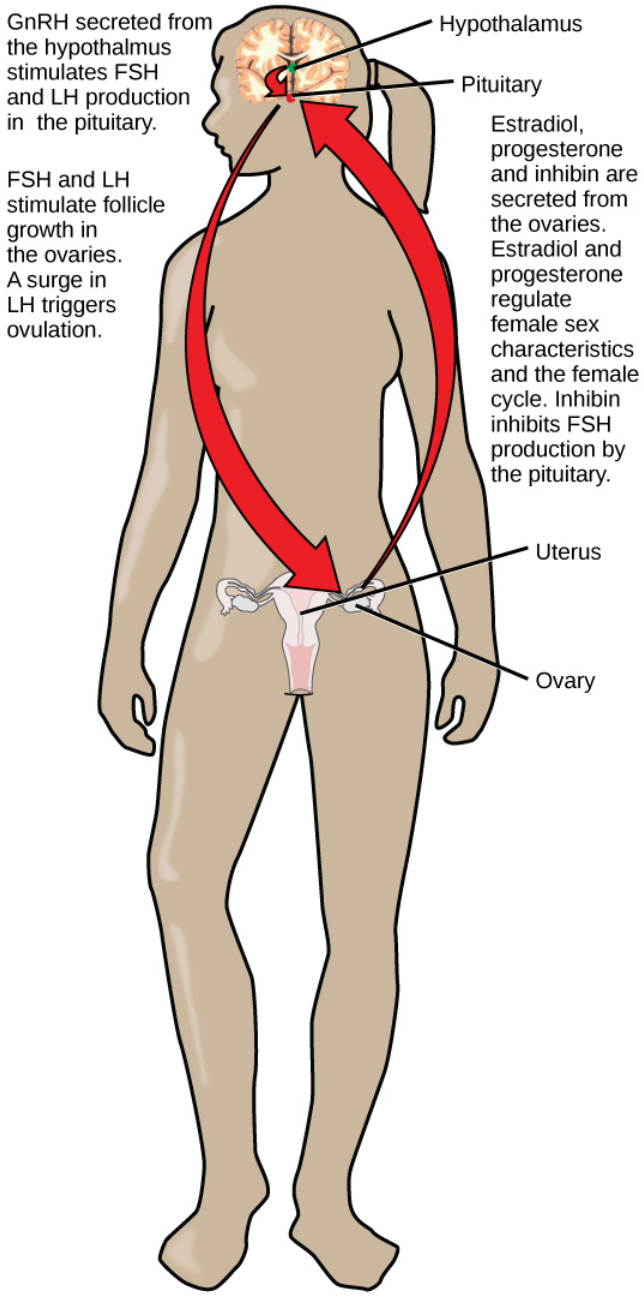


Figure 44.4.3: Hormonal regulation of the female reproductive system involves hormones from the hypothalamus, pituitary, and ovaries.

In addition to producing FSH and LH, the anterior portion of the pituitary gland also produces the hormone prolactin (PRL) in females. Prolactin stimulates the production of milk by the mammary glands following childbirth. Prolactin levels are regulated by the hypothalamic hormones prolactin-releasing hormone (PRH) and prolactin-inhibiting hormone (PIH), which is now known to be dopamine. PRH stimulates the release of prolactin and PIH inhibits it.

The posterior pituitary releases the hormone oxytocin, which stimulates uterine contractions during childbirth. The uterine smooth muscles are not very sensitive to oxytocin until late in pregnancy when the number of oxytocin receptors in the uterus peaks. Stretching of tissues in the uterus and cervix stimulates oxytocin release during childbirth. Contractions increase in intensity as blood levels of oxytocin rise via a positive feedback mechanism until the birth is complete. Oxytocin also stimulates the contraction of myoepithelial cells around the milk-producing mammary glands. As these cells contract, milk is forced from the secretory alveoli into milk ducts and is ejected from the breasts in milk ejection (“let-down”) reflex. Oxytocin release is stimulated by the

suckling of an infant, which triggers the synthesis of oxytocin in the hypothalamus and its release into circulation at the posterior pituitary.

Hormonal Regulation of Metabolism

Blood glucose levels vary widely over the course of a day as periods of food consumption alternate with periods of fasting. Insulin and glucagon are the two hormones primarily responsible for maintaining homeostasis of blood glucose levels. Additional regulation is mediated by the thyroid hormones.

Regulation of Blood Glucose Levels by Insulin and Glucagon

Cells of the body require nutrients in order to function, and these nutrients are obtained through feeding. In order to manage nutrient intake, storing excess intake and utilizing reserves when necessary, the body uses hormones to moderate energy stores. Insulin is produced by the beta cells of the pancreas, which are stimulated to release insulin as blood glucose levels rise (for example, after a meal is consumed). Insulin lowers blood glucose levels by enhancing the rate of glucose uptake and utilization by target cells, which use glucose for ATP production. It also stimulates the liver to convert glucose to glycogen, which is then stored by cells for later use. Insulin also increases glucose transport into certain cells, such as muscle cells and the liver. This results from an insulin-mediated increase in the number of glucose transporter proteins in cell membranes, which remove glucose from circulation by facilitated diffusion. As insulin binds to its target cell via insulin receptors and signal transduction, it triggers the cell to incorporate glucose transport proteins into its membrane. This allows glucose to enter the cell, where it can be used as an energy source. However, this does not occur in all cells: some cells, including those in the kidneys and brain, can access glucose without the use of insulin. Insulin also stimulates the conversion of glucose to fat in adipocytes and the synthesis of proteins. These actions mediated by insulin cause blood glucose concentrations to fall, called a hypoglycemic “low sugar” effect, which inhibits further insulin release from beta cells through a negative feedback loop.

Link to Learning



This animation describes the role of insulin and the pancreas in diabetes.

Impaired insulin function can lead to a condition called diabetes mellitus, the main symptoms of which are illustrated in Figure 44.4.4. This can be caused by low levels of insulin production by the beta cells of the pancreas, or by reduced sensitivity of tissue cells to insulin. This prevents glucose from being absorbed by cells, causing high levels of blood glucose, or hyperglycemia (high sugar). High blood glucose levels make it difficult for the kidneys to recover all the glucose from nascent urine, resulting in glucose being lost in urine. High glucose levels also result in less water being reabsorbed by the kidneys, causing high amounts of urine to be produced; this may result in dehydration. Over time, high blood glucose levels can cause nerve damage to the eyes and peripheral body tissues, as well as damage to the kidneys and cardiovascular system. Oversecretion of insulin can cause hypoglycemia, low blood glucose levels. This causes insufficient glucose availability to cells, often leading to muscle weakness, and can sometimes cause unconsciousness or death if left untreated.

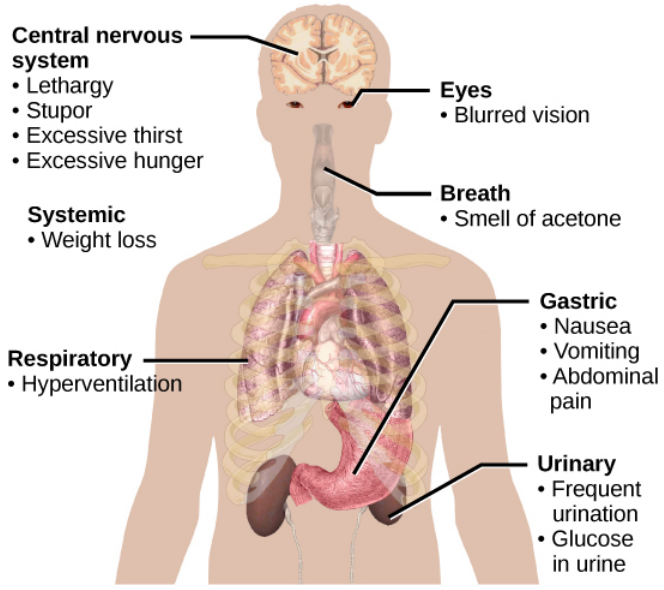


Figure **44.4.4**: The main symptoms of diabetes are shown. (credit: modification of work by Mikael Häggström)

When blood glucose levels decline below normal levels, for example between meals or when glucose is utilized rapidly during exercise, the hormone glucagon is released from the alpha cells of the pancreas. Glucagon raises blood glucose levels, eliciting what is called a hyperglycemic effect, by stimulating the breakdown of glycogen to glucose in skeletal muscle cells and liver cells in a process called glycogenolysis. Glucose can then be utilized as energy by muscle cells and released into circulation by the liver cells. Glucagon also stimulates absorption of amino acids from the blood by the liver, which then converts them to glucose. This process of glucose synthesis is called gluconeogenesis. Glucagon also stimulates adipose cells to release fatty acids into the blood. These actions mediated by glucagon result in an increase in blood glucose levels to normal homeostatic levels. Rising blood glucose levels inhibit further glucagon release by the pancreas via a negative feedback mechanism. In this way, insulin and glucagon work together to maintain homeostatic glucose levels, as shown in Figure **44.4.5**.

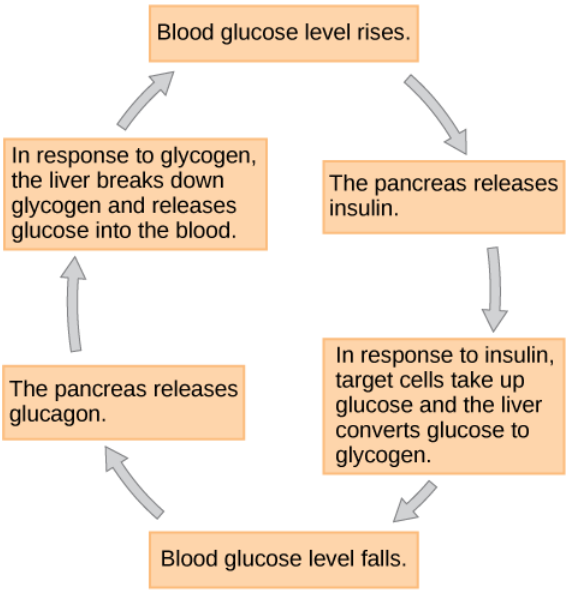


Figure **44.4.5**: Insulin and glucagon regulate blood glucose levels.

Exercise

Pancreatic tumors may cause excess secretion of glucagon. Type I diabetes results from the failure of the pancreas to produce insulin. Which of the following statement about these two conditions is true?

A. A pancreatic tumor and type I diabetes will have the opposite effects on blood sugar levels.

B. A pancreatic tumor and type I diabetes will both cause hyperglycemia.
C. A pancreatic tumor and type I diabetes will both cause hypoglycemia.
D. Both pancreatic tumors and type I diabetes result in the inability of cells to take up glucose.

Answer

B

Regulation of Blood Glucose Levels by Thyroid Hormones

The basal metabolic rate, which is the amount of calories required by the body at rest, is determined by two hormones produced by the thyroid gland: thyroxine, also known as tetraiodothyronine or T_4, and triiodothyronine, also known as T_3. These hormones affect nearly every cell in the body except for the adult brain, uterus, testes, blood cells, and spleen. They are transported across the plasma membrane of target cells and bind to receptors on the mitochondria resulting in increased ATP production. In the nucleus, T_3 and T_4 activate genes involved in energy production and glucose oxidation. This results in increased rates of metabolism and body heat production, which is known as the hormone's calorigenic effect.

T_3 and T_4 release from the thyroid gland is stimulated by thyroid-stimulating hormone (TSH), which is produced by the anterior pituitary. TSH binding at the receptors of the follicle of the thyroid triggers the production of T_3 and T_4 from a glycoprotein called thyroglobulin. Thyroglobulin is present in the follicles of the thyroid, and is converted into thyroid hormones with the addition of iodine. Iodine is formed from iodide ions that are actively transported into the thyroid follicle from the bloodstream. A peroxidase enzyme then attaches the iodine to the tyrosine amino acid found in thyroglobulin. T_3 has three iodine ions attached, while T_4 has four iodine ions attached. T_3 and T_4 are then released into the bloodstream, with T_4 being released in much greater amounts than T_3. As T_3 is more active than T_4 and is responsible for most of the effects of thyroid hormones, tissues of the body convert T_4 to T_3 by the removal of an iodine ion. Most of the released T_3 and T_4 becomes attached to transport proteins in the bloodstream and is unable to cross the plasma membrane of cells. These protein-bound molecules are only released when blood levels of the unattached hormone begin to decline. In this way, a week's worth of reserve hormone is maintained in the blood. Increased T_3 and T_4 levels in the blood inhibit the release of TSH, which results in lower T_3 and T_4 release from the thyroid.

The follicular cells of the thyroid require iodides (anions of iodine) in order to synthesize T_3 and T_4. Iodides obtained from the diet are actively transported into follicle cells resulting in a concentration that is approximately 30 times higher than in blood. The typical diet in North America provides more iodine than required due to the addition of iodide to table salt. Inadequate iodine intake, which occurs in many developing countries, results in an inability to synthesize T_3 and T_4 hormones. The thyroid gland enlarges in a condition called goiter, which is caused by overproduction of TSH without the formation of thyroid hormone. Thyroglobulin is contained in a fluid called colloid, and TSH stimulation results in higher levels of colloid accumulation in the thyroid. In the absence of iodine, this is not converted to thyroid hormone, and colloid begins to accumulate more and more in the thyroid gland, leading to goiter.

Disorders can arise from both the underproduction and overproduction of thyroid hormones. Hypothyroidism, underproduction of the thyroid hormones, can cause a low metabolic rate leading to weight gain, sensitivity to cold, and reduced mental activity, among other symptoms. In children, hypothyroidism can cause cretinism, which can lead to mental retardation and growth defects. Hyperthyroidism, the overproduction of thyroid hormones, can lead to an increased metabolic rate and its effects: weight loss, excess heat production, sweating, and an increased heart rate. Graves' disease is one example of a hyperthyroid condition.

Hormonal Control of Blood Calcium Levels

Regulation of blood calcium concentrations is important for generation of muscle contractions and nerve impulses, which are electrically stimulated. If calcium levels get too high, membrane permeability to sodium decreases and membranes become less responsive. If calcium levels get too low, membrane permeability to sodium increases and convulsions or muscle spasms can result.

Blood calcium levels are regulated by parathyroid hormone (PTH), which is produced by the parathyroid glands, as illustrated in Figure **44.4.6**. PTH is released in response to low blood Ca^{2+} levels. PTH increases Ca^{2+} levels by targeting the skeleton, the kidneys, and the intestine. In the skeleton, PTH stimulates osteoclasts, which causes bone to be reabsorbed, releasing Ca^{2+} from bone into the blood. PTH also inhibits osteoblasts, reducing Ca^{2+} deposition in bone. In the intestines, PTH increases dietary Ca^{2+} absorption, and in the kidneys, PTH stimulates reabsorption of the CA^{2+}. While PTH acts directly on the kidneys to increase Ca^{2+}

reabsorption, its effects on the intestine are indirect. PTH triggers the formation of calcitriol, an active form of vitamin D, which acts on the intestines to increase absorption of dietary calcium. PTH release is inhibited by rising blood calcium levels.

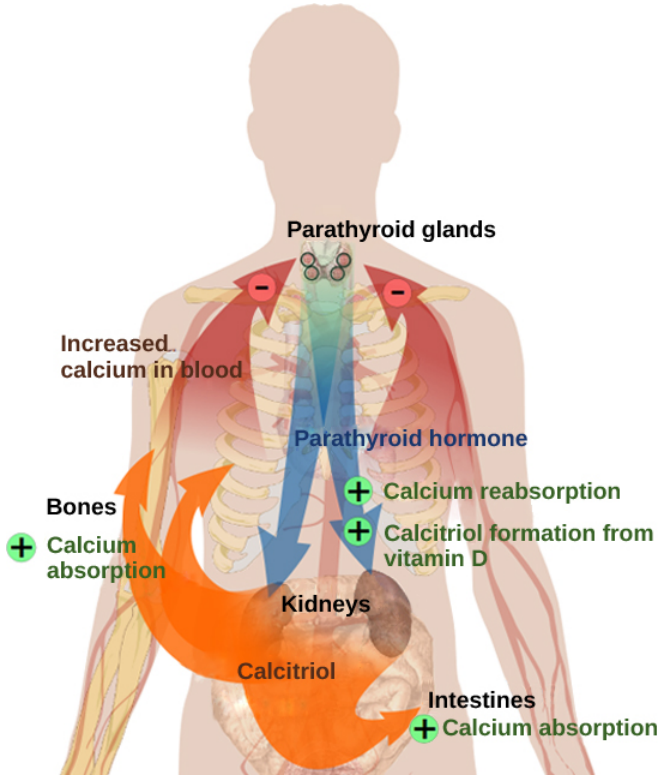


Figure 44.4.6: Parathyroid hormone (PTH) is released in response to low blood calcium levels. It increases blood calcium levels by targeting the skeleton, the kidneys, and the intestine. (credit: modification of work by Mikael Häggström)

Hyperparathyroidism results from an overproduction of parathyroid hormone. This results in excessive calcium being removed from bones and introduced into blood circulation, producing structural weakness of the bones, which can lead to deformation and fractures, plus nervous system impairment due to high blood calcium levels. Hypoparathyroidism, the underproduction of PTH, results in extremely low levels of blood calcium, which causes impaired muscle function and may result in tetany (severe sustained muscle contraction).

The hormone calcitonin, which is produced by the parafollicular or C cells of the thyroid, has the opposite effect on blood calcium levels as does PTH. Calcitonin decreases blood calcium levels by inhibiting osteoclasts, stimulating osteoblasts, and stimulating calcium excretion by the kidneys. This results in calcium being added to the bones to promote structural integrity. Calcitonin is most important in children (when it stimulates bone growth), during pregnancy (when it reduces maternal bone loss), and during prolonged starvation (because it reduces bone mass loss). In healthy nonpregnant, unstarved adults, the role of calcitonin is unclear.

Hormonal Regulation of Growth

Hormonal regulation is required for the growth and replication of most cells in the body. Growth hormone (GH), produced by the anterior portion of the pituitary gland, accelerates the rate of protein synthesis, particularly in skeletal muscle and bones. Growth hormone has direct and indirect mechanisms of action. The first direct action of GH is stimulation of triglyceride breakdown (lipolysis) and release into the blood by adipocytes. This results in a switch by most tissues from utilizing glucose as an energy source to utilizing fatty acids. This process is called a glucose-sparing effect. In another direct mechanism, GH stimulates glycogen breakdown in the liver; the glycogen is then released into the blood as glucose. Blood glucose levels increase as most tissues are utilizing fatty acids instead of glucose for their energy needs. The GH mediated increase in blood glucose levels is called a diabetogenic effect because it is similar to the high blood glucose levels seen in diabetes mellitus.

The indirect mechanism of GH action is mediated by insulin-like growth factors (IGFs) or somatomedins, which are a family of growth-promoting proteins produced by the liver, which stimulates tissue growth. IGFs stimulate the uptake of amino acids from the blood, allowing the formation of new proteins, particularly in skeletal muscle cells, cartilage cells, and other target cells, as

shown in Figure **44.4.7**. This is especially important after a meal, when glucose and amino acid concentration levels are high in the blood. GH levels are regulated by two hormones produced by the hypothalamus. GH release is stimulated by growth hormone-releasing hormone (GHRH) and is inhibited by growth hormone-inhibiting hormone (GHIH), also called somatostatin.

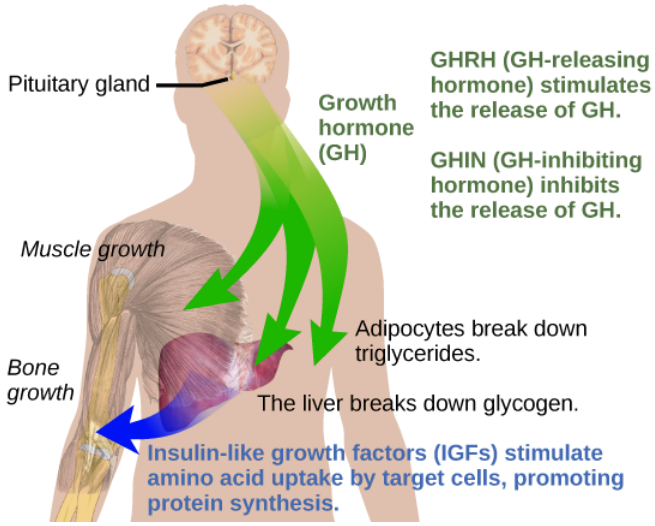


Figure **44.4.7**: Growth hormone directly accelerates the rate of protein synthesis in skeletal muscle and bones. Insulin-like growth factor 1 (IGF-1) is activated by growth hormone and also allows formation of new proteins in muscle cells and bone. (credit: modification of work by Mikael Häggström)

A balanced production of growth hormone is critical for proper development. Underproduction of GH in adults does not appear to cause any abnormalities, but in children it can result in pituitary dwarfism, in which growth is reduced. Pituitary dwarfism is characterized by symmetric body formation. In some cases, individuals are under 30 inches in height. Oversecretion of growth hormone can lead to gigantism in children, causing excessive growth. In some documented cases, individuals can reach heights of over eight feet. In adults, excessive GH can lead to acromegaly, a condition in which there is enlargement of bones in the face, hands, and feet that are still capable of growth.

Hormonal Regulation of Stress

When a threat or danger is perceived, the body responds by releasing hormones that will ready it for the “fight-or-flight” response. The effects of this response are familiar to anyone who has been in a stressful situation: increased heart rate, dry mouth, and hair standing up.

Evolution Connection: Fight-or-Flight Response

Interactions of the endocrine hormones have evolved to ensure the body’s internal environment remains stable. Stressors are stimuli that disrupt homeostasis. The sympathetic division of the vertebrate autonomic nervous system has evolved the fight-or-flight response to counter stress-induced disruptions of homeostasis. In the initial alarm phase, the sympathetic nervous system stimulates an increase in energy levels through increased blood glucose levels. This prepares the body for physical activity that may be required to respond to stress: to either fight for survival or to flee from danger.

However, some stresses, such as illness or injury, can last for a long time. Glycogen reserves, which provide energy in the short-term response to stress, are exhausted after several hours and cannot meet long-term energy needs. If glycogen reserves were the only energy source available, neural functioning could not be maintained once the reserves became depleted due to the nervous system’s high requirement for glucose. In this situation, the body has evolved a response to counter long-term stress through the actions of the glucocorticoids, which ensure that long-term energy requirements can be met. The glucocorticoids mobilize lipid and protein reserves, stimulate gluconeogenesis, conserve glucose for use by neural tissue, and stimulate the conservation of salts and water. The mechanisms to maintain homeostasis that are described here are those observed in the human body. However, the fight-or-flight response exists in some form in all vertebrates.

The sympathetic nervous system regulates the stress response via the hypothalamus. Stressful stimuli cause the hypothalamus to signal the adrenal medulla (which mediates short-term stress responses) via nerve impulses, and the adrenal cortex, which

mediates long-term stress responses, via the hormone adrenocorticotropic hormone (ACTH), which is produced by the anterior pituitary.

Short-term Stress Response

When presented with a stressful situation, the body responds by calling for the release of hormones that provide a burst of energy. The hormones epinephrine (also known as adrenaline) and norepinephrine (also known as noradrenaline) are released by the adrenal medulla. How do these hormones provide a burst of energy? Epinephrine and norepinephrine increase blood glucose levels by stimulating the liver and skeletal muscles to break down glycogen and by stimulating glucose release by liver cells. Additionally, these hormones increase oxygen availability to cells by increasing the heart rate and dilating the bronchioles. The hormones also prioritize body function by increasing blood supply to essential organs such as the heart, brain, and skeletal muscles, while restricting blood flow to organs not in immediate need, such as the skin, digestive system, and kidneys. Epinephrine and norepinephrine are collectively called catecholamines.

Link to Learning



Watch this Discovery Channel animation describing the flight-or-flight response.

Long-term Stress Response

Long-term stress response differs from short-term stress response. The body cannot sustain the bursts of energy mediated by epinephrine and norepinephrine for long times. Instead, other hormones come into play. In a long-term stress response, the hypothalamus triggers the release of ACTH from the anterior pituitary gland. The adrenal cortex is stimulated by ACTH to release steroid hormones called corticosteroids. Corticosteroids turn on transcription of certain genes in the nuclei of target cells. They change enzyme concentrations in the cytoplasm and affect cellular metabolism. There are two main corticosteroids: glucocorticoids such as cortisol, and mineralocorticoids such as aldosterone. These hormones target the breakdown of fat into fatty acids in the adipose tissue. The fatty acids are released into the bloodstream for other tissues to use for ATP production. The glucocorticoids primarily affect glucose metabolism by stimulating glucose synthesis. Glucocorticoids also have anti-inflammatory properties through inhibition of the immune system. For example, cortisone is used as an anti-inflammatory medication; however, it cannot be used long term as it increases susceptibility to disease due to its immune-suppressing effects.

Mineralocorticoids function to regulate ion and water balance of the body. The hormone aldosterone stimulates the reabsorption of water and sodium ions in the kidney, which results in increased blood pressure and volume.

Hypersecretion of glucocorticoids can cause a condition known as Cushing's disease, characterized by a shifting of fat storage areas of the body. This can cause the accumulation of adipose tissue in the face and neck, and excessive glucose in the blood.

Hyposecretion of the corticosteroids can cause Addison's disease, which may result in bronzing of the skin, hypoglycemia, and low electrolyte levels in the blood.

Summary

Water levels in the body are controlled by antidiuretic hormone (ADH), which is produced in the hypothalamus and triggers the reabsorption of water by the kidneys. Underproduction of ADH can cause diabetes insipidus. Aldosterone, a hormone produced by the adrenal cortex of the kidneys, enhances Na^+ reabsorption from the extracellular fluids and subsequent water reabsorption by diffusion. The renin-angiotensin-aldosterone system is one way that aldosterone release is controlled.

The reproductive system is controlled by the gonadotropins follicle-stimulating hormone (FSH) and luteinizing hormone (LH), which are produced by the pituitary gland. Gonadotropin release is controlled by the hypothalamic hormone gonadotropin-releasing hormone (GnRH). FSH stimulates the maturation of sperm cells in males and is inhibited by the hormone inhibin, while LH stimulates the production of the androgen testosterone. FSH stimulates egg maturation in females, while LH stimulates the production of estrogens and progesterone. Estrogens are a group of steroid hormones produced by the ovaries that trigger the development of secondary sex characteristics in females as well as control the maturation of the ova. In females, the pituitary also produces prolactin, which stimulates milk production after childbirth, and oxytocin, which stimulates uterine contraction during childbirth and milk let-down during suckling.

Insulin is produced by the pancreas in response to rising blood glucose levels and allows cells to utilize blood glucose and store excess glucose for later use. Diabetes mellitus is caused by reduced insulin activity and causes high blood glucose levels, or hyperglycemia. Glucagon is released by the pancreas in response to low blood glucose levels and stimulates the breakdown of glycogen into glucose, which can be used by the body. The body's basal metabolic rate is controlled by the thyroid hormones thyroxine (T_4) and triiodothyronine (T_3). The anterior pituitary produces thyroid stimulating hormone (TSH), which controls the release of T_3 and T_4 from the thyroid gland. Iodine is necessary in the production of thyroid hormone, and the lack of iodine can lead to a condition called goiter.

Parathyroid hormone (PTH) is produced by the parathyroid glands in response to low blood Ca^{2+} levels. The parafollicular cells of the thyroid produce calcitonin, which reduces blood Ca^{2+} levels. Growth hormone (GH) is produced by the anterior pituitary and controls the growth rate of muscle and bone. GH action is indirectly mediated by insulin-like growth factors (IGFs). Short-term stress causes the hypothalamus to trigger the adrenal medulla to release epinephrine and norepinephrine, which trigger the fight or flight response. Long-term stress causes the hypothalamus to trigger the anterior pituitary to release adrenocorticotropic hormone (ACTH), which causes the release of corticosteroids, glucocorticoids, and mineralocorticoids, from the adrenal cortex.

Glossary

acromegaly
: condition caused by overproduction of GH in adults

Addison's disease
: disorder caused by the hyposecretion of corticosteroids

adrenocorticotropic hormone (ACTH)
: hormone released by the anterior pituitary, which stimulates the adrenal cortex to release corticosteroids during the long-term stress response

aldosterone
: steroid hormone produced by the adrenal cortex that stimulates the reabsorption of Na^+ from extracellular fluids and secretion of K^+.

androgen
: male sex hormone such as testosterone

antidiuretic hormone (ADH)

hormone produced by the hypothalamus and released by the posterior pituitary that increases water reabsorption by the kidneys

calcitonin
hormone produced by the parafollicular cells of the thyroid gland that functions to lower blood Ca^{2+} levels and promote bone growth

corticosteroid
hormone released by the adrenal cortex in response to long-term stress

cortisol
glucocorticoid produced in response to stress

Cushing's disease
disorder caused by the hypersecretion of glucocorticoids

diabetes insipidus
disorder caused by underproduction of ADH

diabetes mellitus
disorder caused by low levels of insulin activity

diabetogenic effect
effect of GH that causes blood glucose levels to rise similar to diabetes mellitus

epinephrine
hormone released by the adrenal medulla in response to a short term stress

estrogens
- a group of steroid hormones, including estradiol and several others, that are produced by the ovaries and elicit secondary sex characteristics in females as well as control the maturation of the ova

follicle-stimulating hormone (FSH)
hormone produced by the anterior pituitary that stimulates gamete production

gigantism
condition caused by overproduction of GH in children

glucagon
hormone produced by the alpha cells of the pancreas in response to low blood sugar; functions to raise blood sugar levels

glucocorticoid
corticosteroid that affects glucose metabolism

gluconeogenesis
synthesis of glucose from amino acids

glucose-sparing effect
effect of GH that causes tissues to use fatty acids instead of glucose as an energy source

glycogenolysis
breakdown of glycogen into glucose

goiter
enlargement of the thyroid gland caused by insufficient dietary iodine levels

gonadotropin
hormone that regulates the gonads, including FSH and LH

growth hormone (GH)
hormone produced by the anterior pituitary that promotes protein synthesis and body growth

growth hormone-inhibiting hormone (GHIH)
hormone produced by the hypothalamus that inhibits growth hormone production, also called somatostatin

growth hormone-releasing hormone (GHRH)
hormone released by the hypothalamus that triggers the release of GH

hyperglycemia
high blood sugar level

hyperthyroidism
overactivity of the thyroid gland

hypoglycemia
low blood sugar level

hypothyroidism
underactivity of the thyroid gland

insulin
hormone produced by the beta cells of the pancreas in response to high blood glucose levels; functions to lower blood glucose levels

insulin-like growth factor (IGF)
growth-promoting protein produced by the liver

mineralocorticoid
corticosteroid that affects ion and water balance

norepinephrine
hormone released by the adrenal medulla in response to a short-term stress hormone production by the gonads

osmoreceptor
receptor in the hypothalamus that monitors the concentration of electrolytes in the blood

oxytocin
hormone released by the posterior pituitary to stimulate uterine contractions during childbirth and milk let-down in the mammary glands

parathyroid hormone (PTH)
hormone produced by the parathyroid glands in response to low blood Ca^{2+} levels; functions to raise blood Ca^{2+} levels

pituitary dwarfism
condition caused by underproduction of GH in children

prolactin (PRL)
hormone produced by the anterior pituitary that stimulates milk production

prolactin-inhibiting hormone

hormone produced by the hypothalamus that inhibits the release of prolactin

prolactin-releasing hormone
hormone produced by the hypothalamus that stimulates the release of prolactin

renin
enzyme produced by the juxtaglomerular apparatus of the kidneys that reacts with angiotensinogen to cause the release of aldosterone

thyroglobulin
glycoprotein found in the thyroid that is converted into thyroid hormone

thyroid-stimulating hormone (TSH)
hormone produced by the anterior pituitary that controls the release of T_3 and T_4 from the thyroid gland

thyroxine (tetraiodothyronine, T_4)
thyroid hormone that controls the basal metabolic rate

triiodothyronine (T_3)
thyroid hormone that controls the basal metabolic rate

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44.5: Other Hormones and Their Effects

Skills to Develop

- Describe the role of different glands in the endocrine system
- Explain how the different glands work together to maintain homeostasis

Both the endocrine and nervous systems use chemical signals to communicate and regulate the body's physiology. The endocrine system releases hormones that act on target cells to regulate development, growth, energy metabolism, reproduction, and many behaviors. The nervous system releases neurotransmitters or neurohormones that regulate neurons, muscle cells, and endocrine cells. Because the neurons can regulate the release of hormones, the nervous and endocrine systems work in a coordinated manner to regulate the body's physiology.

Hypothalamic-Pituitary Axis

The hypothalamus in vertebrates integrates the endocrine and nervous systems. The hypothalamus is an endocrine organ located in the diencephalon of the brain. It receives input from the body and other brain areas and initiates endocrine responses to environmental changes. The hypothalamus acts as an endocrine organ, synthesizing hormones and transporting them along axons to the posterior pituitary gland. It synthesizes and secretes regulatory hormones that control the endocrine cells in the anterior pituitary gland. The hypothalamus contains autonomic centers that control endocrine cells in the adrenal medulla via neuronal control.

The pituitary gland, sometimes called the hypophysis or “master gland” is located at the base of the brain in the sella turcica, a groove of the sphenoid bone of the skull, illustrated in Figure **44.5.1**. It is attached to the hypothalamus via a stalk called the pituitary stalk (or infundibulum). The anterior portion of the pituitary gland is regulated by releasing or release-inhibiting hormones produced by the hypothalamus, and the posterior pituitary receives signals via neurosecretory cells to release hormones produced by the hypothalamus. The pituitary has two distinct regions—the anterior pituitary and the posterior pituitary—which between them secrete nine different peptide or protein hormones. The posterior lobe of the pituitary gland contains axons of the hypothalamic neurons.

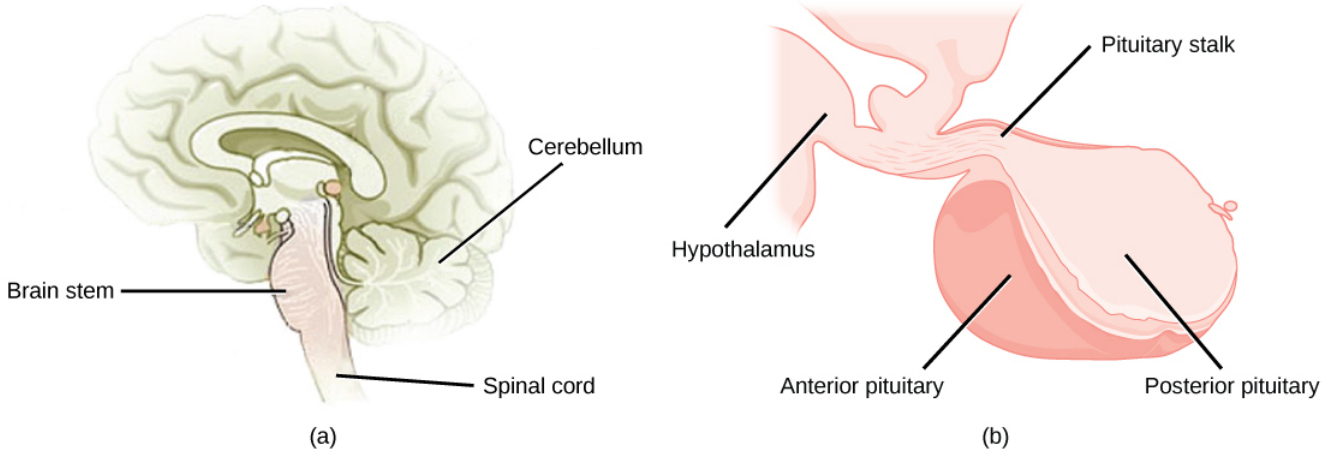


Figure **44.5.1**: The pituitary gland is located at (a) the base of the brain and (b) connected to the hypothalamus by the pituitary stalk. (credit a: modification of work by NCI; credit b: modification of work by Gray’s Anatomy)

Anterior Pituitary

The anterior pituitary gland, or adenohypophysis, is surrounded by a capillary network that extends from the hypothalamus, down along the infundibulum, and to the anterior pituitary. This capillary network is a part of the hypophyseal portal system that carries substances from the hypothalamus to the anterior pituitary and hormones from the anterior pituitary into the circulatory system. A portal system carries blood from one capillary network to another; therefore, the hypophyseal portal system allows hormones produced by the hypothalamus to be carried directly to the anterior pituitary without first entering the circulatory system.

The anterior pituitary produces seven hormones: growth hormone (GH), prolactin (PRL), thyroid-stimulating hormone (TSH), melanin-stimulating hormone (MSH), adrenocorticotropic hormone (ACTH), follicle-stimulating hormone (FSH), and luteinizing hormone (LH). Anterior pituitary hormones are sometimes referred to as tropic hormones, because they control the functioning of other organs. While these hormones are produced by the anterior pituitary, their production is controlled by regulatory hormones produced by the hypothalamus. These regulatory hormones can be releasing hormones or inhibiting hormones, causing more or less of the anterior pituitary hormones to be secreted. These travel from the hypothalamus through the hypophyseal portal system to the anterior pituitary where they exert their effect. Negative feedback then regulates how much of these regulatory hormones are released and how much anterior pituitary hormone is secreted.

Posterior Pituitary

The posterior pituitary is significantly different in structure from the anterior pituitary. It is a part of the brain, extending down from the hypothalamus, and contains mostly nerve fibers and neuroglial cells, which support axons that extend from the hypothalamus to the posterior pituitary. The posterior pituitary and the infundibulum together are referred to as the neurohypophysis.

The hormones antidiuretic hormone (ADH), also known as vasopressin, and oxytocin are produced by neurons in the hypothalamus and transported within these axons along the infundibulum to the posterior pituitary. They are released into the circulatory system via neural signaling from the hypothalamus. These hormones are considered to be posterior pituitary hormones, even though they are produced by the hypothalamus, because that is where they are released into the circulatory system. The posterior pituitary itself does not produce hormones, but instead stores hormones produced by the hypothalamus and releases them into the blood stream.

Thyroid Gland

The thyroid gland is located in the neck, just below the larynx and in front of the trachea, as shown in Figure **44.5.2**. It is a butterfly-shaped gland with two lobes that are connected by the isthmus. It has a dark red color due to its extensive vascular system. When the thyroid swells due to dysfunction, it can be felt under the skin of the neck.

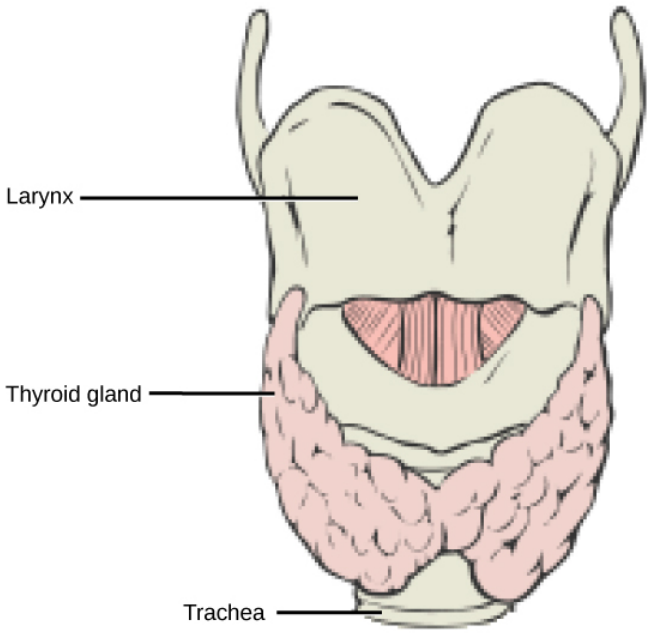


Figure **44.5.2**: This illustration shows the location of the thyroid gland.

The thyroid gland is made up of many spherical thyroid follicles, which are lined with a simple cuboidal epithelium. These follicles contain a viscous fluid, called colloid, which stores the glycoprotein thyroglobulin, the precursor to the thyroid hormones. The follicles produce hormones that can be stored in the colloid or released into the surrounding capillary network for transport to the rest of the body via the circulatory system.

Thyroid follicle cells synthesize the hormone thyroxine, which is also known as T_4 because it contains four atoms of iodine, and triiodothyronine, also known as T_3 because it contains three atoms of iodine. Follicle cells are stimulated to release stored T_3 and T_4

by thyroid stimulating hormone (TSH), which is produced by the anterior pituitary. These thyroid hormones increase the rates of mitochondrial ATP production.

A third hormone, calcitonin, is produced by parafollicular cells of the thyroid either releasing hormones or inhibiting hormones. Calcitonin release is not controlled by TSH, but instead is released when calcium ion concentrations in the blood rise. Calcitonin functions to help regulate calcium concentrations in body fluids. It acts in the bones to inhibit osteoclast activity and in the kidneys to stimulate excretion of calcium. The combination of these two events lowers body fluid levels of calcium.

Parathyroid Glands

Most people have four parathyroid glands; however, the number can vary from two to six. These glands are located on the posterior surface of the thyroid gland, as shown in Figure **44.5.3**. Normally, there is a superior gland and an inferior gland associated with each of the thyroid's two lobes. Each parathyroid gland is covered by connective tissue and contains many secretory cells that are associated with a capillary network.

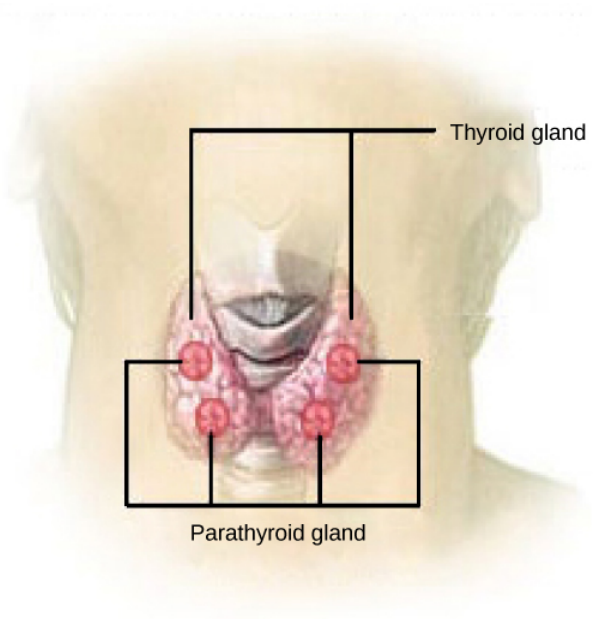


Figure **44.5.3**: The parathyroid glands are located on the posterior of the thyroid gland. (credit: modification of work by NCI)

The parathyroid glands produce parathyroid hormone (PTH). PTH increases blood calcium concentrations when calcium ion levels fall below normal. PTH (1) enhances reabsorption of Ca^{2+} by the kidneys, (2) stimulates osteoclast activity and inhibits osteoblast activity, and (3) it stimulates synthesis and secretion of calcitriol by the kidneys, which enhances Ca^{2+} absorption by the digestive system. PTH is produced by chief cells of the parathyroid. PTH and calcitonin work in opposition to one another to maintain homeostatic Ca^{2+} levels in body fluids. Another type of cells, oxyphil cells, exist in the parathyroid but their function is not known. These hormones encourage bone growth, muscle mass, and blood cell formation in children and women.

Adrenal Glands

The adrenal glands are associated with the kidneys; one gland is located on top of each kidney as illustrated in Figure **44.5.4**. The adrenal glands consist of an outer adrenal cortex and an inner adrenal medulla. These regions secrete different hormones.

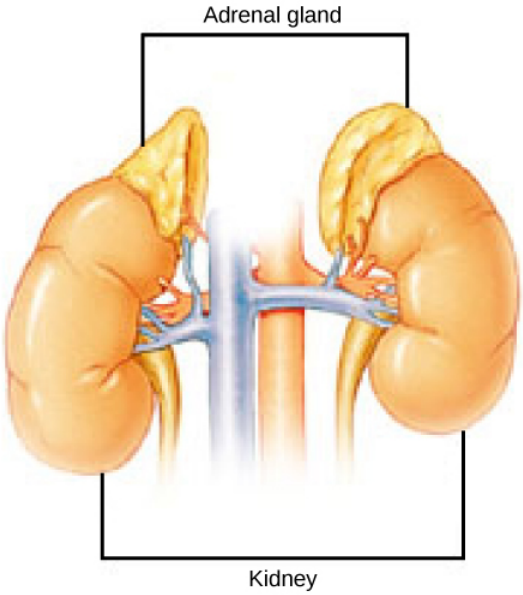


Figure **44.5.4**: The location of the adrenal glands on top of the kidneys is shown. (credit: modification of work by NCI)

Adrenal Cortex

The adrenal cortex is made up of layers of epithelial cells and associated capillary networks. These layers form three distinct regions: an outer zona glomerulosa that produces mineralocorticoids, a middle zona fasciculata that produces glucocorticoids, and an inner zona reticularis that produces androgens.

The main mineralocorticoid is aldosterone, which regulates the concentration of Na^+ ions in urine, sweat, pancreas, and saliva. Aldosterone release from the adrenal cortex is stimulated by a decrease in blood concentrations of sodium ions, blood volume, or blood pressure, or by an increase in blood potassium levels.

The three main glucocorticoids are cortisol, corticosterone, and cortisone. The glucocorticoids stimulate the synthesis of glucose and gluconeogenesis (converting a non-carbohydrate to glucose) by liver cells and they promote the release of fatty acids from adipose tissue. These hormones increase blood glucose levels to maintain levels within a normal range between meals. These hormones are secreted in response to ACTH and levels are regulated by negative feedback.

Androgens are sex hormones that promote masculinity. They are produced in small amounts by the adrenal cortex in both males and females. They do not affect sexual characteristics and may supplement sex hormones released from the gonads.

Adrenal Medulla

The adrenal medulla contains large, irregularly shaped cells that are closely associated with blood vessels. These cells are innervated by preganglionic autonomic nerve fibers from the central nervous system.

The adrenal medulla contains two types of secretory cells: one that produces epinephrine (adrenaline) and another that produces norepinephrine (noradrenaline). Epinephrine is the primary adrenal medulla hormone accounting for 75 to 80 percent of its secretions. Epinephrine and norepinephrine increase heart rate, breathing rate, cardiac muscle contractions, blood pressure, and blood glucose levels. They also accelerate the breakdown of glucose in skeletal muscles and stored fats in adipose tissue.

The release of epinephrine and norepinephrine is stimulated by neural impulses from the sympathetic nervous system. Secretion of these hormones is stimulated by acetylcholine release from preganglionic sympathetic fibers innervating the adrenal medulla. These neural impulses originate from the hypothalamus in response to stress to prepare the body for the fight-or-flight response.

Pancreas

The pancreas, illustrated in Figure **44.5.5**, is an elongated organ that is located between the stomach and the proximal portion of the small intestine. It contains both exocrine cells that excrete digestive enzymes and endocrine cells that release hormones. It is sometimes referred to as a heterocrine gland because it has both endocrine and exocrine functions.

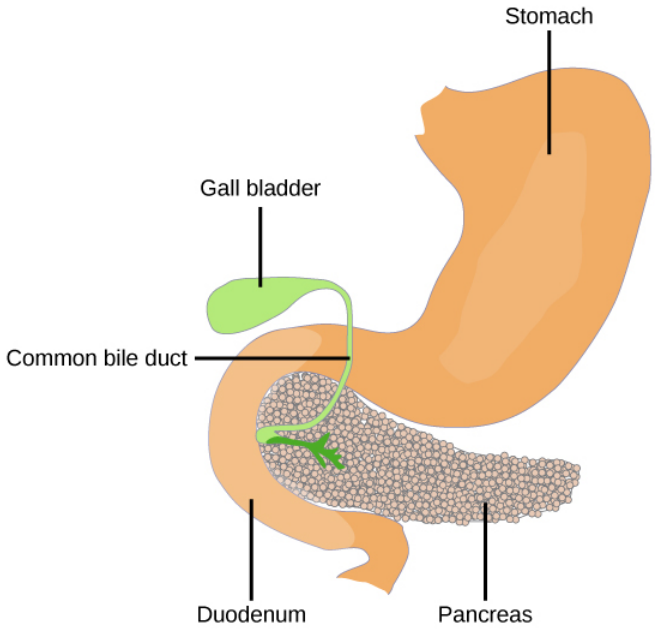


Figure **44.5.5**: The pancreas is found underneath the stomach and points toward the spleen. (credit: modification of work by NCI)

The endocrine cells of the pancreas form clusters called pancreatic islets or the islets of Langerhans, as visible in the micrograph shown in Figure **44.5.6**. The pancreatic islets contain two primary cell types: alpha cells, which produce the hormone glucagon, and beta cells, which produce the hormone insulin. These hormones regulate blood glucose levels. As blood glucose levels decline, alpha cells release glucagon to raise the blood glucose levels by increasing rates of glycogen breakdown and glucose release by the liver. When blood glucose levels rise, such as after a meal, beta cells release insulin to lower blood glucose levels by increasing the rate of glucose uptake in most body cells, and by increasing glycogen synthesis in skeletal muscles and the liver. Together, glucagon and insulin regulate blood glucose levels.

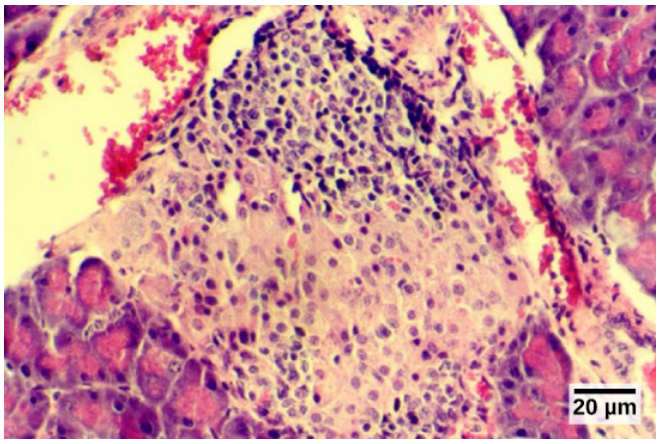


Figure **44.5.6**: The islets of Langerhans are clusters of endocrine cells found in the pancreas; they stain lighter than surrounding cells. (credit: modification of work by Muhammad T. Tabiin, Christopher P. White, Grant Morahan, and Bernard E. Tuch; scale-bar data from Matt Russell)

Pineal Gland

The pineal gland produces melatonin. The rate of melatonin production is affected by the photoperiod. Collaterals from the visual pathways innervate the pineal gland. During the day photoperiod, little melatonin is produced; however, melatonin production increases during the dark photoperiod (night). In some mammals, melatonin has an inhibitory affect on reproductive functions by decreasing production and maturation of sperm, oocytes, and reproductive organs. Melatonin is an effective antioxidant, protecting the CNS from free radicals such as nitric oxide and hydrogen peroxide. Lastly, melatonin is involved in biological rhythms, particularly circadian rhythms such as the sleep-wake cycle and eating habits.

Gonads

The gonads—the male testes and female ovaries—produce steroid hormones. The testes produce androgens, testosterone being the most prominent, which allow for the development of secondary sex characteristics and the production of sperm cells. The ovaries produce estradiol and progesterone, which cause secondary sex characteristics and prepare the body for childbirth.

Table 44.5.1: Endocrine Glands and their Associated Hormones

https://bio.libretexts.org/@go/page/74357

Endocrine Gland	Associated Hormones	Effect
Hypothalamus	releasing and inhibiting hormones	regulate hormone release from pituitary gland; produce oxytocin; produce uterine contractions and milk secretion in females
	antidiuretic hormone (ADH)	water reabsorption from kidneys; vasoconstriction to increase blood pressure
Pituitary (Anterior)	growth hormone (GH)	promotes growth of body tissues, protein synthesis; metabolic functions
	prolactin (PRL)	promotes milk production
	thyroid stimulating hormone (TSH)	stimulates thyroid hormone release
	adrenocorticotropic hormone (ACTH)	stimulates hormone release by adrenal cortex, glucocorticoids
	follicle-stimulating hormone (FSH)	stimulates gamete production (both ova and sperm); secretion of estradiol
	luteinizing hormone (LH)	stimulates androgen production by gonads; ovulation, secretion of progesterone
	melanocyte-stimulating hormone (MSH)	stimulates melanocytes of the skin increasing melanin pigment production.
Pituitary (Posterior)	antidiuretic hormone (ADH)	stimulates water reabsorption by kidneys
	oxytocin	stimulates uterine contractions during childbirth; milk ejection; stimulates ductus deferens and prostate gland contraction during emission
Thyroid	thyroxine, triiodothyronine	stimulate and maintain metabolism; growth and development
	calcitonin	reduces blood Ca^{2+} levels
Parathyroid	parathyroid hormone (PTH)	increases blood Ca^{2+} levels
Adrenal (Cortex)	aldosterone	increases blood Na^{+} levels; increase K^{+} secretion
	cortisol, corticosterone, cortisone	increase blood glucose levels; anti-inflammatory effects
Adrenal (Medulla)	epinephrine, norepinephrine	stimulate fight-or-flight response; increase blood gluclose levels; increase metabolic activities
Pancreas	insulin	reduces blood glucose levels
	glucagon	increases blood glucose levels
Pineal gland	melatonin	regulates some biological rhythms and protects CNS from free radicals
Testes	androgens	regulate, promote, increase or maintain sperm production; male secondary sexual characteristics
Ovaries	estrogen	promotes uterine lining growth; female

Endocrine Gland	Associated Hormones	Effect
		secondary sexual characteristics
	progestins	promote and maintain uterine lining growth

Organs with Secondary Endocrine Functions

There are several organs whose primary functions are non-endocrine but that also possess endocrine functions. These include the heart, kidneys, intestines, thymus, gonads, and adipose tissue.

The heart possesses endocrine cells in the walls of the atria that are specialized cardiac muscle cells. These cells release the hormone atrial natriuretic peptide (ANP) in response to increased blood volume. High blood volume causes the cells to be stretched, resulting in hormone release. ANP acts on the kidneys to reduce the reabsorption of Na^+, causing Na^+ and water to be excreted in the urine. ANP also reduces the amounts of renin released by the kidneys and aldosterone released by the adrenal cortex, further preventing the retention of water. In this way, ANP causes a reduction in blood volume and blood pressure, and reduces the concentration of Na^+ in the blood.

The gastrointestinal tract produces several hormones that aid in digestion. The endocrine cells are located in the mucosa of the GI tract throughout the stomach and small intestine. Some of the hormones produced include gastrin, secretin, and cholecystokinin, which are secreted in the presence of food, and some of which act on other organs such as the pancreas, gallbladder, and liver. They trigger the release of gastric juices, which help to break down and digest food in the GI tract.

While the adrenal glands associated with the kidneys are major endocrine glands, the kidneys themselves also possess endocrine function. Renin is released in response to decreased blood volume or pressure and is part of the renin-angiotensin-aldosterone system that leads to the release of aldosterone. Aldosterone then causes the retention of Na^+ and water, raising blood volume. The kidneys also release calcitriol, which aids in the absorption of Ca^{2+} and phosphate ions. Erythropoietin (EPO) is a protein hormone that triggers the formation of red blood cells in the bone marrow. EPO is released in response to low oxygen levels. Because red blood cells are oxygen carriers, increased production results in greater oxygen delivery throughout the body. EPO has been used by athletes to improve performance, as greater oxygen delivery to muscle cells allows for greater endurance. Because red blood cells increase the viscosity of blood, artificially high levels of EPO can cause severe health risks.

The thymus is found behind the sternum; it is most prominent in infants, becoming smaller in size through adulthood. The thymus produces hormones referred to as thymosins, which contribute to the development of the immune response.

Adipose tissue is a connective tissue found throughout the body. It produces the hormone leptin in response to food intake. Leptin increases the activity of anorexigenic neurons and decreases that of orexigenic neurons, producing a feeling of satiety after eating, thus affecting appetite and reducing the urge for further eating. Leptin is also associated with reproduction. It must be present for GnRH and gonadotropin synthesis to occur. Extremely thin females may enter puberty late; however, if adipose levels increase, more leptin will be produced, improving fertility.

Summary

The pituitary gland is located at the base of the brain and is attached to the hypothalamus by the infundibulum. The anterior pituitary receives products from the hypothalamus by the hypophyseal portal system and produces six hormones. The posterior pituitary is an extension of the brain and releases hormones (antidiuretic hormone and oxytocin) produced by the hypothalamus.

The thyroid gland is located in the neck and is composed of two lobes connected by the isthmus. The thyroid is made up of follicle cells that produce the hormones thyroxine and triiodothyronine. Parafollicular cells of the thyroid produce calcitonin. The parathyroid glands lie on the posterior surface of the thyroid gland and produce parathyroid hormone.

The adrenal glands are located on top of the kidneys and consist of the renal cortex and renal medulla. The adrenal cortex is the outer part of the adrenal gland and produces the corticosteroids, glucocorticoids, and mineralocorticoids. The adrenal medulla is the inner part of the adrenal gland and produces the catecholamines epinephrine and norepinephrine.

The pancreas lies in the abdomen between the stomach and the small intestine. Clusters of endocrine cells in the pancreas form the islets of Langerhans, which are composed of alpha cells that release glucagon and beta cells that release insulin.

Some organs possess endocrine activity as a secondary function but have another primary function. The heart produces the hormone atrial natriuretic peptide, which functions to reduce blood volume, pressure, and Na^+ concentration. The gastrointestinal tract produces various hormones that aid in digestion. The kidneys produce renin, calcitriol, and erythropoietin. Adipose tissue produces leptin, which promotes satiety signals in the brain.

Glossary

adrenal cortex
outer portion of adrenal glands that produces corticosteroids

adrenal gland
endocrine glands associated with the kidneys

adrenal medulla
inner portion of adrenal glands that produces epinephrine and norepinephrine

alpha cell
endocrine cell of the pancreatic islets that produces the hormone glucagon

anterior pituitary
portion of the pituitary gland that produces six hormones; also called adenohypophysis

atrial natriuretic peptide (ANP)
hormone produced by the heart to reduce blood volume, pressure, and Na^+ concentration

beta cell
endocrine cell of the pancreatic islets that produces the hormone insulin

colloid
fluid inside the thyroid gland that contains the glycoprotein thyroglobulin

endocrine gland
gland that secretes hormones into the surrounding interstitial fluid, which then diffuse into blood and are carried to various organs and tissues within the body

erythropoietin (EPO)
hormone produced by the kidneys to stimulate red blood cell production in the bone marrow

hypophyseal portal system
system of blood vessels that carries hormones from the hypothalamus to the anterior pituitary

islets of Langerhans (pancreatic islets)
endocrine cells of the pancreas

isthmus
tissue mass that connects the two lobes of the thyroid gland

leptin
hormone produced by adipose tissue that promotes feelings of satiety and reduces hunger

pancreas
organ located between the stomach and the small intestine that contains exocrine and endocrine cells

parafollicular cell

thyroid cell that produces the hormone calcitonin

parathyroid gland
gland located on the surface of the thyroid that produces parathyroid hormone

pituitary gland
endocrine gland located at the base of the brain composed of an anterior and posterior region; also called hypophysis

pituitary stalk
(also, infundibulum) stalk that connects the pituitary gland to the hypothalamus

posterior pituitary
extension of the brain that releases hormones produced by the hypothalamus; along with the infundibulum, it is also referred to as the neurohypophysis

thymus
gland located behind the sternum that produces thymosin hormones that contribute to the development of the immune system

thyroid gland
endocrine gland located in the neck that produces thyroid hormones thyroxine and triiodothyronine

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CHAPTER OVERVIEW

45: The Musculoskeletal System

45.1: Types of Skeletal Systems

45.2: A Closer Look at Bone

45.3: Joints

45.4: Muscle Contraction

45.5: Vertebrate Skeleton Evolution and Modes of Locomotion

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45.1: Types of Skeletal Systems

Skills to Develop

- Discuss the different types of skeletal systems
- Explain the role of the human skeletal system
- Compare and contrast different skeletal systems

A skeletal system is necessary to support the body, protect internal organs, and allow for the movement of an organism. There are three different skeleton designs that fulfill these functions: hydrostatic skeleton, exoskeleton, and endoskeleton.

Hydrostatic Skeleton

A hydrostatic skeleton is a skeleton formed by a fluid-filled compartment within the body, called the coelom. The organs of the coelom are supported by the aqueous fluid, which also resists external compression. This compartment is under hydrostatic pressure because of the fluid and supports the other organs of the organism. This type of skeletal system is found in soft-bodied animals such as sea anemones, earthworms, Cnidaria, and other invertebrates (Figure **45.1.1**).



Figure **45.1.1**: The skeleton of the red-knobbed sea star (*Protoreaster linckii*) is an example of a hydrostatic skeleton. (credit: "Amada44"/Wikimedia Commons)

Movement in a hydrostatic skeleton is provided by muscles that surround the coelom. The muscles in a hydrostatic skeleton contract to change the shape of the coelom; the pressure of the fluid in the coelom produces movement. For example, earthworms move by waves of muscular contractions of the skeletal muscle of the body wall hydrostatic skeleton, called peristalsis, which alternately shorten and lengthen the body. Lengthening the body extends the anterior end of the organism. Most organisms have a mechanism to fix themselves in the substrate. Shortening the muscles then draws the posterior portion of the body forward. Although a hydrostatic skeleton is well-suited to invertebrate organisms such as earthworms and some aquatic organisms, it is not an efficient skeleton for terrestrial animals.

Exoskeleton

An exoskeleton is an external skeleton that consists of a hard encasement on the surface of an organism. For example, the shells of crabs and insects are exoskeletons (Figure **45.1.2**). This skeleton type provides defence against predators, supports the body, and allows for movement through the contraction of attached muscles. As with vertebrates, muscles must cross a joint inside the exoskeleton. Shortening of the muscle changes the relationship of the two segments of the exoskeleton. Arthropods such as crabs and lobsters have exoskeletons that consist of 30–50 percent chitin, a polysaccharide derivative of glucose that is a strong but flexible material. Chitin is secreted by the epidermal cells. The exoskeleton is further strengthened by the addition of calcium carbonate in organisms such as the lobster. Because the exoskeleton is acellular, arthropods must periodically shed their exoskeletons because the exoskeleton does not grow as the organism grows.



Figure **45.1.2**: Muscles attached to the exoskeleton of the Halloween crab (*Gecarcinus quadratus*) allow it to move.

Endoskeleton

An endoskeleton is a skeleton that consists of hard, mineralized structures located within the soft tissue of organisms. An example of a primitive endoskeletal structure is the spicules of sponges. The bones of vertebrates are composed of tissues, whereas sponges have no true tissues (Figure **45.1.1**). Endoskeletons provide support for the body, protect internal organs, and allow for movement through contraction of muscles attached to the skeleton.



Figure **45.1.3**: The skeletons of humans and horses are examples of endoskeletons. (credit: Ross Murphy)

The human skeleton is an endoskeleton that consists of 206 bones in the adult. It has five main functions: providing support to the body, storing minerals and lipids, producing blood cells, protecting internal organs, and allowing for movement. The skeletal

system in vertebrates is divided into the axial skeleton (which consists of the skull, vertebral column, and rib cage), and the appendicular skeleton (which consists of the shoulders, limb bones, the pectoral girdle, and the pelvic girdle).

Human Axial Skeleton

The axial skeleton forms the central axis of the body and includes the bones of the skull, ossicles of the middle ear, hyoid bone of the throat, vertebral column, and the thoracic cage (ribcage) (Figure **45.1.1**). The function of the axial skeleton is to provide support and protection for the brain, the spinal cord, and the organs in the ventral body cavity. It provides a surface for the attachment of muscles that move the head, neck, and trunk, performs respiratory movements, and stabilizes parts of the appendicular skeleton.

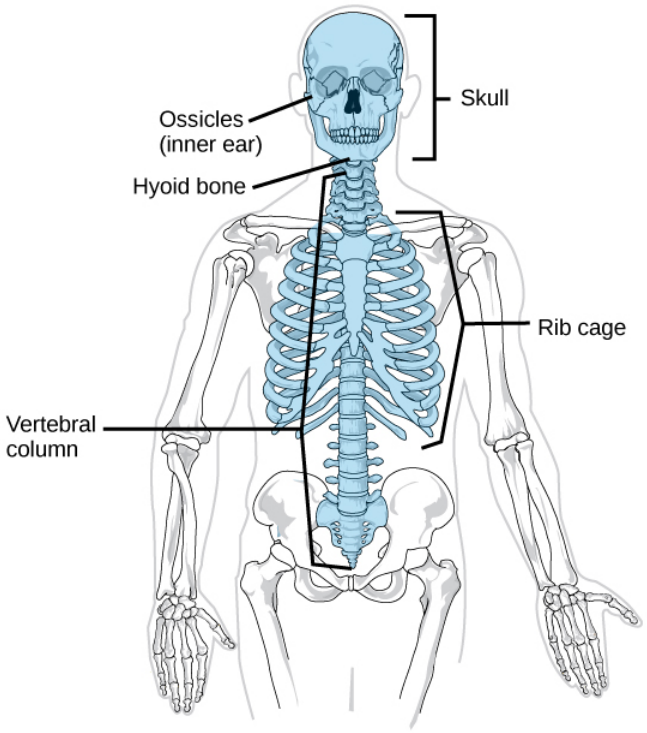


Figure **45.1.4**: The axial skeleton consists of the bones of the skull, ossicles of the middle ear, hyoid bone, vertebral column, and rib cage. (credit: modification of work by Mariana Ruiz Villareal)

The Skull

The bones of the skull support the structures of the face and protect the brain. The skull consists of 22 bones, which are divided into two categories: cranial bones and facial bones. The cranial bones are eight bones that form the cranial cavity, which encloses the brain and serves as an attachment site for the muscles of the head and neck. The eight cranial bones are the frontal bone, two parietal bones, two temporal bones, occipital bone, sphenoid bone, and the ethmoid bone. Although the bones developed separately in the embryo and fetus, in the adult, they are tightly fused with connective tissue and adjoining bones do not move (Figure **45.1.5**).

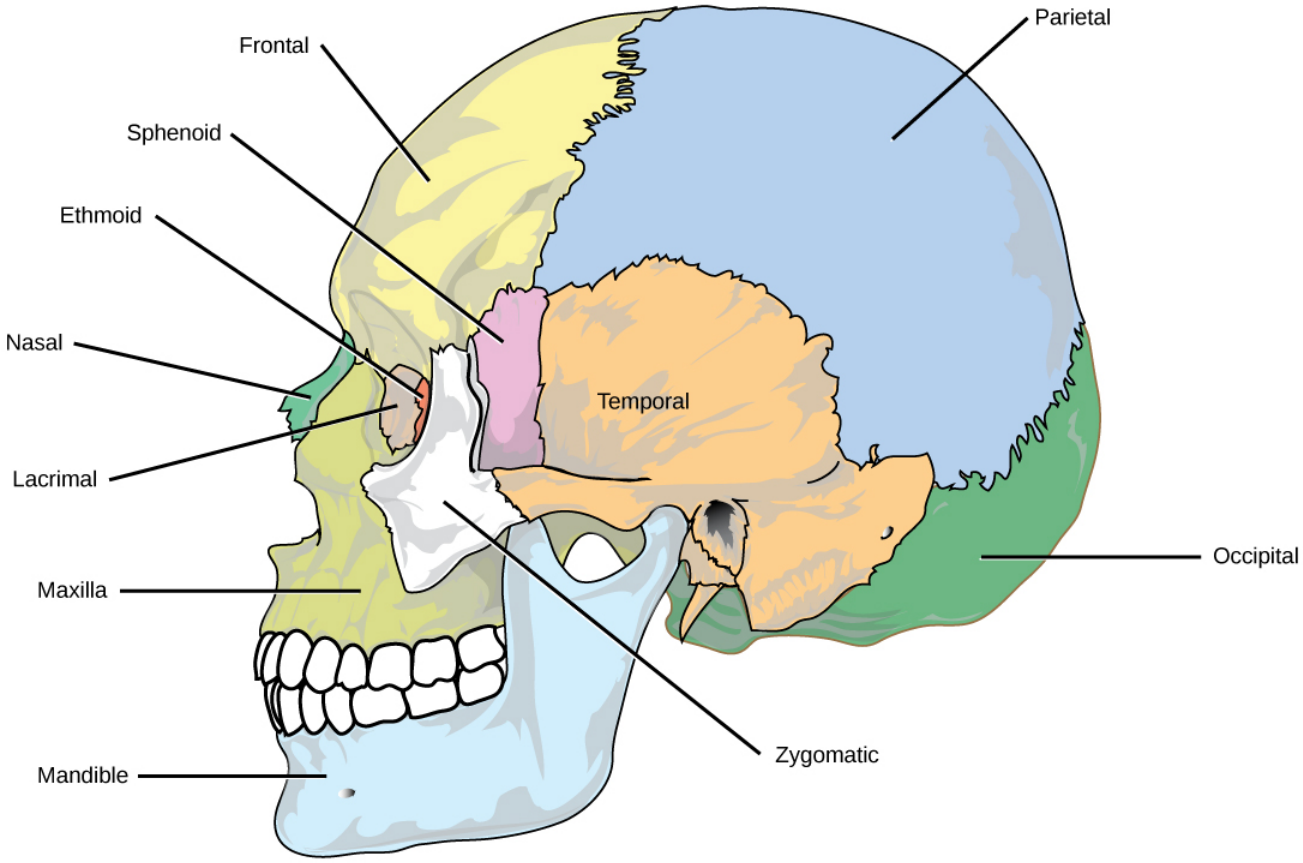


Figure **45.1.5**: The bones of the skull support the structures of the face and protect the brain. (credit: modification of work by Mariana Ruiz Villareal)

The auditory ossicles of the middle ear transmit sounds from the air as vibrations to the fluid-filled cochlea. The auditory ossicles consist of six bones: two malleus bones, two incus bones, and two stapes on each side. These are the smallest bones in the body and are unique to mammals.

Fourteen facial bones form the face, provide cavities for the sense organs (eyes, mouth, and nose), protect the entrances to the digestive and respiratory tracts, and serve as attachment points for facial muscles. The 14 facial bones are the nasal bones, the maxillary bones, zygomatic bones, palatine, vomer, lacrimal bones, the inferior nasal conchae, and the mandible. All of these bones occur in pairs except for the mandible and the vomer (Figure **45.1.6**).

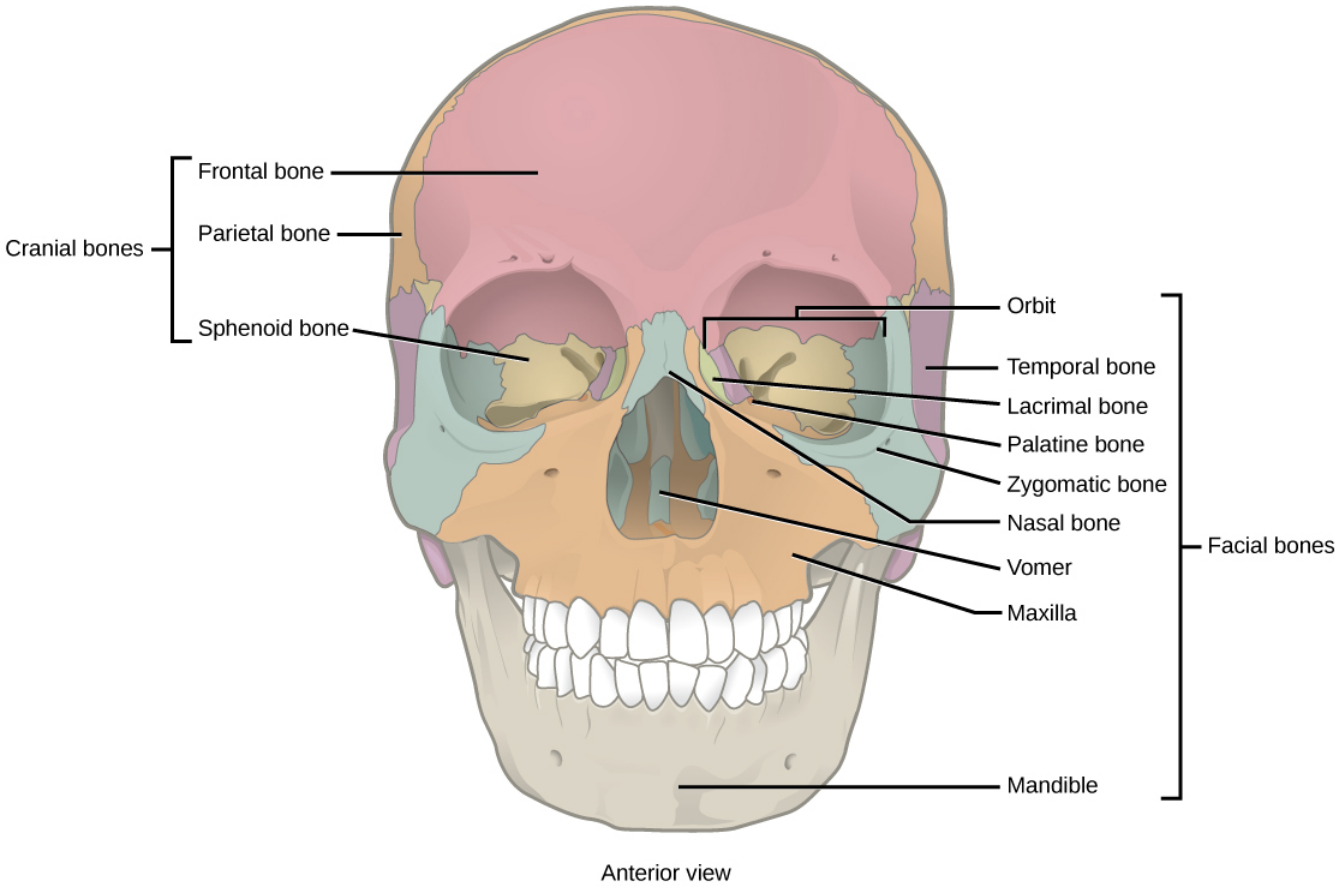


Figure **45.1.6**: The cranial bones, including the frontal, parietal, and sphenoid bones, cover the top of the head. The facial bones of the skull form the face and provide cavities for the eyes, nose, and mouth.

Although it is not found in the skull, the hyoid bone is considered a component of the axial skeleton. The hyoid bone lies below the mandible in the front of the neck. It acts as a movable base for the tongue and is connected to muscles of the jaw, larynx, and tongue. The mandible articulates with the base of the skull. The mandible controls the opening to the airway and gut. In animals with teeth, the mandible brings the surfaces of the teeth in contact with the maxillary teeth.

The Vertebral Column

The vertebral column, or spinal column, surrounds and protects the spinal cord, supports the head, and acts as an attachment point for the ribs and muscles of the back and neck. The adult vertebral column comprises 26 bones: the 24 vertebrae, the sacrum, and the coccyx bones. In the adult, the sacrum is typically composed of five vertebrae that fuse into one. The coccyx is typically 3–4 vertebrae that fuse into one. Around the age of 70, the sacrum and the coccyx may fuse together. We begin life with approximately 33 vertebrae, but as we grow, several vertebrae fuse together. The adult vertebrae are further divided into the 7 cervical vertebrae, 12 thoracic vertebrae, and 5 lumbar vertebrae (Figure **45.1.7**).

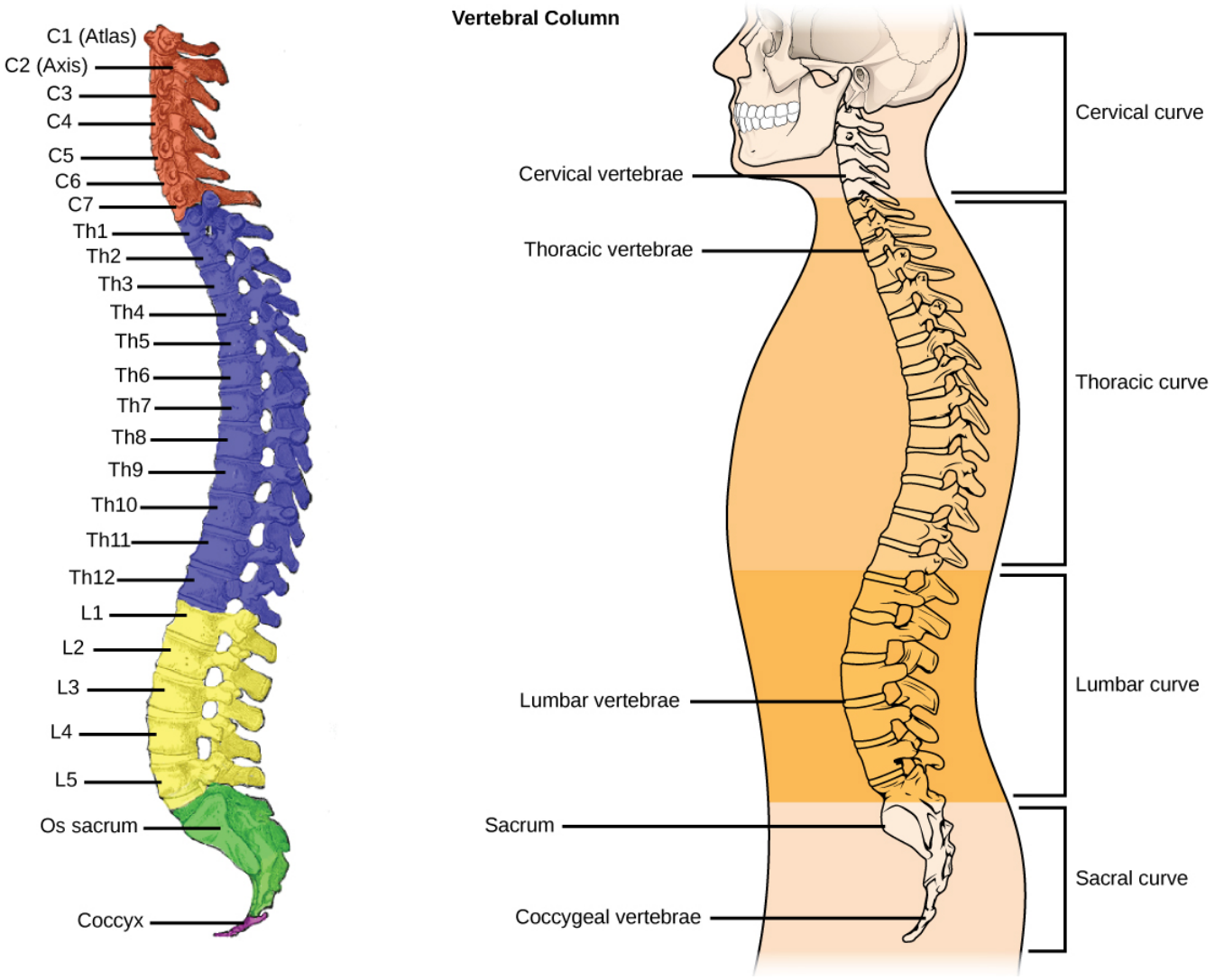


Figure **45.1.7**: (a) The vertebral column consists of seven cervical vertebrae (C1–7) twelve thoracic vertebrae (Th1–12), five lumbar vertebrae (L1–5), the os sacrum, and the coccyx. (b) Spinal curves increase the strength and flexibility of the spine. (credit a: modification of work by Uwe Gille based on original work by Gray's Anatomy; credit b: modification of work by NCI, NIH)

Each vertebral body has a large hole in the center through which the nerves of the spinal cord pass. There is also a notch on each side through which the spinal nerves, which serve the body at that level, can exit from the spinal cord. The vertebral column is approximately 71 cm (28 inches) in adult male humans and is curved, which can be seen from a side view. The names of the spinal curves correspond to the region of the spine in which they occur. The thoracic and sacral curves are concave (curve inwards relative to the front of the body) and the cervical and lumbar curves are convex (curve outwards relative to the front of the body). The arched curvature of the vertebral column increases its strength and flexibility, allowing it to absorb shocks like a spring (Figure **45.1.7**).

Intervertebral discs composed of fibrous cartilage lie between adjacent vertebral bodies from the second cervical vertebra to the sacrum. Each disc is part of a joint that allows for some movement of the spine and acts as a cushion to absorb shocks from movements such as walking and running. Intervertebral discs also act as ligaments to bind vertebrae together. The inner part of discs, the nucleus pulposus, hardens as people age and becomes less elastic. This loss of elasticity diminishes its ability to absorb shocks.

The Thoracic Cage

The thoracic cage, also known as the ribcage, is the skeleton of the chest, and consists of the ribs, sternum, thoracic vertebrae, and costal cartilages (Figure **45.1.8**.8). The thoracic cage encloses and protects the organs of the thoracic cavity, including the heart and

lungs. It also provides support for the shoulder girdles and upper limbs, and serves as the attachment point for the diaphragm, muscles of the back, chest, neck, and shoulders. Changes in the volume of the thorax enable breathing.

The sternum, or breastbone, is a long, flat bone located at the anterior of the chest. It is formed from three bones that fuse in the adult. The ribs are 12 pairs of long, curved bones that attach to the thoracic vertebrae and curve toward the front of the body, forming the ribcage. Costal cartilages connect the anterior ends of the ribs to the sternum, with the exception of rib pairs 11 and 12, which are free-floating ribs.

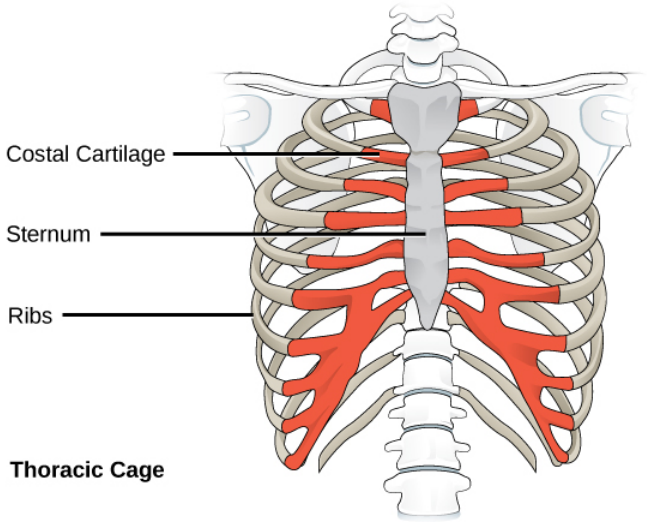


Figure 45.1.8: The thoracic cage, or rib cage, protects the heart and the lungs. (credit: modification of work by NCI, NIH)

Human Appendicular Skeleton

The appendicular skeleton is composed of the bones of the upper limbs (which function to grasp and manipulate objects) and the lower limbs (which permit locomotion). It also includes the pectoral girdle, or shoulder girdle, that attaches the upper limbs to the body, and the pelvic girdle that attaches the lower limbs to the body (Figure 45.1.9).

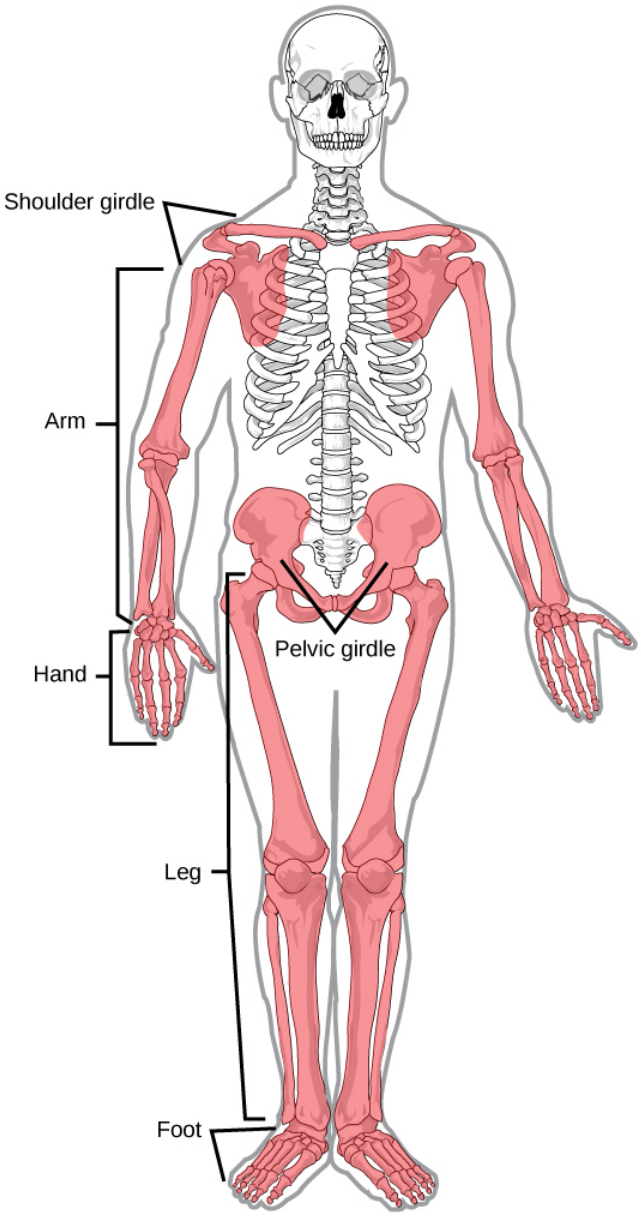


Figure **45.1.9**: The appendicular skeleton is composed of the bones of the pectoral limbs (arm, forearm, hand), the pelvic limbs (thigh, leg, foot), the pectoral girdle, and the pelvic girdle. (credit: modification of work by Mariana Ruiz Villareal)

The Pectoral Girdle

The pectoral girdle bones provide the points of attachment of the upper limbs to the axial skeleton. The human pectoral girdle consists of the clavicle (or collarbone) in the anterior, and the scapula (or shoulder blades) in the posterior (Figure **45.1.10**).

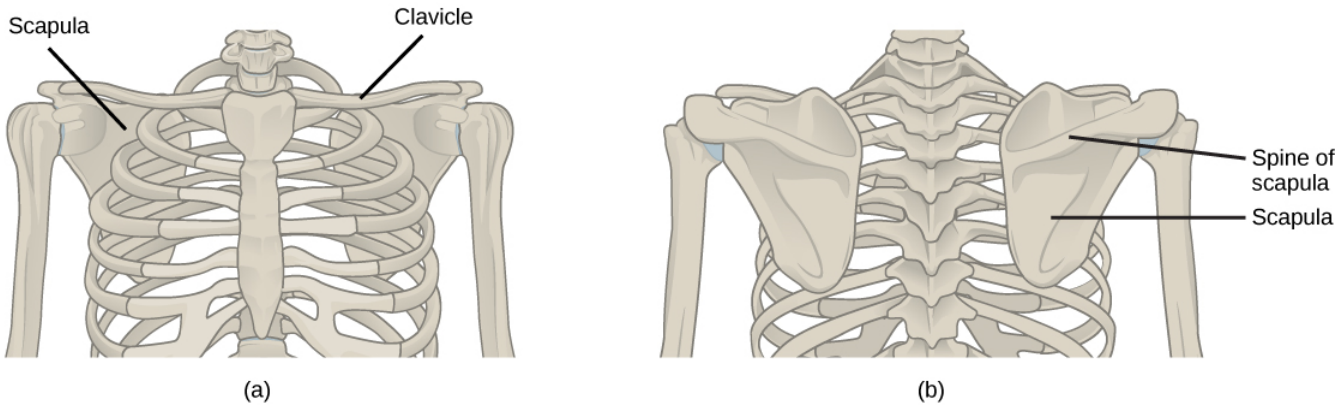


Figure 45.1.10: (a) The pectoral girdle in primates consists of the clavicles and scapulae. (b) The posterior view reveals the spine of the scapula to which muscle attaches.

The clavicles are S-shaped bones that position the arms on the body. The clavicles lie horizontally across the front of the thorax (chest) just above the first rib. These bones are fairly fragile and are susceptible to fractures. For example, a fall with the arms outstretched causes the force to be transmitted to the clavicles, which can break if the force is excessive. The clavicle articulates with the sternum and the scapula.

The scapulae are flat, triangular bones that are located at the back of the pectoral girdle. They support the muscles crossing the shoulder joint. A ridge, called the spine, runs across the back of the scapula and can easily be felt through the skin (Figure 45.1.10). The spine of the scapula is a good example of a bony protrusion that facilitates a broad area of attachment for muscles to bone.

The Upper Limb

The upper limb contains 30 bones in three regions: the arm (shoulder to elbow), the forearm (ulna and radius), and the wrist and hand (Figure 45.1.11).

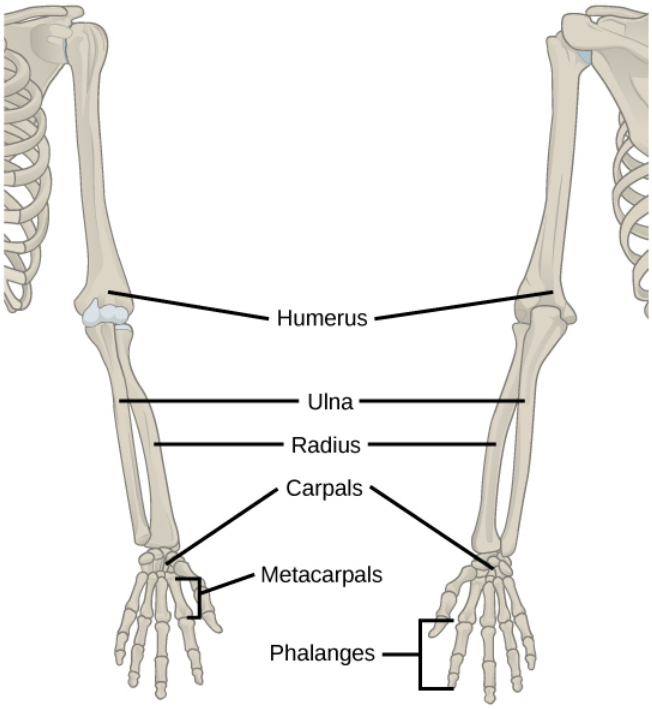


Figure 45.1.11: The upper limb consists of the humerus of the upper arm, the radius and ulna of the forearm, eight bones of the carpus, five bones of the metacarpus, and 14 bones of the phalanges.

An articulation is any place at which two bones are joined. The humerus is the largest and longest bone of the upper limb and the only bone of the arm. It articulates with the scapula at the shoulder and with the forearm at the elbow. The forearm extends from

the elbow to the wrist and consists of two bones: the ulna and the radius. The radius is located along the lateral (thumb) side of the forearm and articulates with the humerus at the elbow. The ulna is located on the medial aspect (pinky-finger side) of the forearm. It is longer than the radius. The ulna articulates with the humerus at the elbow. The radius and ulna also articulate with the carpal bones and with each other, which in vertebrates enables a variable degree of rotation of the carpus with respect to the long axis of the limb. The hand includes the eight bones of the carpus (wrist), the five bones of the metacarpus (palm), and the 14 bones of the phalanges (digits). Each digit consists of three phalanges, except for the thumb, when present, which has only two.

The Pelvic Girdle

The pelvic girdle attaches to the lower limbs of the axial skeleton. Because it is responsible for bearing the weight of the body and for locomotion, the pelvic girdle is securely attached to the axial skeleton by strong ligaments. It also has deep sockets with robust ligaments to securely attach the femur to the body. The pelvic girdle is further strengthened by two large hip bones. In adults, the hip bones, or coxal bones, are formed by the fusion of three pairs of bones: the ilium, ischium, and pubis. The pelvis joins together in the anterior of the body at a joint called the pubic symphysis and with the bones of the sacrum at the posterior of the body.

The female pelvis is slightly different from the male pelvis. Over generations of evolution, females with a wider pubic angle and larger diameter pelvic canal reproduced more successfully. Therefore, their offspring also had pelvic anatomy that enabled successful childbirth (Figure **45.1.12**).

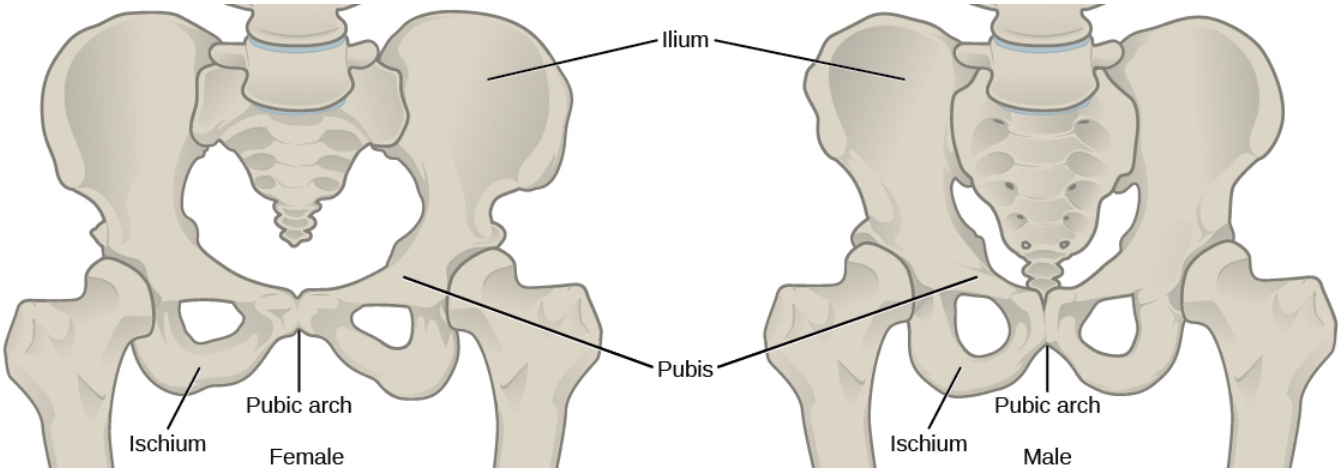


Figure **45.1.12**: To adapt to reproductive fitness, the (a) female pelvis is lighter, wider, shallower, and has a broader angle between the pubic bones than (b) the male pelvis.

The Lower Limb

The lower limb consists of the thigh, the leg, and the foot. The bones of the lower limb are the femur (thigh bone), patella (kneecap), tibia and fibula (bones of the leg), tarsals (bones of the ankle), and metatarsals and phalanges (bones of the foot) (Figure **45.1.13**). The bones of the lower limbs are thicker and stronger than the bones of the upper limbs because of the need to support the entire weight of the body and the resulting forces from locomotion. In addition to evolutionary fitness, the bones of an individual will respond to forces exerted upon them.

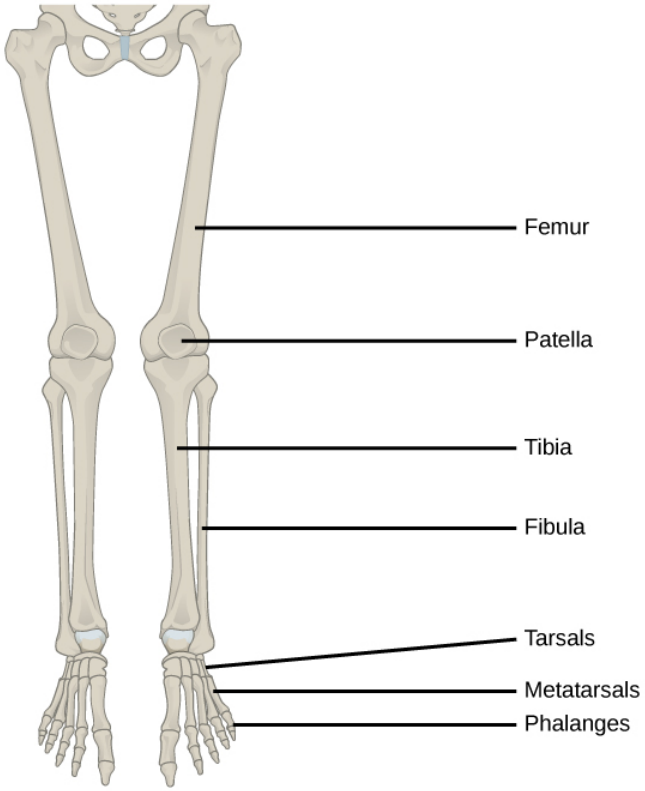


Figure **45.1.13**: The lower limb consists of the thigh (femur), kneecap (patella), leg (tibia and fibula), ankle (tarsals), and foot (metatarsals and phalanges) bones.

The femur, or thighbone, is the longest, heaviest, and strongest bone in the body. The femur and pelvis form the hip joint at the proximal end. At the distal end, the femur, tibia, and patella form the knee joint. The patella, or kneecap, is a triangular bone that lies anterior to the knee joint. The patella is embedded in the tendon of the femoral extensors (quadriceps). It improves knee extension by reducing friction. The tibia, or shinbone, is a large bone of the leg that is located directly below the knee. The tibia articulates with the femur at its proximal end, with the fibula and the tarsal bones at its distal end. It is the second largest bone in the human body and is responsible for transmitting the weight of the body from the femur to the foot. The fibula, or calf bone, parallels and articulates with the tibia. It does not articulate with the femur and does not bear weight. The fibula acts as a site for muscle attachment and forms the lateral part of the ankle joint.

The tarsals are the seven bones of the ankle. The ankle transmits the weight of the body from the tibia and the fibula to the foot. The metatarsals are the five bones of the foot. The phalanges are the 14 bones of the toes. Each toe consists of three phalanges, except for the big toe that has only two (Figure **45.1.14**). Variations exist in other species; for example, the horse's metacarpals and metatarsals are oriented vertically and do not make contact with the substrate.

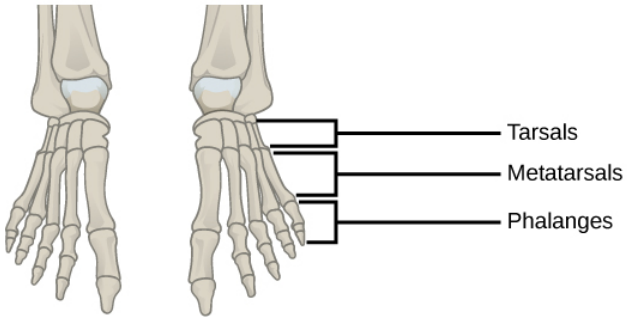


Figure **45.1.14**: This drawing shows the bones of the human foot and ankle, including the metatarsals and the phalanges.

Evolution Connection: Evolution of Body Design for Locomotion on Land

The transition of vertebrates onto land required a number of changes in body design, as movement on land presents a number of challenges for animals that are adapted to movement in water. The buoyancy of water provides a certain amount of lift, and a common form of movement by fish is lateral undulations of the entire body. This back and forth movement pushes the body against the water, creating forward movement. In most fish, the muscles of paired fins attach to girdles within the body, allowing for some control of locomotion. As certain fish began moving onto land, they retained their lateral undulation form of locomotion (anguilliform). However, instead of pushing against water, their fins or flippers became points of contact with the ground, around which they rotated their bodies.

The effect of gravity and the lack of buoyancy on land meant that body weight was suspended on the limbs, leading to increased strengthening and ossification of the limbs. The effect of gravity also required changes to the axial skeleton. Lateral undulations of land animal vertebral columns cause torsional strain. A firmer, more ossified vertebral column became common in terrestrial tetrapods because it reduces strain while providing the strength needed to support the body's weight. In later tetrapods, the vertebrae began allowing for vertical motion rather than lateral flexion. Another change in the axial skeleton was the loss of a direct attachment between the pectoral girdle and the head. This reduced the jarring to the head caused by the impact of the limbs on the ground. The vertebrae of the neck also evolved to allow movement of the head independently of the body.

The appendicular skeleton of land animals is also different from aquatic animals. The shoulders attach to the pectoral girdle through muscles and connective tissue, thus reducing the jarring of the skull. Because of a lateral undulating vertebral column, in early tetrapods, the limbs were splayed out to the side and movement occurred by performing "push-ups." The vertebrae of these animals had to move side-to-side in a similar manner to fish and reptiles. This type of motion requires large muscles to move the limbs toward the midline; it was almost like walking while doing push-ups, and it is not an efficient use of energy. Later tetrapods have their limbs placed under their bodies, so that each stride requires less force to move forward. This resulted in decreased adductor muscle size and an increased range of motion of the scapulae. This also restricts movement primarily to one plane, creating forward motion rather than moving the limbs upward as well as forward. The femur and humerus were also rotated, so that the ends of the limbs and digits were pointed forward, in the direction of motion, rather than out to the side. By placement underneath the body, limbs can swing forward like a pendulum to produce a stride that is more efficient for moving over land.

Summary

The three types of skeleton designs are hydrostatic skeletons, exoskeletons, and endoskeletons. A hydrostatic skeleton is formed by a fluid-filled compartment held under hydrostatic pressure; movement is created by the muscles producing pressure on the fluid. An exoskeleton is a hard external skeleton that protects the outer surface of an organism and enables movement through muscles attached on the inside. An endoskeleton is an internal skeleton composed of hard, mineralized tissue that also enables movement by attachment to muscles. The human skeleton is an endoskeleton that is composed of the axial and appendicular skeleton. The axial skeleton is composed of the bones of the skull, ossicles of the ear, hyoid bone, vertebral column, and ribcage. The skull consists of eight cranial bones and 14 facial bones. Six bones make up the ossicles of the middle ear, while the hyoid bone is located in the neck under the mandible. The vertebral column contains 26 bones, and it surrounds and protects the spinal cord. The thoracic cage consists of the sternum, ribs, thoracic vertebrae, and costal cartilages. The appendicular skeleton is made up of the limbs of the upper and lower limbs. The pectoral girdle is composed of the clavicles and the scapulae. The upper limb contains 30 bones in the arm, the forearm, and the hand. The pelvic girdle attaches the lower limbs to the axial skeleton. The lower limb includes the bones of the thigh, the leg, and the foot.

Glossary

appendicular skeleton

composed of the bones of the upper limbs, which function to grasp and manipulate objects, and the lower limbs, which permit locomotion

articulation

any place where two bones are joined

auditory ossicle
(also, middle ear) transduces sounds from the air into vibrations in the fluid-filled cochlea

axial skeleton
forms the central axis of the body and includes the bones of the skull, the ossicles of the middle ear, the hyoid bone of the throat, the vertebral column, and the thoracic cage (ribcage)

carpus
eight bones that comprise the wrist

clavicle
S-shaped bone that positions the arms laterally

coxal bone
hip bone

cranial bone
one of eight bones that form the cranial cavity that encloses the brain and serves as an attachment site for the muscles of the head and neck

endoskeleton
skeleton of living cells that produce a hard, mineralized tissue located within the soft tissue of organisms

exoskeleton
a secreted cellular product external skeleton that consists of a hard encasement on the surface of an organism

facial bone
one of the 14 bones that form the face; provides cavities for the sense organs (eyes, mouth, and nose) and attachment points for facial muscles

femur
(also, thighbone) longest, heaviest, and strongest bone in the body

fibula
(also, calf bone) parallels and articulates with the tibia

forearm
extends from the elbow to the wrist and consists of two bones: the ulna and the radius

humerus
only bone of the arm

hydrostatic skeleton
skeleton that consists of aqueous fluid held under pressure in a closed body compartment

hyoid bone
lies below the mandible in the front of the neck

intervertebral disc
composed of fibrous cartilage; lies between adjacent vertebrae from the second cervical vertebra to the sacrum

lower limb

consists of the thigh, the leg, and the foot

metacarpus
five bones that comprise the palm

metatarsal
one of the five bones of the foot

patella
(also, kneecap) triangular bone that lies anterior to the knee joint

pectoral girdle
bones that transmit the force generated by the upper limbs to the axial skeleton

phalange
one of the bones of the fingers or toes

pelvic girdle
bones that transmit the force generated by the lower limbs to the axial skeleton

radius
bone located along the lateral (thumb) side of the forearm; articulates with the humerus at the elbow

rib
one of 12 pairs of long, curved bones that attach to the thoracic vertebrae and curve toward the front of the body to form the ribcage

scapula
flat, triangular bone located at the posterior pectoral girdle

skull
bone that supports the structures of the face and protects the brain

sternum
(also, breastbone) long, flat bone located at the front of the chest

tarsal
one of the seven bones of the ankle

thoracic cage
(also, ribcage) skeleton of the chest, which consists of the ribs, thoracic vertebrae, sternum, and costal cartilages

tibia
(also, shinbone) large bone of the leg that is located directly below the knee

ulna
bone located on the medial aspect (pinky-finger side) of the forearm

vertebral column
(also, spine) surrounds and protects the spinal cord, supports the head, and acts as an attachment point for ribs and muscles of the back and neck

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45.2: A Closer Look at Bone

Skills to Develop

- Classify the different types of bones in the skeleton
- Explain the role of the different cell types in bone
- Explain how bone forms during development

Bone, or osseous tissue, is a connective tissue that constitutes the endoskeleton. It contains specialized cells and a matrix of mineral salts and collagen fibers.

The mineral salts primarily include hydroxyapatite, a mineral formed from calcium phosphate. Calcification is the process of deposition of mineral salts on the collagen fiber matrix that crystallizes and hardens the tissue. The process of calcification only occurs in the presence of collagen fibers.

The bones of the human skeleton are classified by their shape: long bones, short bones, flat bones, sutural bones, sesamoid bones, and irregular bones (Figure 45.2.1).

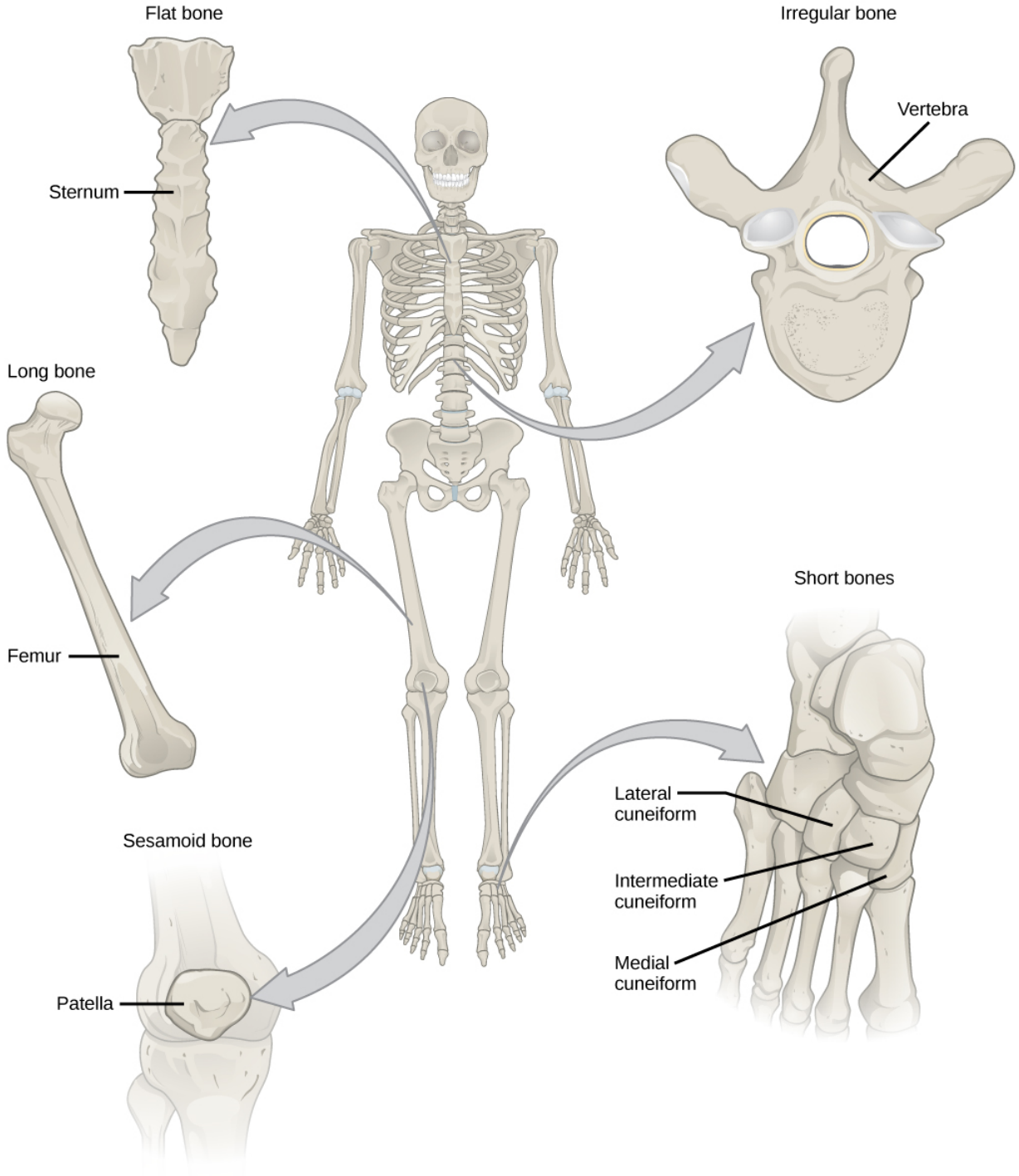


Figure **45.2.1**: Shown are different types of bones: flat, irregular, long, short, and sesamoid.

Long bones are longer than they are wide and have a shaft and two ends. The diaphysis, or central shaft, contains bone marrow in a marrow cavity. The rounded ends, the epiphyses, are covered with articular cartilage and are filled with red bone marrow, which produces blood cells (Figure **45.2.2**). Most of the limb bones are long bones—for example, the femur, tibia, ulna, and radius. Exceptions to this include the patella and the bones of the wrist and ankle.

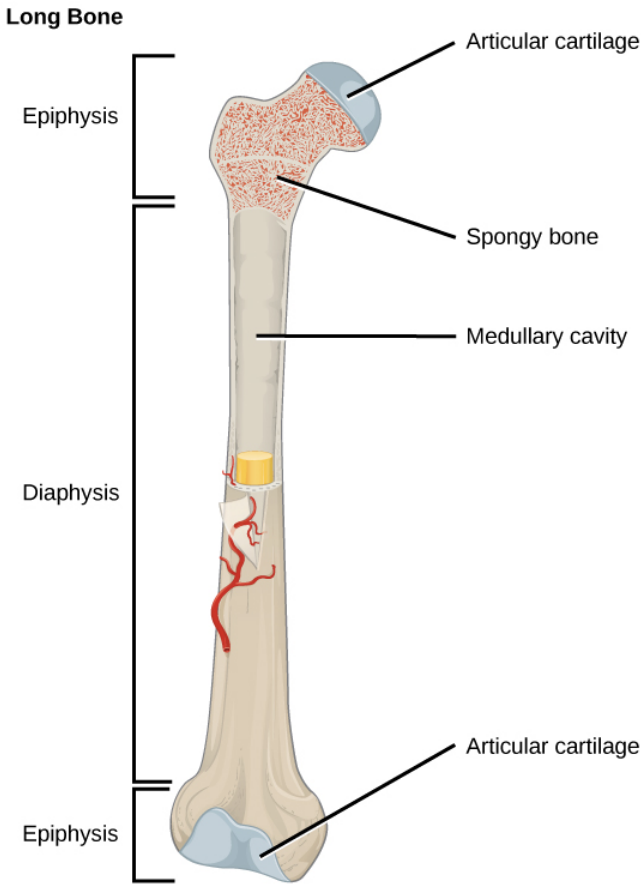


Figure **45.2.2:** The long bone is covered by articular cartilage at either end and contains bone marrow (shown in yellow in this illustration) in the marrow cavity.

Short bones, or cuboidal bones, are bones that are the same width and length, giving them a cube-like shape. For example, the bones of the wrist (carpals) and ankle (tarsals) are short bones (Figure **45.2.1**).

Flat bones are thin and relatively broad bones that are found where extensive protection of organs is required or where broad surfaces of muscle attachment are required. Examples of flat bones are the sternum (breast bone), ribs, scapulae (shoulder blades), and the roof of the skull (Figure **45.2.1**).

Irregular bones are bones with complex shapes. These bones may have short, flat, notched, or ridged surfaces. Examples of irregular bones are the vertebrae, hip bones, and several skull bones.

Sesamoid bones are small, flat bones and are shaped similarly to a sesame seed. The patellae are sesamoid bones (Figure **45.2.3**). Sesamoid bones develop inside tendons and may be found near joints at the knees, hands, and feet.



Figure **45.2.3**: The patella of the knee is an example of a sesamoid bone.

Sutural bones are small, flat, irregularly shaped bones. They may be found between the flat bones of the skull. They vary in number, shape, size, and position.

Bone Tissue

Bones are considered organs because they contain various types of tissue, such as blood, connective tissue, nerves, and bone tissue. Osteocytes, the living cells of bone tissue, form the mineral matrix of bones. There are two types of bone tissue: compact and spongy.

Compact Bone Tissue

Compact bone (or cortical bone) forms the hard external layer of all bones and surrounds the medullary cavity, or bone marrow. It provides protection and strength to bones. Compact bone tissue consists of units called osteons or Haversian systems. Osteons are cylindrical structures that contain a mineral matrix and living osteocytes connected by canaliculi, which transport blood. They are aligned parallel to the long axis of the bone. Each osteon consists of lamellae, which are layers of compact matrix that surround a central canal called the Haversian canal. The Haversian canal (osteonic canal) contains the bone's blood vessels and nerve fibers (Figure **45.2.4**). Osteons in compact bone tissue are aligned in the same direction along lines of stress and help the bone resist bending or fracturing. Therefore, compact bone tissue is prominent in areas of bone at which stresses are applied in only a few directions.

Art Connection

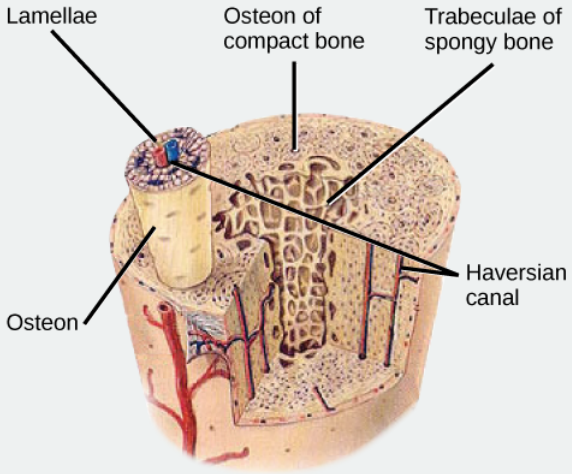


Figure 45.2.4: Compact bone tissue consists of osteons that are aligned parallel to the long axis of the bone, and the Haversian canal that contains the bone's blood vessels and nerve fibers. The inner layer of bones consists of spongy bone tissue. The small dark ovals in the osteon represent the living osteocytes. (credit: modification of work by NCI, NIH)

Which of the following statements about bone tissue is false?

A. Compact bone tissue is made of cylindrical osteons that are aligned such that they travel the length of the bone.
B. Haversian canals contain blood vessels only.
C. Haversian canals contain blood vessels and nerve fibers.
D. Spongy tissue is found on the interior of the bone, and compact bone tissue is found on the exterior.

Spongy Bone Tissue

Whereas compact bone tissue forms the outer layer of all bones, spongy bone or cancellous bone forms the inner layer of all bones. Spongy bone tissue does not contain osteons that constitute compact bone tissue. Instead, it consists of trabeculae, which are lamellae that are arranged as rods or plates. Red bone marrow is found between the trabuculae. Blood vessels within this tissue deliver nutrients to osteocytes and remove waste. The red bone marrow of the femur and the interior of other large bones, such as the ileum, forms blood cells.

Spongy bone reduces the density of bone and allows the ends of long bones to compress as the result of stresses applied to the bone. Spongy bone is prominent in areas of bones that are not heavily stressed or where stresses arrive from many directions. The epiphyses of bones, such as the neck of the femur, are subject to stress from many directions. Imagine laying a heavy framed picture flat on the floor. You could hold up one side of the picture with a toothpick if the toothpick was perpendicular to the floor and the picture. Now drill a hole and stick the toothpick into the wall to hang up the picture. In this case, the function of the toothpick is to transmit the downward pressure of the picture to the wall. The force on the picture is straight down to the floor, but the force on the toothpick is both the picture wire pulling down and the bottom of the hole in the wall pushing up. The toothpick will break off right at the wall.

The neck of the femur is horizontal like the toothpick in the wall. The weight of the body pushes it down near the joint, but the vertical diaphysis of the femur pushes it up at the other end. The neck of the femur must be strong enough to transfer the downward force of the body weight horizontally to the vertical shaft of the femur (Figure 45.2.5).

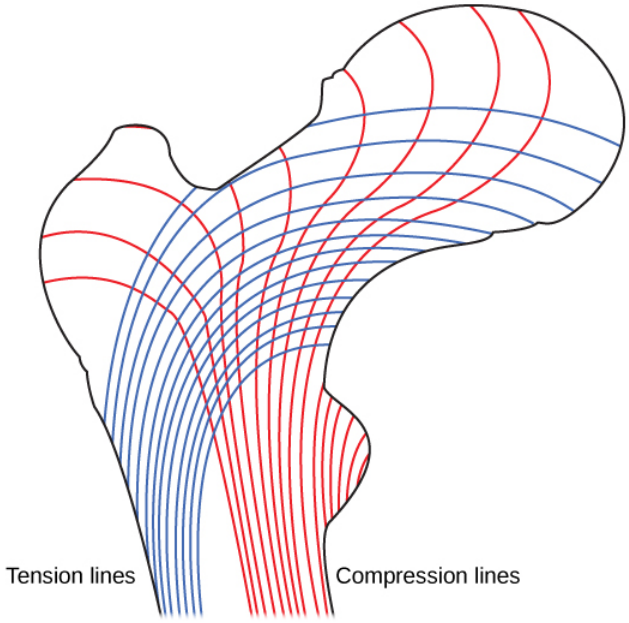


Figure 45.2.5: Trabeculae in spongy bone are arranged such that one side of the bone bears tension and the other withstands compression.

Link to Learning

View micrographs of musculoskeletal tissues as you review the anatomy.

Cell Types in Bones

Bone consists of four types of cells: osteoblasts, osteoclasts, osteocytes, and osteoprogenitor cells. Osteoblasts are bone cells that are responsible for bone formation. Osteoblasts synthesize and secrete the organic part and inorganic part of the extracellular matrix of bone tissue, and collagen fibers. Osteoblasts become trapped in these secretions and differentiate into less active osteocytes. Osteoclasts are large bone cells with up to 50 nuclei. They remove bone structure by releasing lysosomal enzymes and acids that dissolve the bony matrix. These minerals, released from bones into the blood, help regulate calcium concentrations in body fluids. Bone may also be resorbed for remodeling, if the applied stresses have changed. Osteocytes are mature bone cells and are the main cells in bony connective tissue; these cells cannot divide. Osteocytes maintain normal bone structure by recycling the mineral salts in the bony matrix. Osteoprogenitor cells are squamous stem cells that divide to produce daughter cells that differentiate into osteoblasts. Osteoprogenitor cells are important in the repair of fractures.

Development of Bone

Ossification, or osteogenesis, is the process of bone formation by osteoblasts. Ossification is distinct from the process of calcification; whereas calcification takes place during the ossification of bones, it can also occur in other tissues. Ossification begins approximately six weeks after fertilization in an embryo. Before this time, the embryonic skeleton consists entirely of fibrous membranes and hyaline cartilage. The development of bone from fibrous membranes is called intramembranous ossification; development from hyaline cartilage is called endochondral ossification. Bone growth continues until approximately age 25. Bones can grow in thickness throughout life, but after age 25, ossification functions primarily in bone remodeling and repair.

Intramembranous Ossification

Intramembranous ossification is the process of bone development from fibrous membranes. It is involved in the formation of the flat bones of the skull, the mandible, and the clavicles. Ossification begins as mesenchymal cells form a template of the future bone. They then differentiate into osteoblasts at the ossification center. Osteoblasts secrete the extracellular matrix and deposit calcium, which hardens the matrix. The non-mineralized portion of the bone or osteoid continues to form around blood vessels, forming spongy bone. Connective tissue in the matrix differentiates into red bone marrow in the fetus. The spongy bone is remodeled into a thin layer of compact bone on the surface of the spongy bone.

Endochondral Ossification

Endochondral ossification is the process of bone development from hyaline cartilage. All of the bones of the body, except for the flat bones of the skull, mandible, and clavicles, are formed through endochondral ossification.

In long bones, chondrocytes form a template of the hyaline cartilage diaphysis. Responding to complex developmental signals, the matrix begins to calcify. This calcification prevents diffusion of nutrients into the matrix, resulting in chondrocytes dying and the opening up of cavities in the diaphysis cartilage. Blood vessels invade the cavities, and osteoblasts and osteoclasts modify the calcified cartilage matrix into spongy bone. Osteoclasts then break down some of the spongy bone to create a marrow, or medullary, cavity in the center of the diaphysis. Dense, irregular connective tissue forms a sheath (periosteum) around the bones. The periosteum assists in attaching the bone to surrounding tissues, tendons, and ligaments. The bone continues to grow and elongate as the cartilage cells at the epiphyses divide.

In the last stage of prenatal bone development, the centers of the epiphyses begin to calcify. Secondary ossification centers form in the epiphyses as blood vessels and osteoblasts enter these areas and convert hyaline cartilage into spongy bone. Until adolescence, hyaline cartilage persists at the epiphyseal plate (growth plate), which is the region between the diaphysis and epiphysis that is responsible for the lengthwise growth of long bones (Figure **45.2.6**).

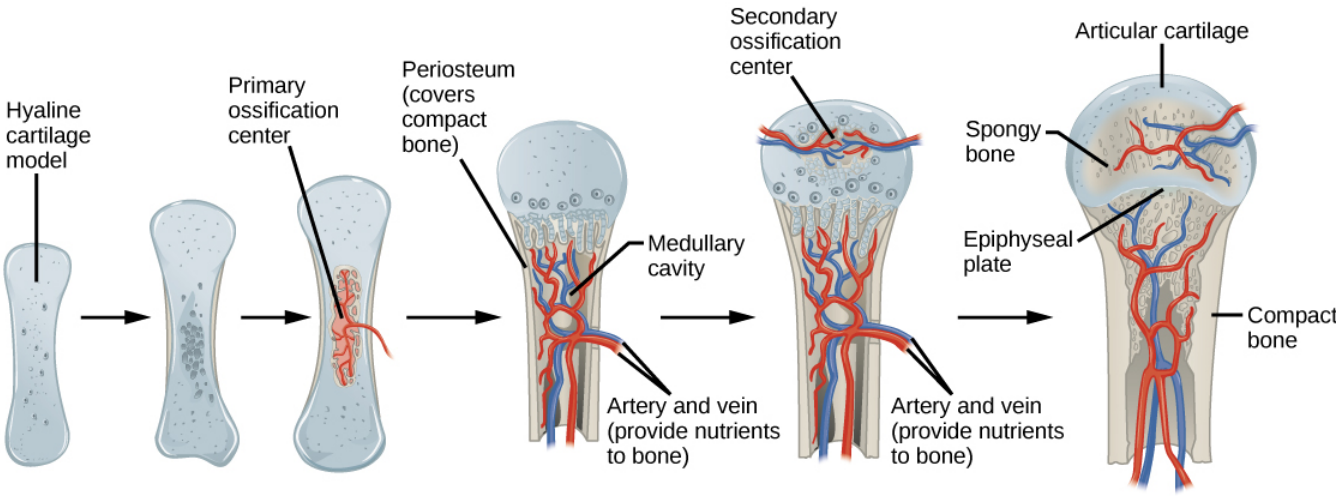


Figure **45.2.6**: Endochondral ossification is the process of bone development from hyaline cartilage. The periosteum is the connective tissue on the outside of bone that acts as the interface between bone, blood vessels, tendons, and ligaments.

Growth of Bone

Long bones continue to lengthen, potentially until adolescence, through the addition of bone tissue at the epiphyseal plate. They also increase in width through appositional growth.

Lengthening of Long Bones

Chondrocytes on the epiphyseal side of the epiphyseal plate divide; one cell remains undifferentiated near the epiphysis, and one cell moves toward the diaphysis. The cells, which are pushed from the epiphysis, mature and are destroyed by calcification. This process replaces cartilage with bone on the diaphyseal side of the plate, resulting in a lengthening of the bone.

Long bones stop growing at around the age of 18 in females and the age of 21 in males in a process called epiphyseal plate closure. During this process, cartilage cells stop dividing and all of the cartilage is replaced by bone. The epiphyseal plate fades, leaving a structure called the epiphyseal line or epiphyseal remnant, and the epiphysis and diaphysis fuse.

Thickening of Long Bones

Appositional growth is the increase in the diameter of bones by the addition of bony tissue at the surface of bones. Osteoblasts at the bone surface secrete bone matrix, and osteoclasts on the inner surface break down bone. The osteoblasts differentiate into osteocytes. A balance between these two processes allows the bone to thicken without becoming too heavy.

Bone Remodeling and Repair

Bone renewal continues after birth into adulthood. Bone remodeling is the replacement of old bone tissue by new bone tissue. It involves the processes of bone deposition by osteoblasts and bone resorption by osteoclasts. Normal bone growth requires vitamins D, C, and A, plus minerals such as calcium, phosphorous, and magnesium. Hormones such as parathyroid hormone, growth hormone, and calcitonin are also required for proper bone growth and maintenance.

Bone turnover rates are quite high, with five to seven percent of bone mass being recycled every week. Differences in turnover rate exist in different areas of the skeleton and in different areas of a bone. For example, the bone in the head of the femur may be fully replaced every six months, whereas the bone along the shaft is altered much more slowly.

Bone remodeling allows bones to adapt to stresses by becoming thicker and stronger when subjected to stress. Bones that are not subject to normal stress, for example when a limb is in a cast, will begin to lose mass. A fractured or broken bone undergoes repair through four stages:

1. Blood vessels in the broken bone tear and hemorrhage, resulting in the formation of clotted blood, or a hematoma, at the site of the break. The severed blood vessels at the broken ends of the bone are sealed by the clotting process, and bone cells that are deprived of nutrients begin to die.
2. Within days of the fracture, capillaries grow into the hematoma, and phagocytic cells begin to clear away the dead cells. Though fragments of the blood clot may remain, fibroblasts and osteoblasts enter the area and begin to reform bone. Fibroblasts produce collagen fibers that connect the broken bone ends, and osteoblasts start to form spongy bone. The repair tissue between the broken bone ends is called the fibrocartilaginous callus, as it is composed of both hyaline and fibrocartilage (Figure 45.2.7). Some bone spicules may also appear at this point.
3. The fibrocartilaginous callus is converted into a bony callus of spongy bone. It takes about two months for the broken bone ends to be firmly joined together after the fracture. This is similar to the endochondral formation of bone, as cartilage becomes ossified; osteoblasts, osteoclasts, and bone matrix are present.
4. The bony callus is then remodelled by osteoclasts and osteoblasts, with excess material on the exterior of the bone and within the medullary cavity being removed. Compact bone is added to create bone tissue that is similar to the original, unbroken bone. This remodeling can take many months, and the bone may remain uneven for years.



Figure 45.2.7: After this bone is set, a callus will knit the two ends together. (credit: Bill Rhodes)

Scientific Method Connection: Decalcification of Bones

Question: What effect does the removal of calcium and collagen have on bone structure?

Background: Conduct a literature search on the role of calcium and collagen in maintaining bone structure. Conduct a literature search on diseases in which bone structure is compromised.

Hypothesis: Develop a hypothesis that states predictions of the flexibility, strength, and mass of bones that have had the calcium and collagen components removed. Develop a hypothesis regarding the attempt to add calcium back to decalcified bones.

Test the hypothesis: Test the prediction by removing calcium from chicken bones by placing them in a jar of vinegar for seven days. Test the hypothesis regarding adding calcium back to decalcified bone by placing the decalcified chicken bones into a jar of water with calcium supplements added. Test the prediction by denaturing the collagen from the bones by baking them at 250°C for three hours.

Analyze the data: Create a table showing the changes in bone flexibility, strength, and mass in the three different environments.

Report the results: Under which conditions was the bone most flexible? Under which conditions was the bone the strongest?

Draw a conclusion: Did the results support or refute the hypothesis? How do the results observed in this experiment correspond to diseases that destroy bone tissue?

Summary

Bone, or osseous tissue, is connective tissue that includes specialized cells, mineral salts, and collagen fibers. The human skeleton can be divided into long bones, short bones, flat bones, and irregular bones. Compact bone tissue is composed of osteons and forms

the external layer of all bones. Spongy bone tissue is composed of trabeculae and forms the inner part of all bones. Four types of cells compose bony tissue: osteocytes, osteoclasts, osteoprogenitor cells, and osteoblasts. Ossification is the process of bone formation by osteoblasts. Intramembranous ossification is the process of bone development from fibrous membranes. Endochondral ossification is the process of bone development from hyaline cartilage. Long bones lengthen as chondrocytes divide and secrete hyaline cartilage. Osteoblasts replace cartilage with bone. Appositional growth is the increase in the diameter of bones by the addition of bone tissue at the surface of bones. Bone remodeling involves the processes of bone deposition by osteoblasts and bone resorption by osteoclasts. Bone repair occurs in four stages and can take several months.

Art Exercise

Figure 45.2.4: Which of the following statements about bone tissue is false?

A. Compact bone tissue is made of cylindrical osteons that are aligned such that they travel the length of the bone.
B. Haversian canals contain blood vessels only.
C. Haversian canals contain blood vessels and nerve fibers.
D. Spongy tissue is found on the interior of the bone, and compact bone tissue is found on the exterior.

Answer

B

Glossary

appositional growth
increase in the diameter of bones by the addition of bone tissue at the surface of bones

bone
(also, osseous tissue) connective tissue that constitutes the endoskeleton

bone remodeling
replacement of old bone tissue by new bone tissue

calcification
process of deposition of mineral salts in the collagen fiber matrix that crystallizes and hardens the tissue

compact bone
forms the hard external layer of all bones

diaphysis
central shaft of bone, contains bone marrow in a marrow cavity

endochondral ossification
process of bone development from hyaline cartilage

epiphyseal plate
region between the diaphysis and epiphysis that is responsible for the lengthwise growth of long bones

epiphysis
rounded end of bone, covered with articular cartilage and filled with red bone marrow, which produces blood cells

flat bone
thin and relatively broad bone found where extensive protection of organs is required or where broad surfaces of muscle attachment are required

Haversian canal
contains the bone's blood vessels and nerve fibers

intramembranous ossification
process of bone development from fibrous membranes

irregular bone
bone with complex shapes; examples include vertebrae and hip bones

lamella
layer of compact tissue that surrounds a central canal called the Haversian canal

long bone
bone that is longer than wide, and has a shaft and two ends

osteoblast
bone cell responsible for bone formation

osteoclast
large bone cells with up to 50 nuclei, responsible for bone remodeling

osteocyte
mature bone cells and the main cell in bone tissue

osseous tissue
connective tissue that constitutes the endoskeleton

ossification
(also, osteogenesis) process of bone formation by osteoblasts

osteon
cylindrical structure aligned parallel to the long axis of the bone

resorption
process by which osteoclasts release minerals stored in bones

sesamoid bone
small, flat bone shaped like a sesame seed; develops inside tendons

short bone
bone that has the same width and length, giving it a cube-like shape

spongy bone tissue
forms the inner layer of all bones

suture bone
small, flat, irregularly shaped bone that forms between the flat bones of the cranium

trabeculae
lamellae that are arranged as rods or plates

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45.3: Joints

Skills to Develop

- Classify the different types of joints on the basis of structure
- Explain the role of joints in skeletal movement

The point at which two or more bones meet is called a joint, or articulation. Joints are responsible for movement, such as the movement of limbs, and stability, such as the stability found in the bones of the skull.

Classification of Joints on the Basis of Structure

There are two ways to classify joints: on the basis of their structure or on the basis of their function. The structural classification divides joints into bony, fibrous, cartilaginous, and synovial joints depending on the material composing the joint and the presence or absence of a cavity in the joint.

Fibrous Joints

The bones of fibrous joints are held together by fibrous connective tissue. There is no cavity, or space, present between the bones and so most fibrous joints do not move at all, or are only capable of minor movements. There are three types of fibrous joints: sutures, syndesmoses, and gomphoses. Sutures are found only in the skull and possess short fibers of connective tissue that hold the skull bones tightly in place (Figure **45.3.1**).

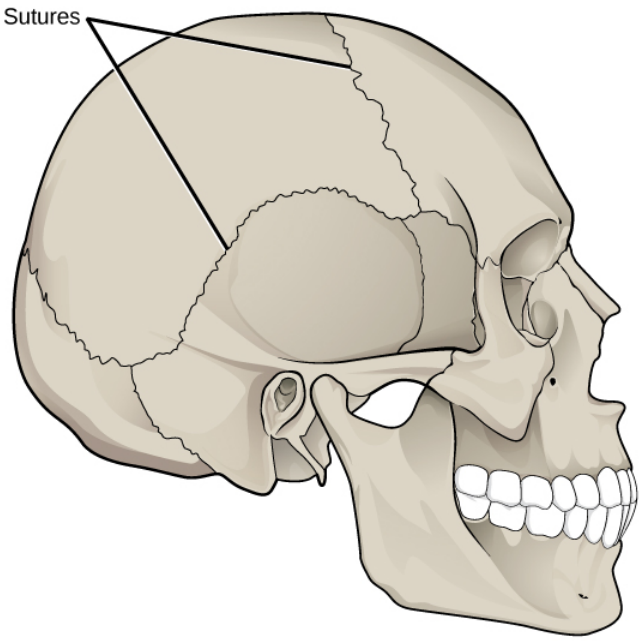


Figure **45.3.1**: Sutures are fibrous joints found only in the skull.

Syndesmoses are joints in which the bones are connected by a band of connective tissue, allowing for more movement than in a suture. An example of a syndesmosis is the joint of the tibia and fibula in the ankle. The amount of movement in these types of joints is determined by the length of the connective tissue fibers. Gomphoses occur between teeth and their sockets; the term refers to the way the tooth fits into the socket like a peg (Figure **45.3.2**). The tooth is connected to the socket by a connective tissue referred to as the periodontal ligament.

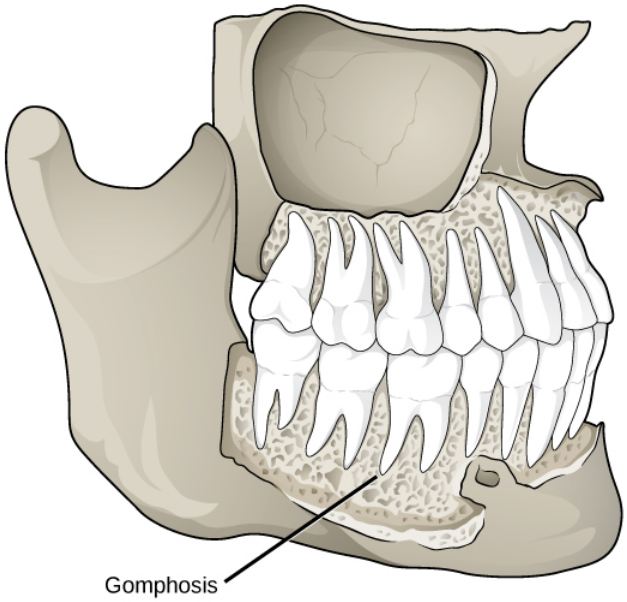


Figure **45.3.2**: Gomphoses are fibrous joints between the teeth and their sockets. (credit: modification of work by Gray's Anatomy)

Cartilaginous Joints

Cartilaginous joints are joints in which the bones are connected by cartilage. There are two types of cartilaginous joints: synchondroses and symphyses. In a synchondrosis, the bones are joined by hyaline cartilage. Synchondroses are found in the epiphyseal plates of growing bones in children. In symphyses, hyaline cartilage covers the end of the bone but the connection between bones occurs through fibrocartilage. Symphyses are found at the joints between vertebrae. Either type of cartilaginous joint allows for very little movement.

Synovial Joints

Synovial joints are the only joints that have a space between the adjoining bones (Figure **45.3.3**). This space is referred to as the synovial (or joint) cavity and is filled with synovial fluid. Synovial fluid lubricates the joint, reducing friction between the bones and allowing for greater movement. The ends of the bones are covered with articular cartilage, a hyaline cartilage, and the entire joint is surrounded by an articular capsule composed of connective tissue that allows movement of the joint while resisting dislocation. Articular capsules may also possess ligaments that hold the bones together. Synovial joints are capable of the greatest movement of the three structural joint types; however, the more mobile a joint, the weaker the joint. Knees, elbows, and shoulders are examples of synovial joints.

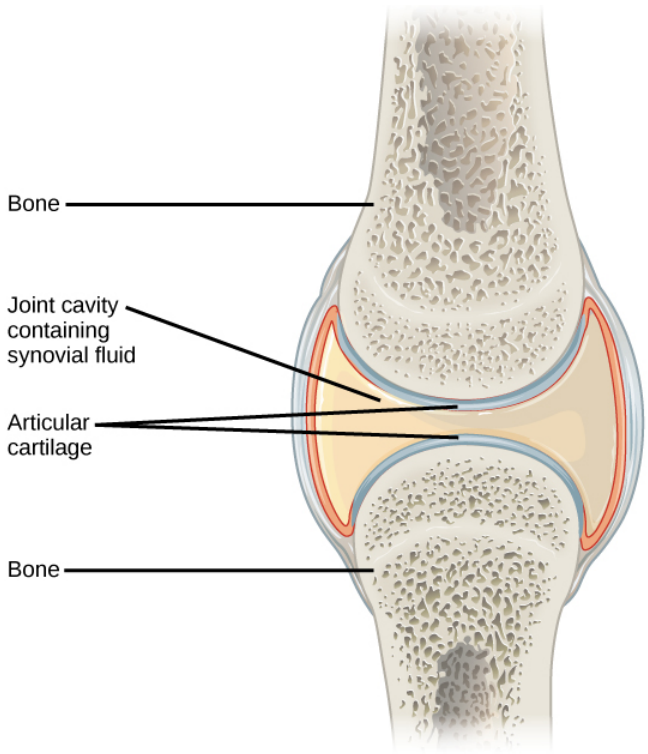


Figure **45.3.3**: Synovial joints are the only joints that have a space or "synovial cavity" in the joint.

Classification of Joints on the Basis of Function

The functional classification divides joints into three categories: synarthroses, amphiarthroses, and diarthroses. A synarthrosis is a joint that is immovable. This includes sutures, gomphoses, and synchondroses. Amphiarthroses are joints that allow slight movement, including syndesmoses and symphyses. Diarthroses are joints that allow for free movement of the joint, as in synovial joints.

Movement at Synovial Joints

The wide range of movement allowed by synovial joints produces different types of movements. The movement of synovial joints can be classified as one of four different types: gliding, angular, rotational, or special movement.

Gliding Movement

Gliding movements occur as relatively flat bone surfaces move past each other. Gliding movements produce very little rotation or angular movement of the bones. The joints of the carpal and tarsal bones are examples of joints that produce gliding movements.

Angular Movement

Angular movements are produced when the angle between the bones of a joint changes. There are several different types of angular movements, including flexion, extension, hyperextension, abduction, adduction, and circumduction. Flexion, or bending, occurs when the angle between the bones decreases. Moving the forearm upward at the elbow or moving the wrist to move the hand toward the forearm are examples of flexion. Extension is the opposite of flexion in that the angle between the bones of a joint increases. Straightening a limb after flexion is an example of extension. Extension past the regular anatomical position is referred to as hyperextension. This includes moving the neck back to look upward, or bending the wrist so that the hand moves away from the forearm.

Abduction occurs when a bone moves away from the midline of the body. Examples of abduction are moving the arms or legs laterally to lift them straight out to the side. Adduction is the movement of a bone toward the midline of the body. Movement of the limbs inward after abduction is an example of adduction. Circumduction is the movement of a limb in a circular motion, as in moving the arm in a circular motion.

Rotational Movement

Rotational movement is the movement of a bone as it rotates around its longitudinal axis. Rotation can be toward the midline of the body, which is referred to as medial rotation, or away from the midline of the body, which is referred to as lateral rotation. Movement of the head from side to side is an example of rotation.

Special Movements

Some movements that cannot be classified as gliding, angular, or rotational are called special movements. Inversion involves the soles of the feet moving inward, toward the midline of the body. Eversion is the opposite of inversion, movement of the sole of the foot outward, away from the midline of the body. Protraction is the anterior movement of a bone in the horizontal plane. Retraction occurs as a joint moves back into position after protraction. Protraction and retraction can be seen in the movement of the mandible as the jaw is thrust outwards and then back inwards. Elevation is the movement of a bone upward, such as when the shoulders are shrugged, lifting the scapulae. Depression is the opposite of elevation—movement downward of a bone, such as after the shoulders are shrugged and the scapulae return to their normal position from an elevated position. Dorsiflexion is a bending at the ankle such that the toes are lifted toward the knee. Plantar flexion is a bending at the ankle when the heel is lifted, such as when standing on the toes. Supination is the movement of the radius and ulna bones of the forearm so that the palm faces forward. Pronation is the opposite movement, in which the palm faces backward. Opposition is the movement of the thumb toward the fingers of the same hand, making it possible to grasp and hold objects.

Types of Synovial Joints

Synovial joints are further classified into six different categories on the basis of the shape and structure of the joint. The shape of the joint affects the type of movement permitted by the joint (Figure **45.3.4**). These joints can be described as planar, hinge, pivot, condyloid, saddle, or ball-and-socket joints.

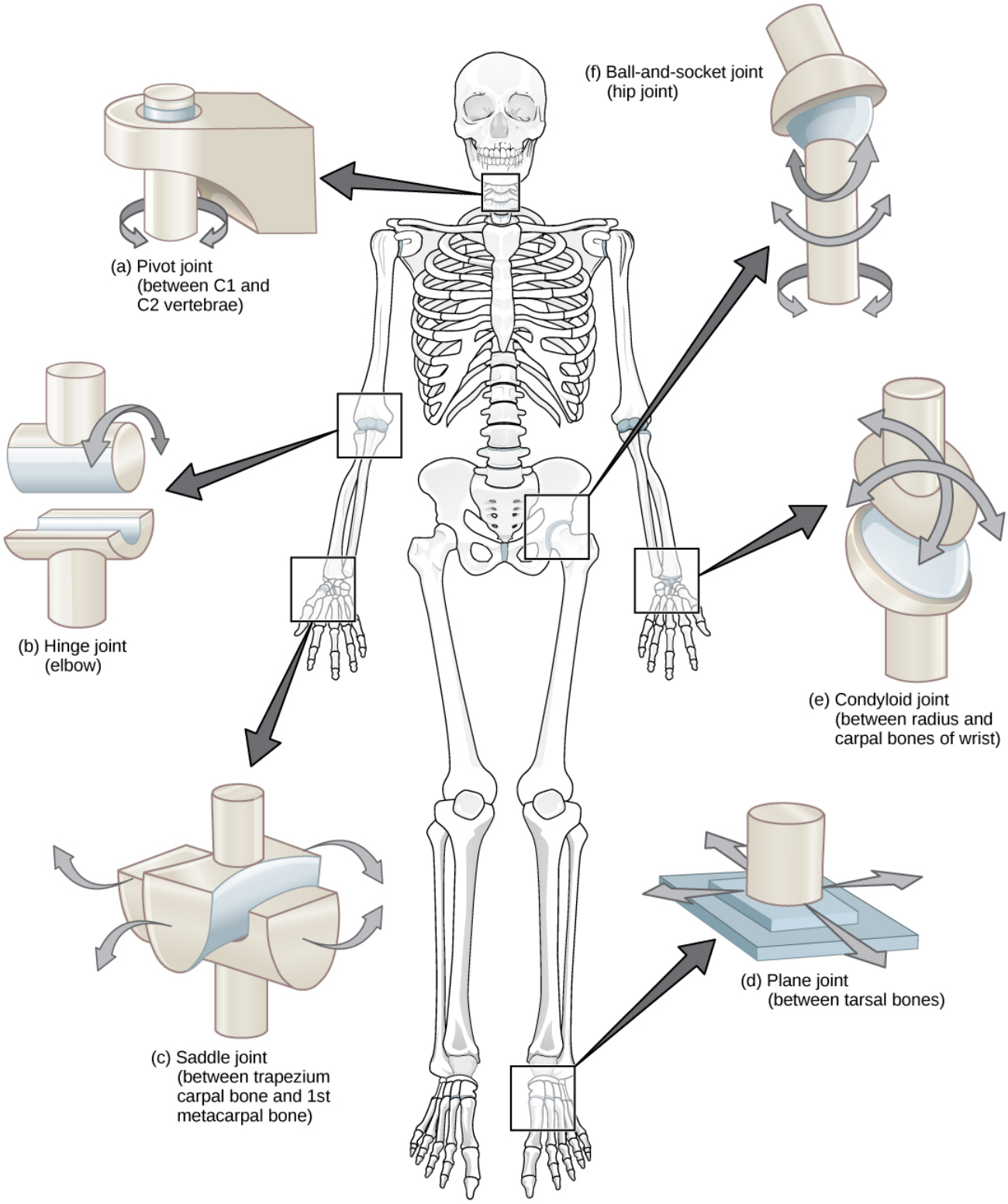


Figure 45.3.4: Different types of joints allow different types of movement. Planar, hinge, pivot, condyloid, saddle, and ball-and-socket are all types of synovial joints.

Planar Joints

Planar joints have bones with articulating surfaces that are flat or slightly curved faces. These joints allow for gliding movements, and so the joints are sometimes referred to as gliding joints. The range of motion is limited in these joints and does not involve

rotation. Planar joints are found in the carpal bones in the hand and the tarsal bones of the foot, as well as between vertebrae (Figure 45.3.5).

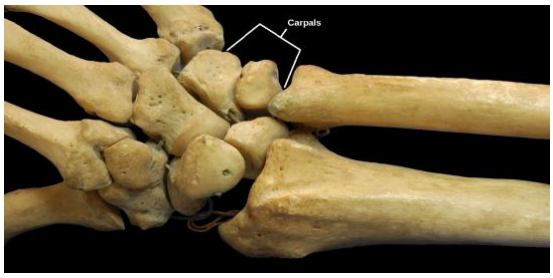


Figure 45.3.5: The joints of the carpal bones in the wrist are examples of planar joints. (credit: modification of work by Brian C. Goss)

Hinge Joints

In hinge joints, the slightly rounded end of one bone fits into the slightly hollow end of the other bone. In this way, one bone moves while the other remains stationary, like the hinge of a door. The elbow is an example of a hinge joint. The knee is sometimes classified as a modified hinge joint (Figure 45.3.6).



Figure 45.3.6: The elbow joint, where the radius articulates with the humerus, is an example of a hinge joint. (credit: modification of work by Brian C. Goss)

Pivot Joints

Pivot joints consist of the rounded end of one bone fitting into a ring formed by the other bone. This structure allows rotational movement, as the rounded bone moves around its own axis. An example of a pivot joint is the joint of the first and second vertebrae of the neck that allows the head to move back and forth (Figure 45.3.7). The joint of the wrist that allows the palm of the hand to be turned up and down is also a pivot joint.

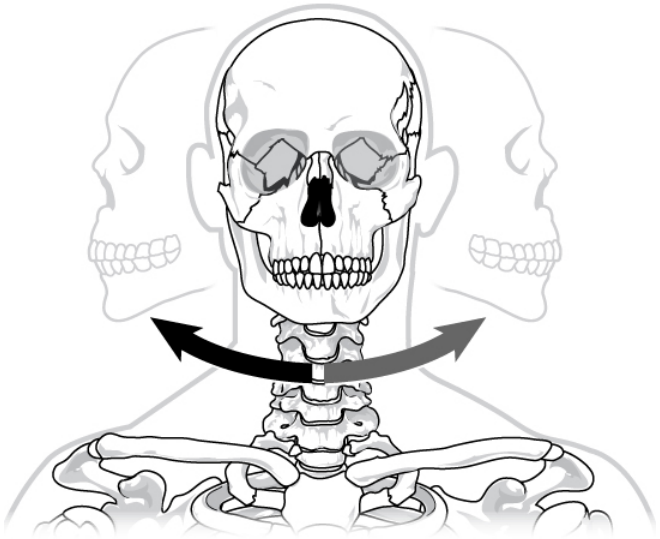


Figure **45.3.7**: The joint in the neck that allows the head to move back and forth is an example of a pivot joint.

Condyloid Joints

Condyloid joints consist of an oval-shaped end of one bone fitting into a similarly oval-shaped hollow of another bone (Figure **45.3.8**). This is also sometimes called an ellipsoidal joint. This type of joint allows angular movement along two axes, as seen in the joints of the wrist and fingers, which can move both side to side and up and down.

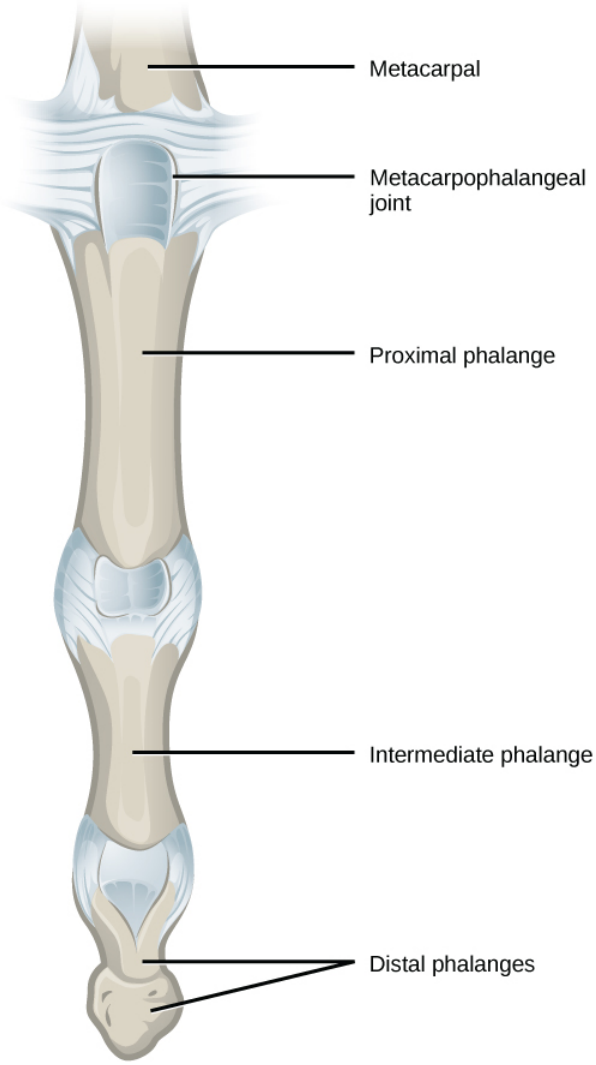


Figure **45.3.8**: The metacarpophalangeal joints in the finger are examples of condyloid joints. (credit: modification of work by Gray's Anatomy)

Saddle Joints

Saddle joints are so named because the ends of each bone resemble a saddle, with concave and convex portions that fit together. Saddle joints allow angular movements similar to condyloid joints but with a greater range of motion. An example of a saddle joint is the thumb joint, which can move back and forth and up and down, but more freely than the wrist or fingers (Figure **45.3.9**).

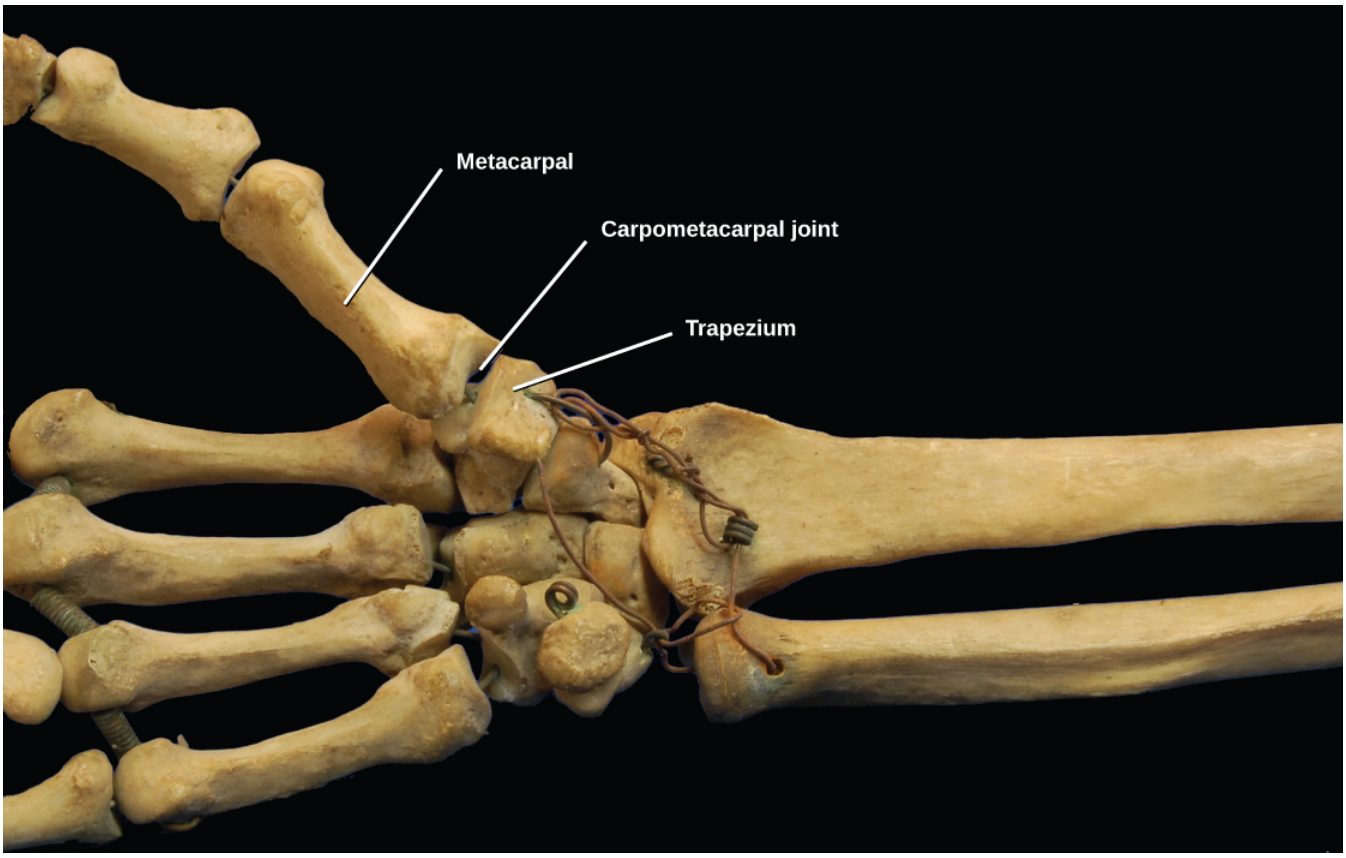


Figure 45.3.9: The carpometacarpal joints in the thumb are examples of saddle joints. (credit: modification of work by Brian C. Goss)

Ball-and-Socket Joints

Ball-and-socket joints possess a rounded, ball-like end of one bone fitting into a cuplike socket of another bone. This organization allows the greatest range of motion, as all movement types are possible in all directions. Examples of ball-and-socket joints are the shoulder and hip joints (Figure 45.3.10).

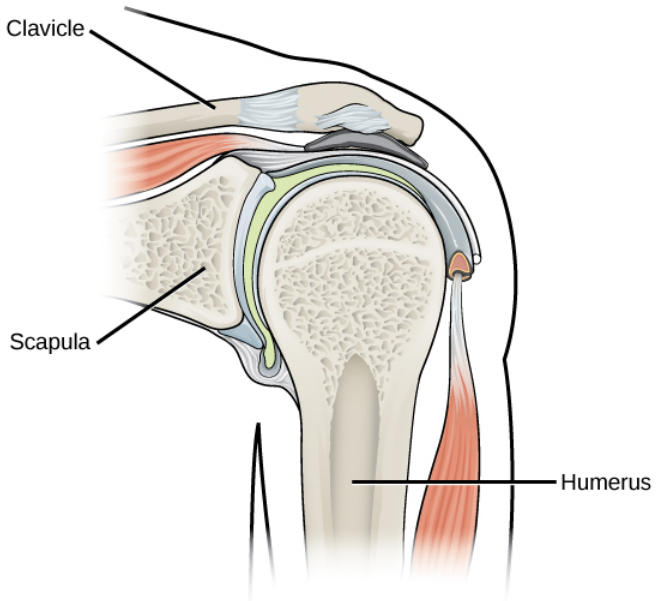


Figure 45.3.10: The shoulder joint is an example of a ball-and-socket joint.

Link to Learning



Watch this animation showing the six types of synovial joints.

Career Connection: Rheumatologist

Rheumatologists are medical doctors who specialize in the diagnosis and treatment of disorders of the joints, muscles, and bones. They diagnose and treat diseases such as arthritis, musculoskeletal disorders, osteoporosis, and autoimmune diseases such as ankylosing spondylitis and rheumatoid arthritis.

Rheumatoid arthritis (RA) is an inflammatory disorder that primarily affects the synovial joints of the hands, feet, and cervical spine. Affected joints become swollen, stiff, and painful. Although it is known that RA is an autoimmune disease in which the body's immune system mistakenly attacks healthy tissue, the cause of RA remains unknown. Immune cells from the blood enter joints and the synovium causing cartilage breakdown, swelling, and inflammation of the joint lining. Breakdown of cartilage causes bones to rub against each other causing pain. RA is more common in women than men and the age of onset is usually 40–50 years of age.

Rheumatologists can diagnose RA on the basis of symptoms such as joint inflammation and pain, X-ray and MRI imaging, and blood tests. Arthrography is a type of medical imaging of joints that uses a contrast agent, such as a dye, that is opaque to X-rays. This allows the soft tissue structures of joints—such as cartilage, tendons, and ligaments—to be visualized. An arthrogram differs from a regular X-ray by showing the surface of soft tissues lining the joint in addition to joint bones. An arthrogram allows early degenerative changes in joint cartilage to be detected before bones become affected.

There is currently no cure for RA; however, rheumatologists have a number of treatment options available. Early stages can be treated with rest of the affected joints by using a cane or by using joint splints that minimize inflammation. When inflammation has decreased, exercise can be used to strengthen the muscles that surround the joint and to maintain joint flexibility. If joint damage is more extensive, medications can be used to relieve pain and decrease inflammation. Anti-inflammatory drugs such as aspirin, topical pain relievers, and corticosteroid injections may be used. Surgery may be required in cases in which joint damage is severe.

Summary

The structural classification of joints divides them into bony, fibrous, cartilaginous, and synovial joints. The bones of fibrous joints are held together by fibrous connective tissue; the three types of fibrous joints are sutures, syndesomes, and gomphoses. Cartilaginous joints are joints in which the bones are connected by cartilage; the two types of cartilaginous joints are synchondroses and symphyses. Synovial joints are joints that have a space between the adjoining bones. The functional classification divides joints into three categories: synarthroses, amphiarthroses, and diarthroses. The movement of synovial joints can be classified as one of four different types: gliding, angular, rotational, or special movement. Gliding movements occur as relatively flat bone surfaces move past each other. Angular movements are produced when the angle between the bones of a joint changes. Rotational movement is the movement of a bone as it rotates around its own longitudinal axis. Special movements include inversion, eversion, protraction, retraction, elevation, depression, dorsiflexion, plantar flexion, supination, pronation, and opposition. Synovial joints

are also classified into six different categories on the basis of the shape and structure of the joint: planar, hinge, pivot, condyloid, saddle, and ball-and-socket.

Glossary

abduction
when a bone moves away from the midline of the body

adduction
movement of the limbs inward after abduction

amphiarthrosis
joint that allows slight movement; includes syndesmoses and symphyses

angular movement
produced when the angle between the bones of a joint changes

ball-and-socket joint
joint with a rounded, ball-like end of one bone fitting into a cuplike socket of another bone

cartilaginous joint
joint in which the bones are connected by cartilage

circumduction
movement of a limb in a circular motion.

condyloid joint
oval-shaped end of one bone fitting into a similarly oval-shaped hollow of another bone

depression
movement downward of a bone, such as after the shoulders are shrugged and the scapulae return to their normal position from an elevated position; opposite of elevation

diarthrosis
joint that allows for free movement of the joint; found in synovial joints

dorsiflexion
bending at the ankle such that the toes are lifted toward the knee

elevation
movement of a bone upward, such as when the shoulders are shrugged, lifting the scapulae

eversion
movement of the sole of the foot outward, away from the midline of the body; opposite of inversion

extension
movement in which the angle between the bones of a joint increases; opposite of flexion

fibrous joint
joint held together by fibrous connective tissue

flexion
movement in which the angle between the bones decreases; opposite of extension

gliding movement
when relatively flat bone surfaces move past each other

gomphosis
the joint in which the tooth fits into the socket like a peg

hinge joint
slightly rounded end of one bone fits into the slightly hollow end of the other bone

hyperextension
extension past the regular anatomical position

inversion
soles of the feet moving inward, toward the midline of the body

joint
point at which two or more bones meet

lateral rotation
rotation away from the midline of the body

medial rotation
rotation toward the midline of the body

opposition
movement of the thumb toward the fingers of the same hand, making it possible to grasp and hold objects

plantar flexion
bending at the ankle such that the heel is lifted, such as when standing on the toes

planar joint
joint with bones whose articulating surfaces are flat

pivot joint
joint with the rounded end of one bone fitting into a ring formed by the other bone

pronation
movement in which the palm faces backward

protraction
anterior movement of a bone in the horizontal plane

retraction
movement in which a joint moves back into position after protraction

rotational movement
movement of a bone as it rotates around its own longitudinal axis

saddle joint
joint with concave and convex portions that fit together; named because the ends of each bone resemble a saddle

supination
movement of the radius and ulna bones of the forearm so that the palm faces forward

suture

short fiber of connective tissue that holds the skull bones tightly in place; found only in the skull

synarthrosis

joint that is immovable

symphysis

hyaline cartilage covers the end of the bone, but the connection between bones occurs through fibrocartilage; symphyses are found at the joints between vertebrae

synchondrosis

bones joined by hyaline cartilage; synchondroses are found in the epiphyseal plates of growing bones in children

syndesmosis

joint in which the bones are connected by a band of connective tissue, allowing for more movement than in a suture

synovial joint

only joint that has a space between the adjoining bones

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45.4: Muscle Contraction

Skills to Develop

- Classify the different types of muscle tissue
- Explain the role of muscles in locomotion

Muscle cells are specialized for contraction. Muscles allow for motions such as walking, and they also facilitate bodily processes such as respiration and digestion. The body contains three types of muscle tissue: skeletal muscle, cardiac muscle, and smooth muscle (Figure 45.4.1).

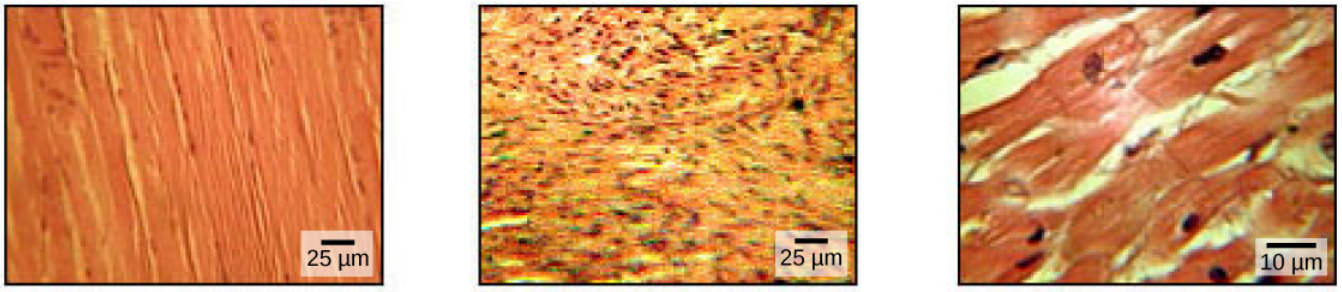


Figure 45.4.1: The body contains three types of muscle tissue: skeletal muscle, smooth muscle, and cardiac muscle, visualized here using light microscopy. Smooth muscle cells are short, tapered at each end, and have only one plump nucleus in each. Cardiac muscle cells are branched and striated, but short. The cytoplasm may branch, and they have one nucleus in the center of the cell. (credit: modification of work by NCI, NIH; scale-bar data from Matt Russell)

Skeletal muscle tissue forms skeletal muscles, which attach to bones or skin and control locomotion and any movement that can be consciously controlled. Because it can be controlled by thought, skeletal muscle is also called voluntary muscle. Skeletal muscles are long and cylindrical in appearance; when viewed under a microscope, skeletal muscle tissue has a striped or striated appearance. The striations are caused by the regular arrangement of contractile proteins (actin and myosin). Actin is a globular contractile protein that interacts with myosin for muscle contraction. Skeletal muscle also has multiple nuclei present in a single cell.

Smooth muscle tissue occurs in the walls of hollow organs such as the intestines, stomach, and urinary bladder, and around passages such as the respiratory tract and blood vessels. Smooth muscle has no striations, is not under voluntary control, has only one nucleus per cell, is tapered at both ends, and is called involuntary muscle.

Cardiac muscle tissue is only found in the heart, and cardiac contractions pump blood throughout the body and maintain blood pressure. Like skeletal muscle, cardiac muscle is striated, but unlike skeletal muscle, cardiac muscle cannot be consciously controlled and is called involuntary muscle. It has one nucleus per cell, is branched, and is distinguished by the presence of intercalated disks.

Skeletal Muscle Fiber Structure

Each skeletal muscle fiber is a skeletal muscle cell. These cells are incredibly large, with diameters of up to 100 µm and lengths of up to 30 cm. The plasma membrane of a skeletal muscle fiber is called the sarcolemma. The sarcolemma is the site of action potential conduction, which triggers muscle contraction. Within each muscle fiber are myofibrils—long cylindrical structures that lie parallel to the muscle fiber. Myofibrils run the entire length of the muscle fiber, and because they are only approximately 1.2 µm in diameter, hundreds to thousands can be found inside one muscle fiber. They attach to the sarcolemma at their ends, so that as myofibrils shorten, the entire muscle cell contracts (Figure 45.4.2).

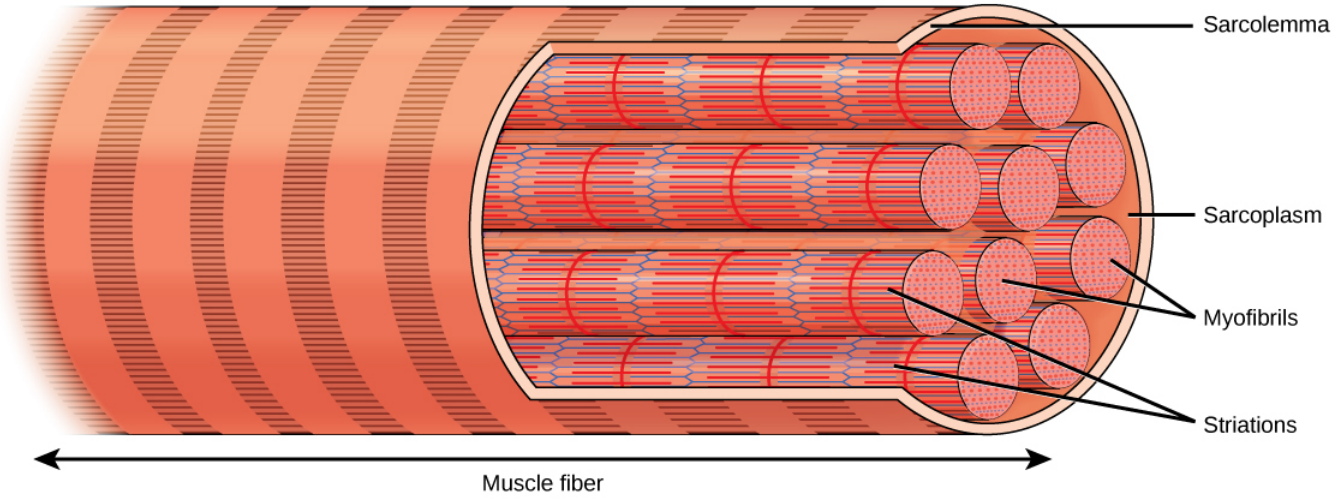


Figure 45.4.2: A skeletal muscle cell is surrounded by a plasma membrane called the sarcolemma with a cytoplasm called the sarcoplasm. A muscle fiber is composed of many fibrils, packaged into orderly units.

The striated appearance of skeletal muscle tissue is a result of repeating bands of the proteins actin and myosin that are present along the length of myofibrils. Dark A bands and light I bands repeat along myofibrils, and the alignment of myofibrils in the cell causes the entire cell to appear striated or banded.

Each I band has a dense line running vertically through the middle called a Z disc or Z line. The Z discs mark the border of units called sarcomeres, which are the functional units of skeletal muscle. One sarcomere is the space between two consecutive Z discs and contains one entire A band and two halves of an I band, one on either side of the A band. A myofibril is composed of many sarcomeres running along its length, and as the sarcomeres individually contract, the myofibrils and muscle cells shorten (Figure 45.4.3).

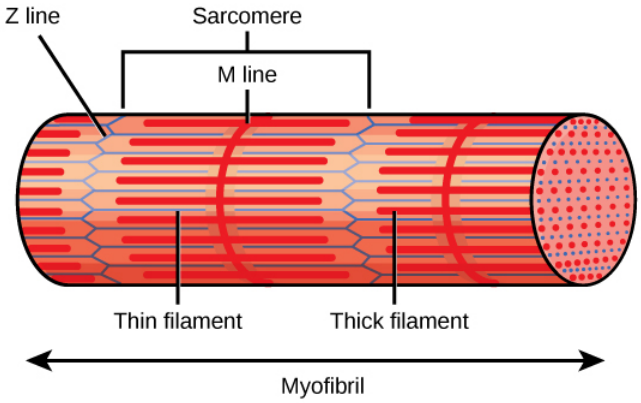
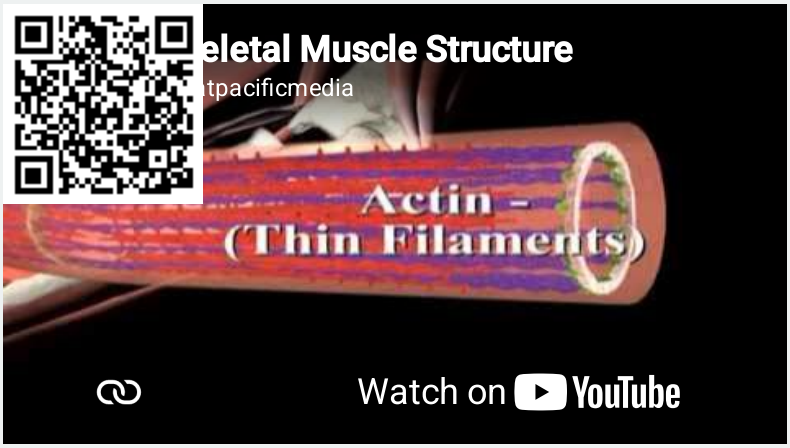


Figure 45.4.3: A sarcomere is the region from one Z line to the next Z line. Many sarcomeres are present in a myofibril, resulting in the striation pattern characteristic of skeletal muscle.

Myofibrils are composed of smaller structures called myofilaments. There are two main types of filaments: thick filaments and thin filaments; each has different compositions and locations. Thick filaments occur only in the A band of a myofibril. Thin filaments attach to a protein in the Z disc called alpha-actinin and occur across the entire length of the I band and partway into the A band. The region at which thick and thin filaments overlap has a dense appearance, as there is little space between the filaments. Thin filaments do not extend all the way into the A bands, leaving a central region of the A band that only contains thick filaments. This central region of the A band looks slightly lighter than the rest of the A band and is called the H zone. The middle of the H zone has a vertical line called the M line, at which accessory proteins hold together thick filaments. Both the Z disc and the M line hold myofilaments in place to maintain the structural arrangement and layering of the myofibril. Myofibrils are connected to each other by intermediate, or desmin, filaments that attach to the Z disc.

Thick and thin filaments are themselves composed of proteins. Thick filaments are composed of the protein myosin. The tail of a myosin molecule connects with other myosin molecules to form the central region of a thick filament near the M line, whereas the heads align on either side of the thick filament where the thin filaments overlap. The primary component of thin filaments is the actin protein. Two other components of the thin filament are tropomyosin and troponin. Actin has binding sites for myosin attachment. Strands of tropomyosin block the binding sites and prevent actin–myosin interactions when the muscles are at rest. Troponin consists of three globular subunits. One subunit binds to tropomyosin, one subunit binds to actin, and one subunit binds Ca^{2+} ions.

Link to Learning



View this animation showing the organization of muscle fibers.

Sliding Filament Model of Contraction

For a muscle cell to contract, the sarcomere must shorten. However, thick and thin filaments—the components of sarcomeres—do not shorten. Instead, they slide by one another, causing the sarcomere to shorten while the filaments remain the same length. The sliding filament theory of muscle contraction was developed to fit the differences observed in the named bands on the sarcomere at different degrees of muscle contraction and relaxation. The mechanism of contraction is the binding of myosin to actin, forming cross-bridges that generate filament movement (Figure 45.4.4).

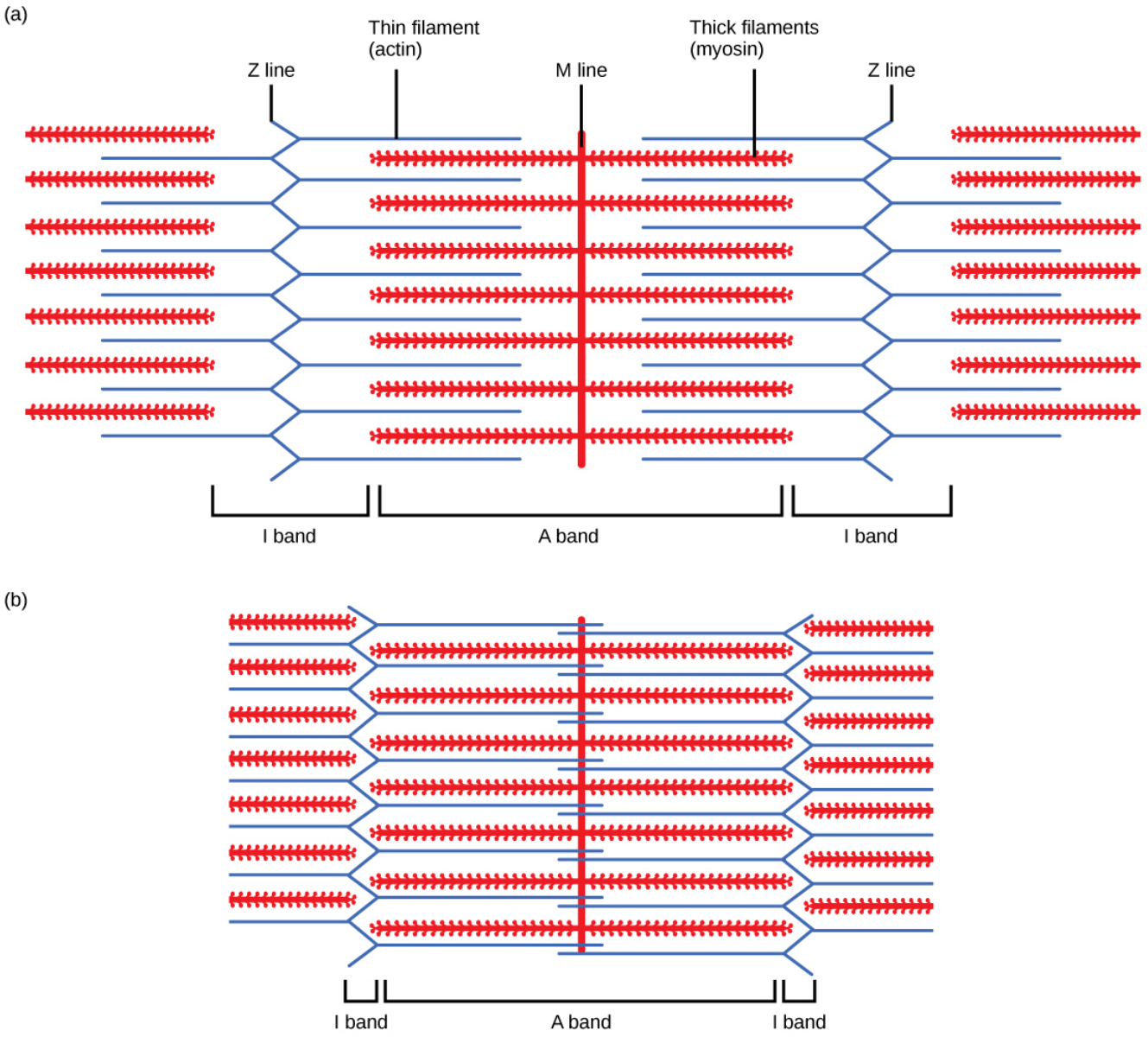


Figure 45.4.4: When (a) a sarcomere (b) contracts, the Z lines move closer together and the I band gets smaller. The A band stays the same width and, at full contraction, the thin filaments overlap.

When a sarcomere shortens, some regions shorten whereas others stay the same length. A sarcomere is defined as the distance between two consecutive Z discs or Z lines; when a muscle contracts, the distance between the Z discs is reduced. The H zone—the central region of the A zone—contains only thick filaments and is shortened during contraction. The I band contains only thin filaments and also shortens. The A band does not shorten—it remains the same length—but A bands of different sarcomeres move closer together during contraction, eventually disappearing. Thin filaments are pulled by the thick filaments toward the center of the sarcomere until the Z discs approach the thick filaments. The zone of overlap, in which thin filaments and thick filaments occupy the same area, increases as the thin filaments move inward.

ATP and Muscle Contraction

The motion of muscle shortening occurs as myosin heads bind to actin and pull the actin inwards. This action requires energy, which is provided by ATP. Myosin binds to actin at a binding site on the globular actin protein. Myosin has another binding site for ATP at which enzymatic activity hydrolyzes ATP to ADP, releasing an inorganic phosphate molecule and energy.

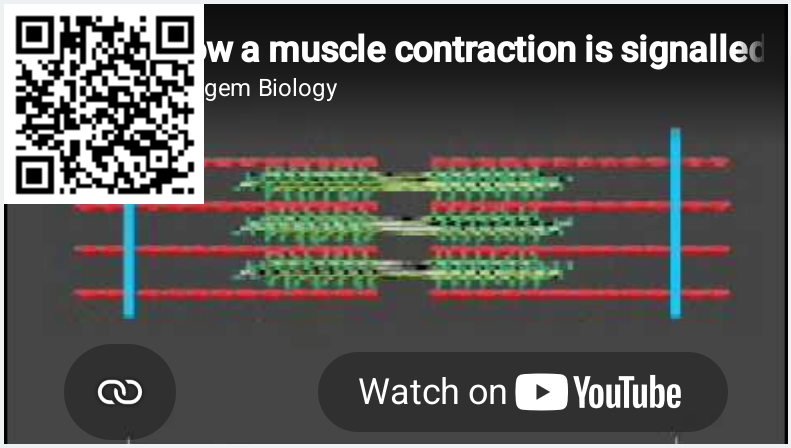
ATP binding causes myosin to release actin, allowing actin and myosin to detach from each other. After this happens, the newly bound ATP is converted to ADP and inorganic phosphate, P_i. The enzyme at the binding site on myosin is called ATPase. The

energy released during ATP hydrolysis changes the angle of the myosin head into a “cocked” position. The myosin head is then in a position for further movement, possessing potential energy, but ADP and P_i are still attached. If actin binding sites are covered and unavailable, the myosin will remain in the high energy configuration with ATP hydrolyzed, but still attached.

If the actin binding sites are uncovered, a cross-bridge will form; that is, the myosin head spans the distance between the actin and myosin molecules. P_i is then released, allowing myosin to expend the stored energy as a conformational change. The myosin head moves toward the M line, pulling the actin along with it. As the actin is pulled, the filaments move approximately 10 nm toward the M line. This movement is called the power stroke, as it is the step at which force is produced. As the actin is pulled toward the M line, the sarcomere shortens and the muscle contracts.

When the myosin head is “cocked,” it contains energy and is in a high-energy configuration. This energy is expended as the myosin head moves through the power stroke; at the end of the power stroke, the myosin head is in a low-energy position. After the power stroke, ADP is released; however, the cross-bridge formed is still in place, and actin and myosin are bound together. ATP can then attach to myosin, which allows the cross-bridge cycle to start again and further muscle contraction can occur (Figure **45.4.5**).

Link to Learning



Watch this video explaining how a muscle contraction is signaled.

Art Connection

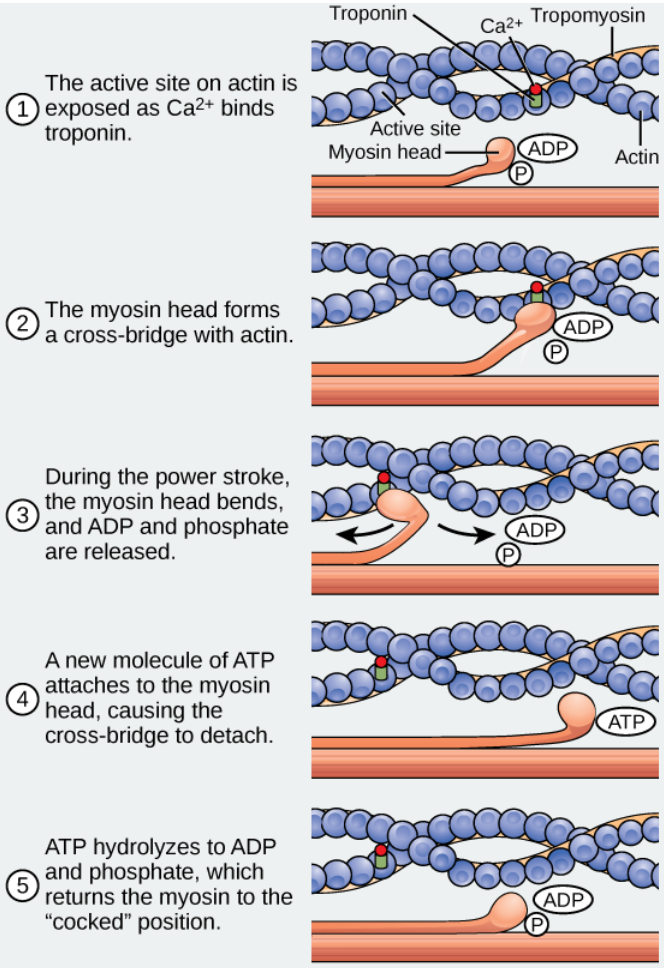
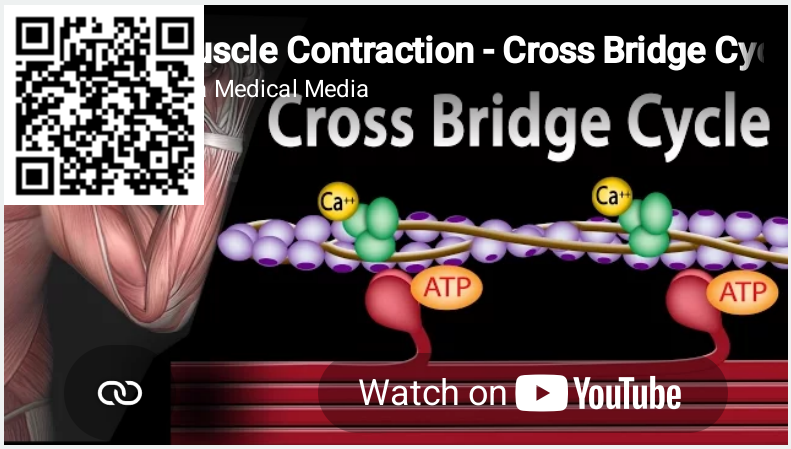


Figure **45.4.5**: The cross-bridge muscle contraction cycle, which is triggered by Ca^{2+} binding to the actin active site, is shown. With each contraction cycle, actin moves relative to myosin.

Which of the following statements about muscle contraction is true?

A. The power stroke occurs when ATP is hydrolyzed to ADP and phosphate.
B. The power stroke occurs when ADP and phosphate dissociate from the myosin head.
C. The power stroke occurs when ADP and phosphate dissociate from the actin active site.
D. The power stroke occurs when Ca^{2+} binds the calcium head.

Link to Learning



View this animation of the cross-bridge muscle contraction.

Regulatory Proteins

When a muscle is in a resting state, actin and myosin are separated. To keep actin from binding to the active site on myosin, regulatory proteins block the molecular binding sites. Tropomyosin blocks myosin binding sites on actin molecules, preventing cross-bridge formation and preventing contraction in a muscle without nervous input. Troponin binds to tropomyosin and helps to position it on the actin molecule; it also binds calcium ions.

To enable a muscle contraction, tropomyosin must change conformation, uncovering the myosin-binding site on an actin molecule and allowing cross-bridge formation. This can only happen in the presence of calcium, which is kept at extremely low concentrations in the sarcoplasm. If present, calcium ions bind to troponin, causing conformational changes in troponin that allow tropomyosin to move away from the myosin binding sites on actin. Once the tropomyosin is removed, a cross-bridge can form between actin and myosin, triggering contraction. Cross-bridge cycling continues until Ca^{2+} ions and ATP are no longer available and tropomyosin again covers the binding sites on actin.

Excitation–Contraction Coupling

Excitation–contraction coupling is the link (transduction) between the action potential generated in the sarcolemma and the start of a muscle contraction. The trigger for calcium release from the sarcoplasmic reticulum into the sarcoplasm is a neural signal. Each skeletal muscle fiber is controlled by a motor neuron, which conducts signals from the brain or spinal cord to the muscle. The area of the sarcolemma on the muscle fiber that interacts with the neuron is called the motor end plate. The end of the neuron's axon is called the synaptic terminal, and it does not actually contact the motor end plate. A small space called the synaptic cleft separates the synaptic terminal from the motor end plate. Electrical signals travel along the neuron's axon, which branches through the muscle and connects to individual muscle fibers at a neuromuscular junction.

The ability of cells to communicate electrically requires that the cells expend energy to create an electrical gradient across their cell membranes. This charge gradient is carried by ions, which are differentially distributed across the membrane. Each ion exerts an electrical influence and a concentration influence. Just as milk will eventually mix with coffee without the need to stir, ions also distribute themselves evenly, if they are permitted to do so. In this case, they are not permitted to return to an evenly mixed state.

The sodium–potassium ATPase uses cellular energy to move K^+ ions inside the cell and Na^+ ions outside. This alone accumulates a small electrical charge, but a big concentration gradient. There is lots of K^+ in the cell and lots of Na^+ outside the cell. Potassium is able to leave the cell through K^+ channels that are open 90% of the time, and it does. However, Na^+ channels are rarely open, so Na^+ remains outside the cell. When K^+ leaves the cell, obeying its concentration gradient, that effectively leaves a negative charge behind. So at rest, there is a large concentration gradient for Na^+ to enter the cell, and there is an accumulation of negative charges left behind in the cell. This is the resting membrane potential. Potential in this context means a separation of electrical charge that is capable of doing work. It is measured in volts, just like a battery. However, the transmembrane potential is considerably smaller (0.07 V); therefore, the small value is expressed as millivolts (mV) or 70 mV. Because the inside of a cell is negative compared with the outside, a minus sign signifies the excess of negative charges inside the cell, −70 mV.

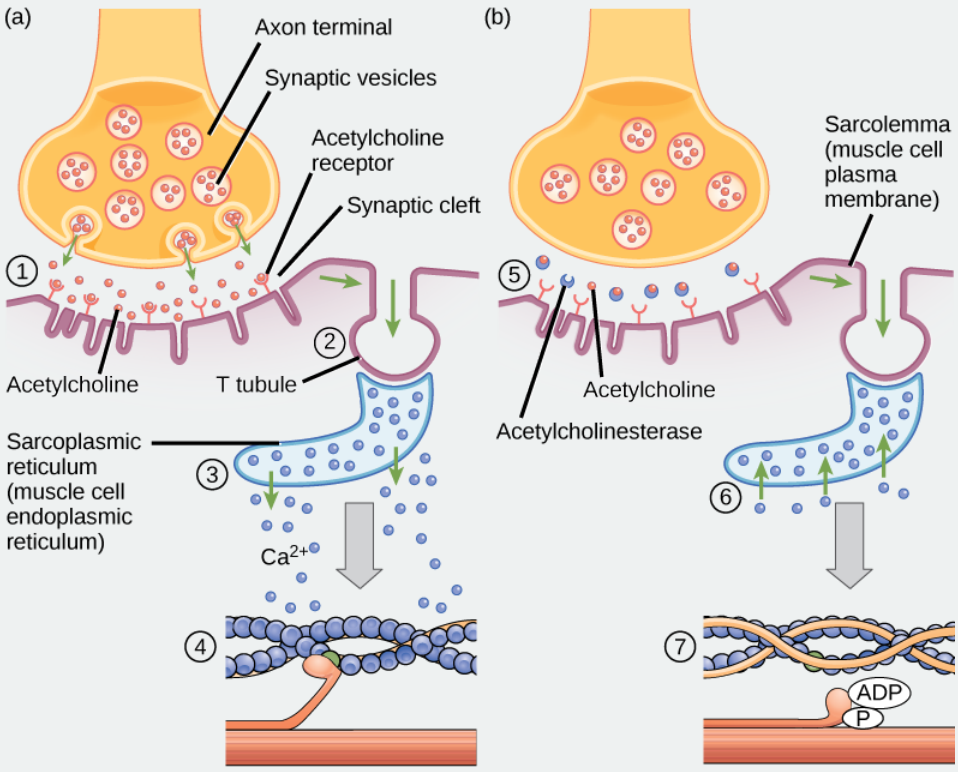
If an event changes the permeability of the membrane to Na^+ ions, they will enter the cell. That will change the voltage. This is an electrical event, called an action potential, that can be used as a cellular signal. Communication occurs between nerves and muscles through neurotransmitters. Neuron action potentials cause the release of neurotransmitters from the synaptic terminal into the synaptic cleft, where they can then diffuse across the synaptic cleft and bind to a receptor molecule on the motor end plate. The motor end plate possesses junctional folds—folds in the sarcolemma that create a large surface area for the neurotransmitter to bind to receptors. The receptors are actually sodium channels that open to allow the passage of Na^+ into the cell when they receive neurotransmitter signal.

Acetylcholine (ACh) is a neurotransmitter released by motor neurons that binds to receptors in the motor end plate. Neurotransmitter release occurs when an action potential travels down the motor neuron's axon, resulting in altered permeability of the synaptic terminal membrane and an influx of calcium. The Ca^{2+} ions allow synaptic vesicles to move to and bind with the presynaptic membrane (on the neuron), and release neurotransmitter from the vesicles into the synaptic cleft. Once released by the synaptic terminal, ACh diffuses across the synaptic cleft to the motor end plate, where it binds with ACh receptors. As a

neurotransmitter binds, these ion channels open, and Na^+ ions cross the membrane into the muscle cell. This reduces the voltage difference between the inside and outside of the cell, which is called depolarization. As ACh binds at the motor end plate, this depolarization is called an end-plate potential. The depolarization then spreads along the sarcolemma, creating an action potential as sodium channels adjacent to the initial depolarization site sense the change in voltage and open. The action potential moves across the entire cell, creating a wave of depolarization.

ACh is broken down by the enzyme acetylcholinesterase (AChE) into acetyl and choline. AChE resides in the synaptic cleft, breaking down ACh so that it does not remain bound to ACh receptors, which would cause unwanted extended muscle contraction (Figure **45.4.6**).

Art Connection



1. Acetylcholine released from the axon terminal binds to receptors on the sarcolemma.
2. An action potential is generated and travels down the T tubule.
3. Ca^{2+} is released from the sarcoplasmic reticulum in response to the change in voltage.
4. Ca^{2+} binds troponin; Cross-bridges form between actin and myosin.
5. Acetylcholinesterase removes acetylcholine from the synaptic cleft.
6. Ca^{2+} is transported back into the sarcoplasmic reticulum.
7. Tropomyosin binds active sites on actin causing the cross-bridge to detach.

Figure **45.4.6**: This diagram shows excitation-contraction coupling in a skeletal muscle contraction. The sarcoplasmic reticulum is a specialized endoplasmic reticulum found in muscle cells.

The deadly nerve gas Sarin irreversibly inhibits acetycholinesterase. What effect would Sarin have on muscle contraction?

After depolarization, the membrane returns to its resting state. This is called repolarization, during which voltage-gated sodium channels close. Potassium channels continue at 90% conductance. Because the plasma membrane sodium–potassium ATPase always transports ions, the resting state (negatively charged inside relative to the outside) is restored. The period immediately following the transmission of an impulse in a nerve or muscle, in which a neuron or muscle cell regains its ability to transmit another impulse, is called the refractory period. During the refractory period, the membrane cannot generate another action potential. . The refractory period allows the voltage-sensitive ion channels to return to their resting configurations. The sodium

potassium ATPase continually moves Na^+ back out of the cell and K^+ back into the cell, and the K^+ leaks out leaving negative charge behind. Very quickly, the membrane repolarizes, so that it can again be depolarized.

Control of Muscle Tension

Neural control initiates the formation of actin–myosin cross-bridges, leading to the sarcomere shortening involved in muscle contraction. These contractions extend from the muscle fiber through connective tissue to pull on bones, causing skeletal movement. The pull exerted by a muscle is called tension, and the amount of force created by this tension can vary. This enables the same muscles to move very light objects and very heavy objects. In individual muscle fibers, the amount of tension produced depends on the cross-sectional area of the muscle fiber and the frequency of neural stimulation.

The number of cross-bridges formed between actin and myosin determine the amount of tension that a muscle fiber can produce. Cross-bridges can only form where thick and thin filaments overlap, allowing myosin to bind to actin. If more cross-bridges are formed, more myosin will pull on actin, and more tension will be produced.

The ideal length of a sarcomere during production of maximal tension occurs when thick and thin filaments overlap to the greatest degree. If a sarcomere at rest is stretched past an ideal resting length, thick and thin filaments do not overlap to the greatest degree, and fewer cross-bridges can form. This results in fewer myosin heads pulling on actin, and less tension is produced. As a sarcomere is shortened, the zone of overlap is reduced as the thin filaments reach the H zone, which is composed of myosin tails. Because it is myosin heads that form cross-bridges, actin will not bind to myosin in this zone, reducing the tension produced by this myofiber. If the sarcomere is shortened even more, thin filaments begin to overlap with each other—reducing cross-bridge formation even further, and producing even less tension. Conversely, if the sarcomere is stretched to the point at which thick and thin filaments do not overlap at all, no cross-bridges are formed and no tension is produced. This amount of stretching does not usually occur because accessory proteins, internal sensory nerves, and connective tissue oppose extreme stretching.

The primary variable determining force production is the number of myofibers within the muscle that receive an action potential from the neuron that controls that fiber. When using the biceps to pick up a pencil, the motor cortex of the brain only signals a few neurons of the biceps, and only a few myofibers respond. In vertebrates, each myofiber responds fully if stimulated. When picking up a piano, the motor cortex signals all of the neurons in the biceps and every myofiber participates. This is close to the maximum force the muscle can produce. As mentioned above, increasing the frequency of action potentials (the number of signals per second) can increase the force a bit more, because the tropomyosin is flooded with calcium.

Summary

The body contains three types of muscle tissue: skeletal muscle, cardiac muscle, and smooth muscle. Skeleton muscle tissue is composed of sarcomeres, the functional units of muscle tissue. Muscle contraction occurs when sarcomeres shorten, as thick and thin filaments slide past each other, which is called the sliding filament model of muscle contraction. ATP provides the energy for cross-bridge formation and filament sliding. Regulatory proteins, such as troponin and tropomyosin, control cross-bridge formation. Excitation–contraction coupling transduces the electrical signal of the neuron, via acetylcholine, to an electrical signal on the muscle membrane, which initiates force production. The number of muscle fibers contracting determines how much force the whole muscle produces.

Art Connections

Figure 45.4.5: Which of the following statements about muscle contraction is true?

A. The power stroke occurs when ATP is hydrolyzed to ADP and phosphate.
B. The power stroke occurs when ADP and phosphate dissociate from the myosin head.
C. The power stroke occurs when ADP and phosphate dissociate from the actin active site.
D. The power stroke occurs when Ca^{2+} binds the calcium head.

Answer

B

Figure 45.4.6: The deadly nerve gas Sarin irreversibly inhibits acetycholinesterase. What effect would Sarin have on muscle contraction?

Answer

In the presence of Sarin, acetycholine is not removed from the synapse, resulting in continuous stimulation of the muscle plasma membrane. At first, muscle activity is intense and uncontrolled, but the ion gradients dissipate, so electrical signals in the T-tubules are no longer possible. The result is paralysis, leading to death by asphyxiation.

Glossary

actin
globular contractile protein that interacts with myosin for muscle contraction

acetylcholinesterase
(AChE) enzyme that breaks down ACh into acetyl and choline

cardiac muscle
tissue muscle tissue found only in the heart; cardiac contractions pump blood throughout the body and maintain blood pressure

motor end plate
sarcolemma of the muscle fiber that interacts with the neuron

myofibril
long cylindrical structures that lie parallel to the muscle fiber

myofilament
small structures that make up myofibrils

myosin
contractile protein that interacts with actin for muscle contraction

sarcolemma
plasma membrane of a skeletal muscle fiber

sarcomere
functional unit of skeletal muscle

skeletal muscle tissue
forms skeletal muscles, which attach to bones and control locomotion and any movement that can be consciously controlled

smooth muscle
tissue occurs in the walls of hollow organs such as the intestines, stomach, and urinary bladder, and around passages such as the respiratory tract and blood vessels

thick filament
a group of myosin molecules

thin filament
two polymers of actin wound together along with tropomyosin and troponin

tropomyosin

acts to block myosin binding sites on actin molecules, preventing cross-bridge formation and preventing contraction until a muscle receives a neuron signal

troponin

binds to tropomyosin and helps to position it on the actin molecule, and also binds calcium ions

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45.5: Vertebrate Skeleton Evolution and Modes of Locomotion

Skills to Develop

- Discuss the different types of skeletal systems
- Explain the role of the human skeletal system
- Compare and contrast different skeletal systems

A skeletal system is necessary to support the body, protect internal organs, and allow for the movement of an organism. There are three different skeleton designs that fulfill these functions: hydrostatic skeleton, exoskeleton, and endoskeleton.

Hydrostatic Skeleton

A hydrostatic skeleton is a skeleton formed by a fluid-filled compartment within the body, called the coelom. The organs of the coelom are supported by the aqueous fluid, which also resists external compression. This compartment is under hydrostatic pressure because of the fluid and supports the other organs of the organism. This type of skeletal system is found in soft-bodied animals such as sea anemones, earthworms, Cnidaria, and other invertebrates (Figure **45.5.1**).



Figure **45.5.1**: The skeleton of the red-knobbed sea star (*Protoreaster linckii*) is an example of a hydrostatic skeleton. (credit: "Amada44"/Wikimedia Commons)

Movement in a hydrostatic skeleton is provided by muscles that surround the coelom. The muscles in a hydrostatic skeleton contract to change the shape of the coelom; the pressure of the fluid in the coelom produces movement. For example, earthworms move by waves of muscular contractions of the skeletal muscle of the body wall hydrostatic skeleton, called peristalsis, which alternately shorten and lengthen the body. Lengthening the body extends the anterior end of the organism. Most organisms have a mechanism to fix themselves in the substrate. Shortening the muscles then draws the posterior portion of the body forward. Although a hydrostatic skeleton is well-suited to invertebrate organisms such as earthworms and some aquatic organisms, it is not an efficient skeleton for terrestrial animals.

Exoskeleton

An exoskeleton is an external skeleton that consists of a hard encasement on the surface of an organism. For example, the shells of crabs and insects are exoskeletons (Figure **45.5.2**). This skeleton type provides defence against predators, supports the body, and allows for movement through the contraction of attached muscles. As with vertebrates, muscles must cross a joint inside the exoskeleton. Shortening of the muscle changes the relationship of the two segments of the exoskeleton. Arthropods such as crabs and lobsters have exoskeletons that consist of 30–50 percent chitin, a polysaccharide derivative of glucose that is a strong but flexible material. Chitin is secreted by the epidermal cells. The exoskeleton is further strengthened by the addition of calcium carbonate in organisms such as the lobster. Because the exoskeleton is acellular, arthropods must periodically shed their exoskeletons because the exoskeleton does not grow as the organism grows.



Figure **45.5.2**: Muscles attached to the exoskeleton of the Halloween crab (*Gecarcinus quadratus*) allow it to move.

Endoskeleton

An endoskeleton is a skeleton that consists of hard, mineralized structures located within the soft tissue of organisms. An example of a primitive endoskeletal structure is the spicules of sponges. The bones of vertebrates are composed of tissues, whereas sponges have no true tissues (Figure **45.5.1**). Endoskeletons provide support for the body, protect internal organs, and allow for movement through contraction of muscles attached to the skeleton.



Figure **45.5.3**: The skeletons of humans and horses are examples of endoskeletons. (credit: Ross Murphy)

The human skeleton is an endoskeleton that consists of 206 bones in the adult. It has five main functions: providing support to the body, storing minerals and lipids, producing blood cells, protecting internal organs, and allowing for movement. The skeletal

system in vertebrates is divided into the axial skeleton (which consists of the skull, vertebral column, and rib cage), and the appendicular skeleton (which consists of the shoulders, limb bones, the pectoral girdle, and the pelvic girdle).

Human Axial Skeleton

The axial skeleton forms the central axis of the body and includes the bones of the skull, ossicles of the middle ear, hyoid bone of the throat, vertebral column, and the thoracic cage (ribcage) (Figure **45.5.1**). The function of the axial skeleton is to provide support and protection for the brain, the spinal cord, and the organs in the ventral body cavity. It provides a surface for the attachment of muscles that move the head, neck, and trunk, performs respiratory movements, and stabilizes parts of the appendicular skeleton.

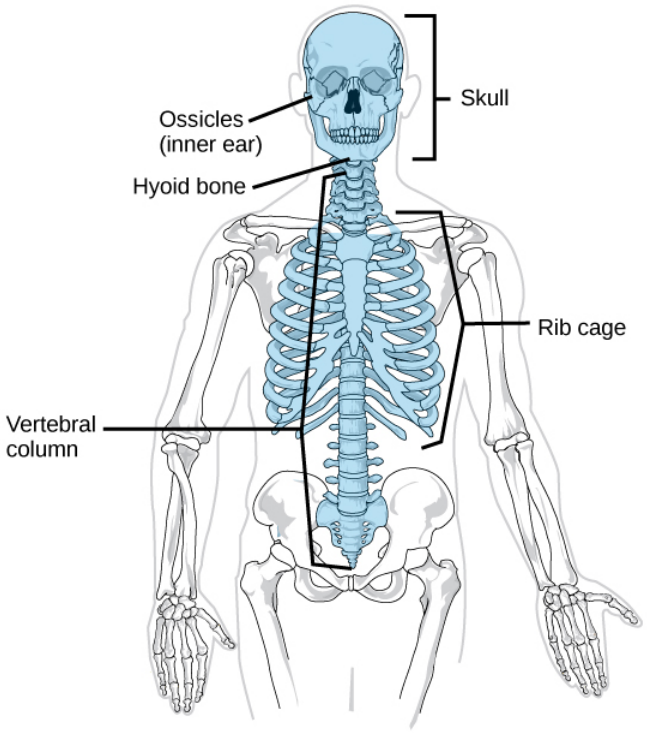


Figure **45.5.4**: The axial skeleton consists of the bones of the skull, ossicles of the middle ear, hyoid bone, vertebral column, and rib cage. (credit: modification of work by Mariana Ruiz Villareal)

The Skull

The bones of the skull support the structures of the face and protect the brain. The skull consists of 22 bones, which are divided into two categories: cranial bones and facial bones. The cranial bones are eight bones that form the cranial cavity, which encloses the brain and serves as an attachment site for the muscles of the head and neck. The eight cranial bones are the frontal bone, two parietal bones, two temporal bones, occipital bone, sphenoid bone, and the ethmoid bone. Although the bones developed separately in the embryo and fetus, in the adult, they are tightly fused with connective tissue and adjoining bones do not move (Figure **45.5.5**).

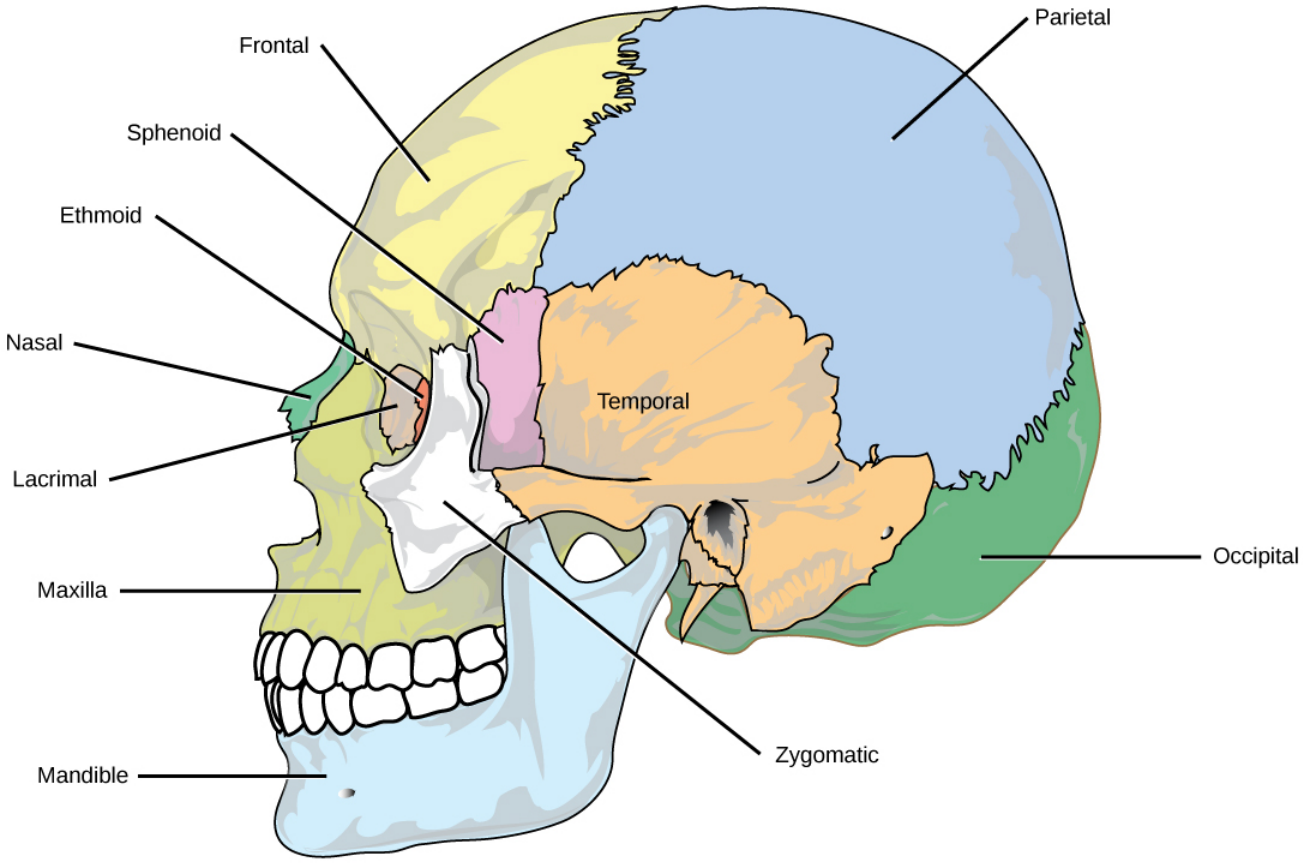


Figure 45.5.5: The bones of the skull support the structures of the face and protect the brain. (credit: modification of work by Mariana Ruiz Villareal)

The auditory ossicles of the middle ear transmit sounds from the air as vibrations to the fluid-filled cochlea. The auditory ossicles consist of six bones: two malleus bones, two incus bones, and two stapes on each side. These are the smallest bones in the body and are unique to mammals.

Fourteen facial bones form the face, provide cavities for the sense organs (eyes, mouth, and nose), protect the entrances to the digestive and respiratory tracts, and serve as attachment points for facial muscles. The 14 facial bones are the nasal bones, the maxillary bones, zygomatic bones, palatine, vomer, lacrimal bones, the inferior nasal conchae, and the mandible. All of these bones occur in pairs except for the mandible and the vomer (Figure 45.5.6).

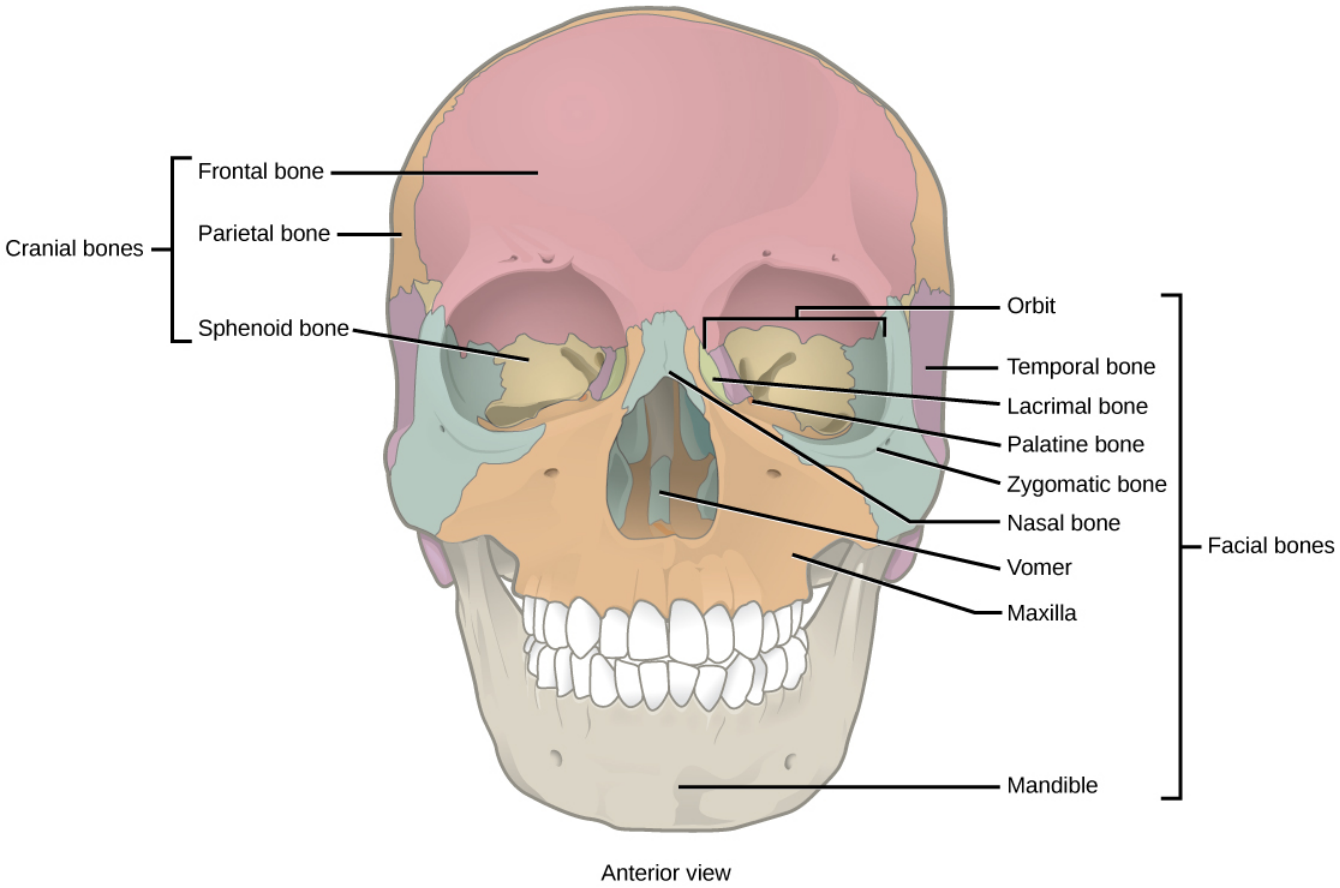


Figure **45.5.6**: The cranial bones, including the frontal, parietal, and sphenoid bones, cover the top of the head. The facial bones of the skull form the face and provide cavities for the eyes, nose, and mouth.

Although it is not found in the skull, the hyoid bone is considered a component of the axial skeleton. The hyoid bone lies below the mandible in the front of the neck. It acts as a movable base for the tongue and is connected to muscles of the jaw, larynx, and tongue. The mandible articulates with the base of the skull. The mandible controls the opening to the airway and gut. In animals with teeth, the mandible brings the surfaces of the teeth in contact with the maxillary teeth.

The Vertebral Column

The vertebral column, or spinal column, surrounds and protects the spinal cord, supports the head, and acts as an attachment point for the ribs and muscles of the back and neck. The adult vertebral column comprises 26 bones: the 24 vertebrae, the sacrum, and the coccyx bones. In the adult, the sacrum is typically composed of five vertebrae that fuse into one. The coccyx is typically 3–4 vertebrae that fuse into one. Around the age of 70, the sacrum and the coccyx may fuse together. We begin life with approximately 33 vertebrae, but as we grow, several vertebrae fuse together. The adult vertebrae are further divided into the 7 cervical vertebrae, 12 thoracic vertebrae, and 5 lumbar vertebrae (Figure **45.5.7**).

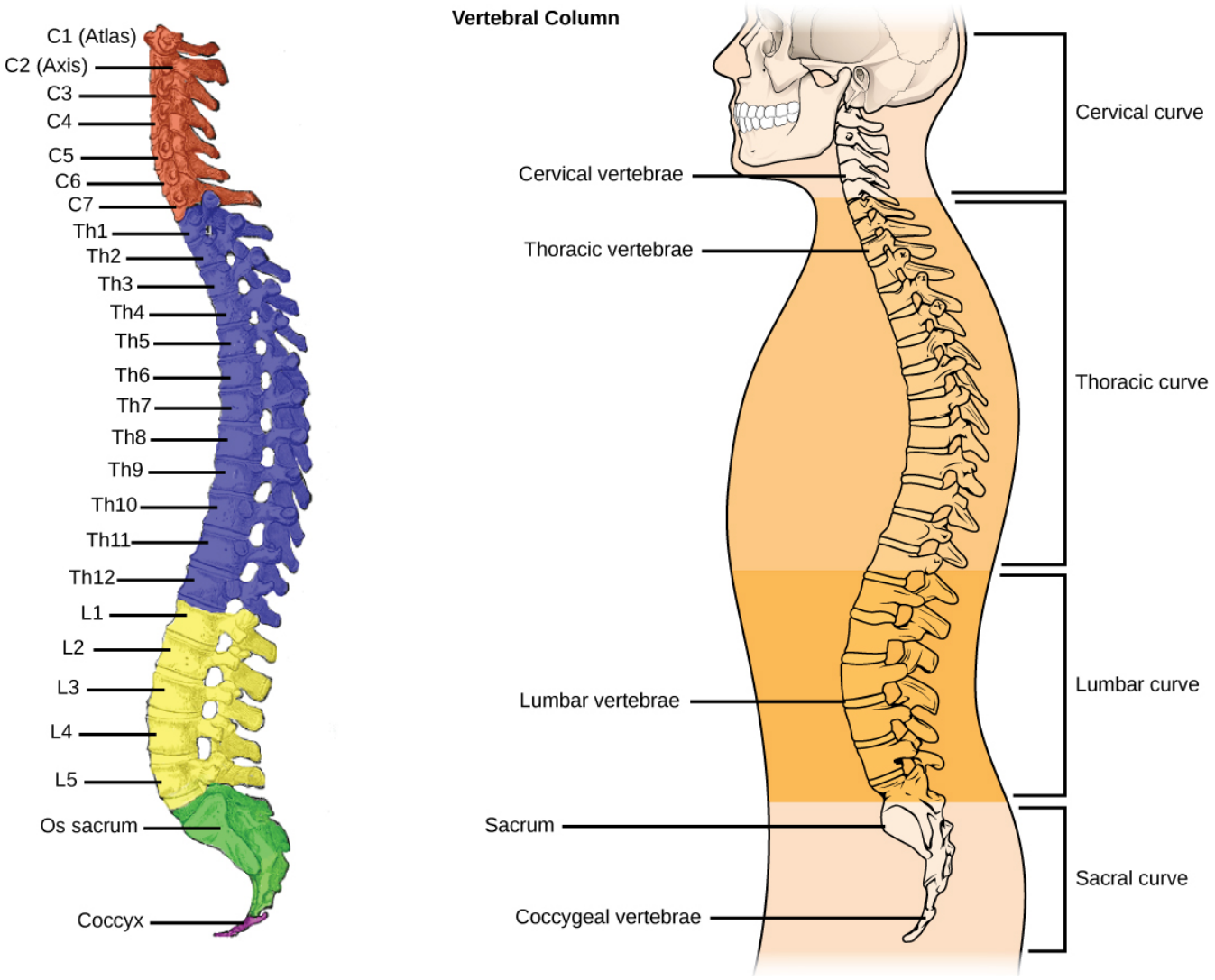


Figure 45.5.7: (a) The vertebral column consists of seven cervical vertebrae (C1–7) twelve thoracic vertebrae (Th1–12), five lumbar vertebrae (L1–5), the os sacrum, and the coccyx. (b) Spinal curves increase the strength and flexibility of the spine. (credit a: modification of work by Uwe Gille based on original work by Gray's Anatomy; credit b: modification of work by NCI, NIH)

Each vertebral body has a large hole in the center through which the nerves of the spinal cord pass. There is also a notch on each side through which the spinal nerves, which serve the body at that level, can exit from the spinal cord. The vertebral column is approximately 71 cm (28 inches) in adult male humans and is curved, which can be seen from a side view. The names of the spinal curves correspond to the region of the spine in which they occur. The thoracic and sacral curves are concave (curve inwards relative to the front of the body) and the cervical and lumbar curves are convex (curve outwards relative to the front of the body). The arched curvature of the vertebral column increases its strength and flexibility, allowing it to absorb shocks like a spring (Figure 45.5.7).

Intervertebral discs composed of fibrous cartilage lie between adjacent vertebral bodies from the second cervical vertebra to the sacrum. Each disc is part of a joint that allows for some movement of the spine and acts as a cushion to absorb shocks from movements such as walking and running. Intervertebral discs also act as ligaments to bind vertebrae together. The inner part of discs, the nucleus pulposus, hardens as people age and becomes less elastic. This loss of elasticity diminishes its ability to absorb shocks.

The Thoracic Cage

The thoracic cage, also known as the ribcage, is the skeleton of the chest, and consists of the ribs, sternum, thoracic vertebrae, and costal cartilages (Figure 45.5.8.8). The thoracic cage encloses and protects the organs of the thoracic cavity, including the heart and

lungs. It also provides support for the shoulder girdles and upper limbs, and serves as the attachment point for the diaphragm, muscles of the back, chest, neck, and shoulders. Changes in the volume of the thorax enable breathing.

The sternum, or breastbone, is a long, flat bone located at the anterior of the chest. It is formed from three bones that fuse in the adult. The ribs are 12 pairs of long, curved bones that attach to the thoracic vertebrae and curve toward the front of the body, forming the ribcage. Costal cartilages connect the anterior ends of the ribs to the sternum, with the exception of rib pairs 11 and 12, which are free-floating ribs.

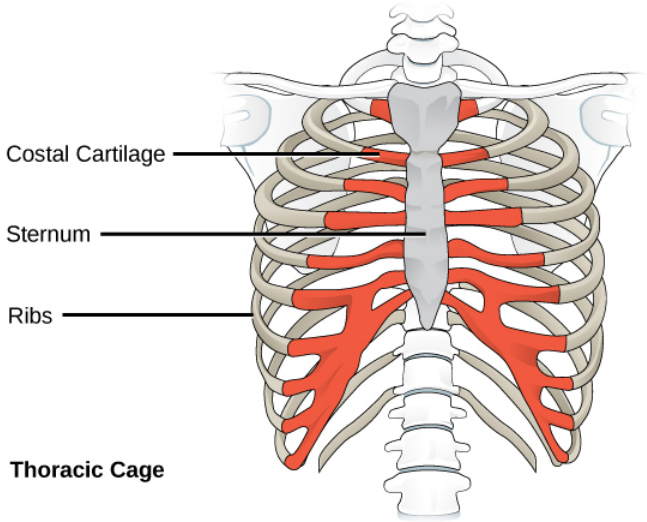


Figure 45.5.8: The thoracic cage, or rib cage, protects the heart and the lungs. (credit: modification of work by NCI, NIH)

Human Appendicular Skeleton

The appendicular skeleton is composed of the bones of the upper limbs (which function to grasp and manipulate objects) and the lower limbs (which permit locomotion). It also includes the pectoral girdle, or shoulder girdle, that attaches the upper limbs to the body, and the pelvic girdle that attaches the lower limbs to the body (Figure 45.5.9).

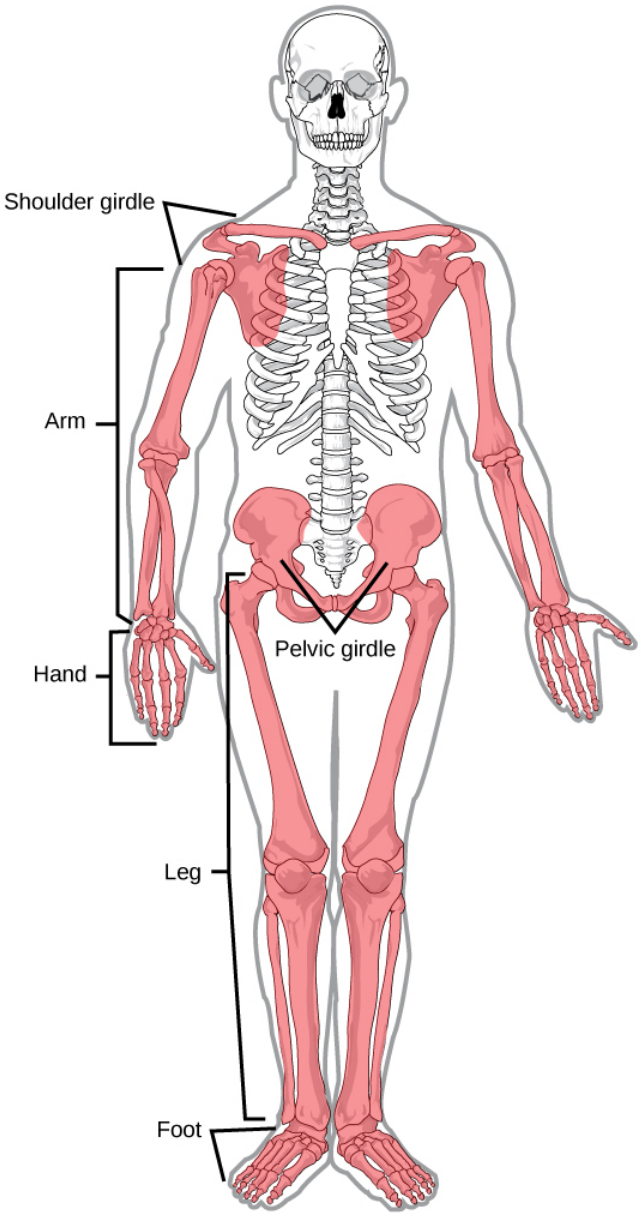


Figure **45.5.9**: The appendicular skeleton is composed of the bones of the pectoral limbs (arm, forearm, hand), the pelvic limbs (thigh, leg, foot), the pectoral girdle, and the pelvic girdle. (credit: modification of work by Mariana Ruiz Villareal)

The Pectoral Girdle

The pectoral girdle bones provide the points of attachment of the upper limbs to the axial skeleton. The human pectoral girdle consists of the clavicle (or collarbone) in the anterior, and the scapula (or shoulder blades) in the posterior (Figure **45.5.10**).

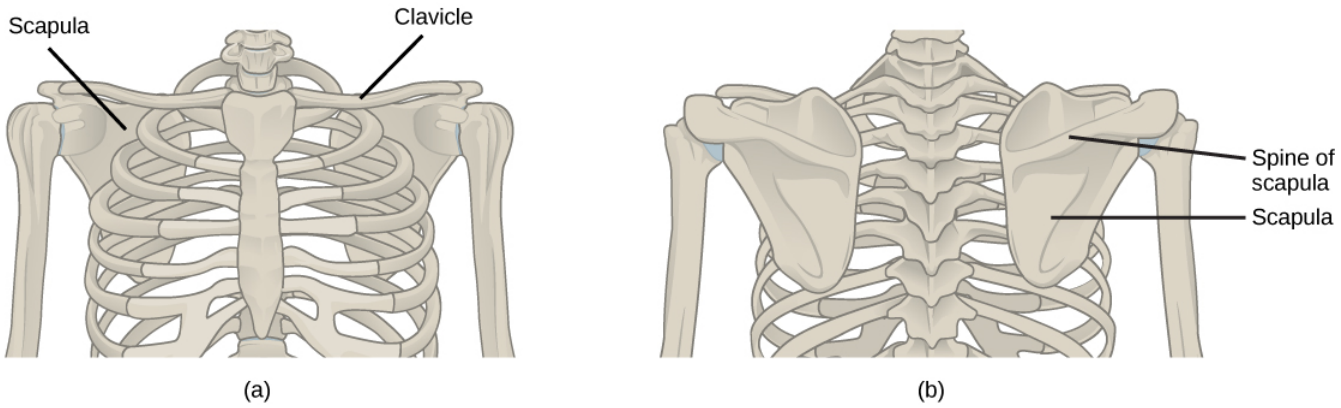


Figure 45.5.10: (a) The pectoral girdle in primates consists of the clavicles and scapulae. (b) The posterior view reveals the spine of the scapula to which muscle attaches.

The clavicles are S-shaped bones that position the arms on the body. The clavicles lie horizontally across the front of the thorax (chest) just above the first rib. These bones are fairly fragile and are susceptible to fractures. For example, a fall with the arms outstretched causes the force to be transmitted to the clavicles, which can break if the force is excessive. The clavicle articulates with the sternum and the scapula.

The scapulae are flat, triangular bones that are located at the back of the pectoral girdle. They support the muscles crossing the shoulder joint. A ridge, called the spine, runs across the back of the scapula and can easily be felt through the skin (Figure 45.5.10). The spine of the scapula is a good example of a bony protrusion that facilitates a broad area of attachment for muscles to bone.

The Upper Limb

The upper limb contains 30 bones in three regions: the arm (shoulder to elbow), the forearm (ulna and radius), and the wrist and hand (Figure 45.5.11).

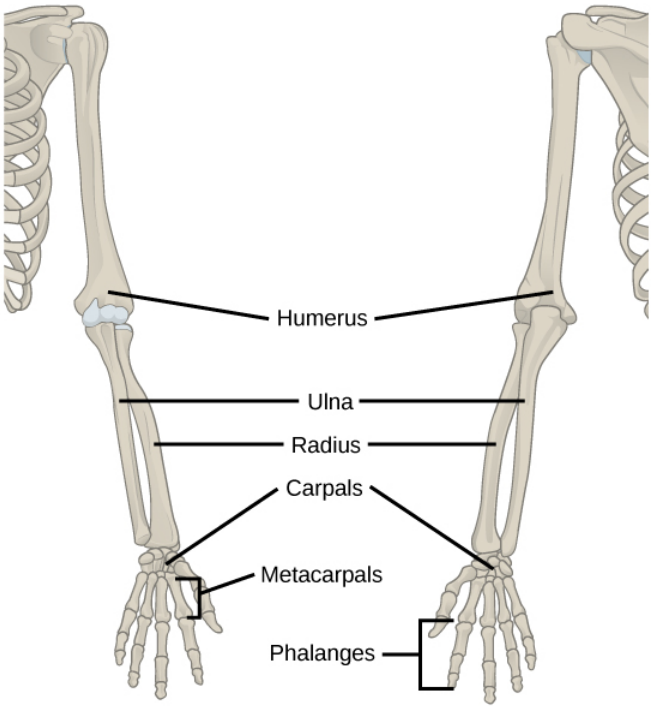


Figure 45.5.11: The upper limb consists of the humerus of the upper arm, the radius and ulna of the forearm, eight bones of the carpus, five bones of the metacarpus, and 14 bones of the phalanges.

An articulation is any place at which two bones are joined. The humerus is the largest and longest bone of the upper limb and the only bone of the arm. It articulates with the scapula at the shoulder and with the forearm at the elbow. The forearm extends from

the elbow to the wrist and consists of two bones: the ulna and the radius. The radius is located along the lateral (thumb) side of the forearm and articulates with the humerus at the elbow. The ulna is located on the medial aspect (pinky-finger side) of the forearm. It is longer than the radius. The ulna articulates with the humerus at the elbow. The radius and ulna also articulate with the carpal bones and with each other, which in vertebrates enables a variable degree of rotation of the carpus with respect to the long axis of the limb. The hand includes the eight bones of the carpus (wrist), the five bones of the metacarpus (palm), and the 14 bones of the phalanges (digits). Each digit consists of three phalanges, except for the thumb, when present, which has only two.

The Pelvic Girdle

The pelvic girdle attaches to the lower limbs of the axial skeleton. Because it is responsible for bearing the weight of the body and for locomotion, the pelvic girdle is securely attached to the axial skeleton by strong ligaments. It also has deep sockets with robust ligaments to securely attach the femur to the body. The pelvic girdle is further strengthened by two large hip bones. In adults, the hip bones, or coxal bones, are formed by the fusion of three pairs of bones: the ilium, ischium, and pubis. The pelvis joins together in the anterior of the body at a joint called the pubic symphysis and with the bones of the sacrum at the posterior of the body.

The female pelvis is slightly different from the male pelvis. Over generations of evolution, females with a wider pubic angle and larger diameter pelvic canal reproduced more successfully. Therefore, their offspring also had pelvic anatomy that enabled successful childbirth (Figure 45.5.12).

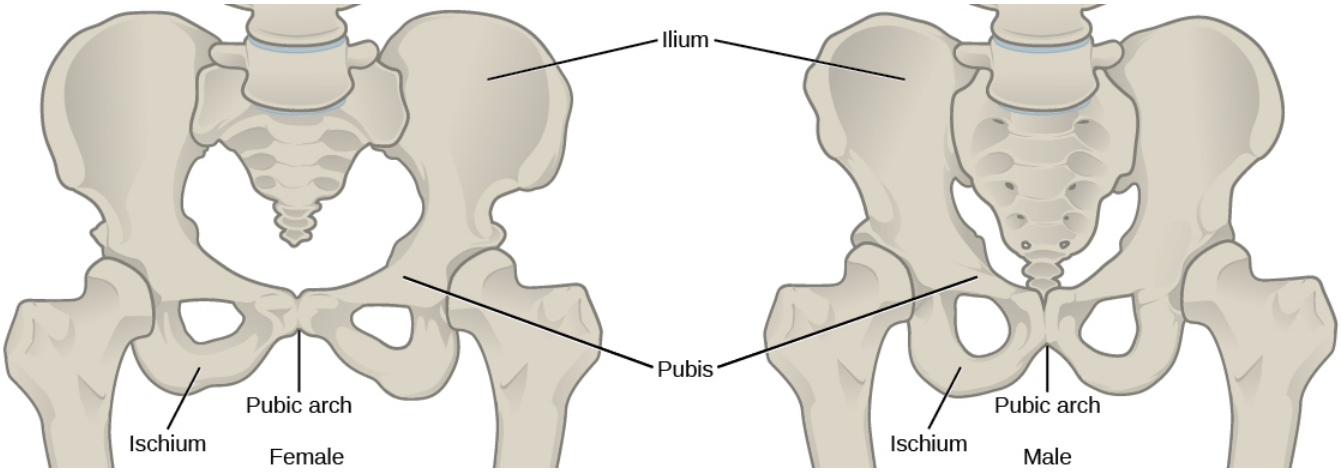


Figure 45.5.12: To adapt to reproductive fitness, the (a) female pelvis is lighter, wider, shallower, and has a broader angle between the pubic bones than (b) the male pelvis.

The Lower Limb

The lower limb consists of the thigh, the leg, and the foot. The bones of the lower limb are the femur (thigh bone), patella (kneecap), tibia and fibula (bones of the leg), tarsals (bones of the ankle), and metatarsals and phalanges (bones of the foot) (Figure 45.5.13). The bones of the lower limbs are thicker and stronger than the bones of the upper limbs because of the need to support the entire weight of the body and the resulting forces from locomotion. In addition to evolutionary fitness, the bones of an individual will respond to forces exerted upon them.

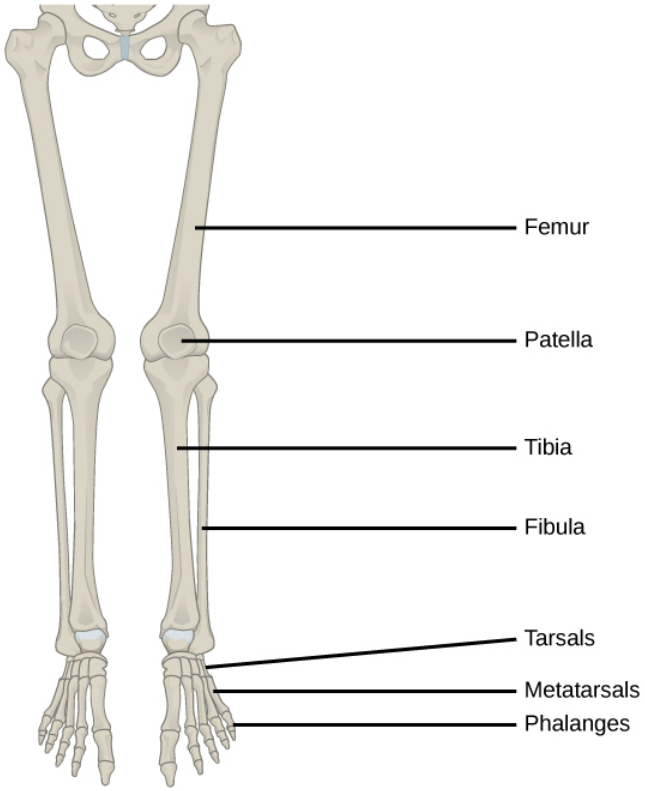


Figure **45.5.13**: The lower limb consists of the thigh (femur), kneecap (patella), leg (tibia and fibula), ankle (tarsals), and foot (metatarsals and phalanges) bones.

The femur, or thighbone, is the longest, heaviest, and strongest bone in the body. The femur and pelvis form the hip joint at the proximal end. At the distal end, the femur, tibia, and patella form the knee joint. The patella, or kneecap, is a triangular bone that lies anterior to the knee joint. The patella is embedded in the tendon of the femoral extensors (quadriceps). It improves knee extension by reducing friction. The tibia, or shinbone, is a large bone of the leg that is located directly below the knee. The tibia articulates with the femur at its proximal end, with the fibula and the tarsal bones at its distal end. It is the second largest bone in the human body and is responsible for transmitting the weight of the body from the femur to the foot. The fibula, or calf bone, parallels and articulates with the tibia. It does not articulate with the femur and does not bear weight. The fibula acts as a site for muscle attachment and forms the lateral part of the ankle joint.

The tarsals are the seven bones of the ankle. The ankle transmits the weight of the body from the tibia and the fibula to the foot. The metatarsals are the five bones of the foot. The phalanges are the 14 bones of the toes. Each toe consists of three phalanges, except for the big toe that has only two (Figure **45.5.14**). Variations exist in other species; for example, the horse's metacarpals and metatarsals are oriented vertically and do not make contact with the substrate.

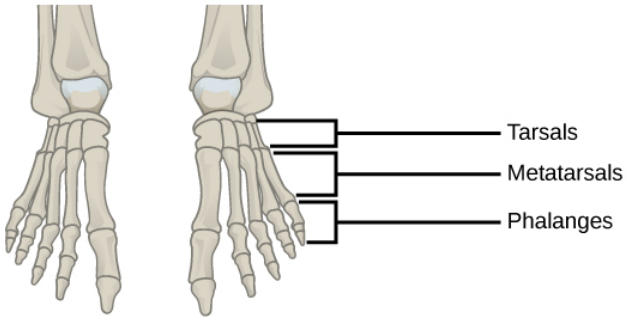


Figure **45.5.14**: This drawing shows the bones of the human foot and ankle, including the metatarsals and the phalanges.

Evolution Connection: Evolution of Body Design for Locomotion on Land

The transition of vertebrates onto land required a number of changes in body design, as movement on land presents a number of challenges for animals that are adapted to movement in water. The buoyancy of water provides a certain amount of lift, and a common form of movement by fish is lateral undulations of the entire body. This back and forth movement pushes the body against the water, creating forward movement. In most fish, the muscles of paired fins attach to girdles within the body, allowing for some control of locomotion. As certain fish began moving onto land, they retained their lateral undulation form of locomotion (anguilliform). However, instead of pushing against water, their fins or flippers became points of contact with the ground, around which they rotated their bodies.

The effect of gravity and the lack of buoyancy on land meant that body weight was suspended on the limbs, leading to increased strengthening and ossification of the limbs. The effect of gravity also required changes to the axial skeleton. Lateral undulations of land animal vertebral columns cause torsional strain. A firmer, more ossified vertebral column became common in terrestrial tetrapods because it reduces strain while providing the strength needed to support the body's weight. In later tetrapods, the vertebrae began allowing for vertical motion rather than lateral flexion. Another change in the axial skeleton was the loss of a direct attachment between the pectoral girdle and the head. This reduced the jarring to the head caused by the impact of the limbs on the ground. The vertebrae of the neck also evolved to allow movement of the head independently of the body.

The appendicular skeleton of land animals is also different from aquatic animals. The shoulders attach to the pectoral girdle through muscles and connective tissue, thus reducing the jarring of the skull. Because of a lateral undulating vertebral column, in early tetrapods, the limbs were splayed out to the side and movement occurred by performing "push-ups." The vertebrae of these animals had to move side-to-side in a similar manner to fish and reptiles. This type of motion requires large muscles to move the limbs toward the midline; it was almost like walking while doing push-ups, and it is not an efficient use of energy. Later tetrapods have their limbs placed under their bodies, so that each stride requires less force to move forward. This resulted in decreased adductor muscle size and an increased range of motion of the scapulae. This also restricts movement primarily to one plane, creating forward motion rather than moving the limbs upward as well as forward. The femur and humerus were also rotated, so that the ends of the limbs and digits were pointed forward, in the direction of motion, rather than out to the side. By placement underneath the body, limbs can swing forward like a pendulum to produce a stride that is more efficient for moving over land.

Summary

The three types of skeleton designs are hydrostatic skeletons, exoskeletons, and endoskeletons. A hydrostatic skeleton is formed by a fluid-filled compartment held under hydrostatic pressure; movement is created by the muscles producing pressure on the fluid. An exoskeleton is a hard external skeleton that protects the outer surface of an organism and enables movement through muscles attached on the inside. An endoskeleton is an internal skeleton composed of hard, mineralized tissue that also enables movement by attachment to muscles. The human skeleton is an endoskeleton that is composed of the axial and appendicular skeleton. The axial skeleton is composed of the bones of the skull, ossicles of the ear, hyoid bone, vertebral column, and ribcage. The skull consists of eight cranial bones and 14 facial bones. Six bones make up the ossicles of the middle ear, while the hyoid bone is located in the neck under the mandible. The vertebral column contains 26 bones, and it surrounds and protects the spinal cord. The thoracic cage consists of the sternum, ribs, thoracic vertebrae, and costal cartilages. The appendicular skeleton is made up of the limbs of the upper and lower limbs. The pectoral girdle is composed of the clavicles and the scapulae. The upper limb contains 30 bones in the arm, the forearm, and the hand. The pelvic girdle attaches the lower limbs to the axial skeleton. The lower limb includes the bones of the thigh, the leg, and the foot.

Glossary

appendicular skeleton

composed of the bones of the upper limbs, which function to grasp and manipulate objects, and the lower limbs, which permit locomotion

articulation

any place where two bones are joined

auditory ossicle
(also, middle ear) transduces sounds from the air into vibrations in the fluid-filled cochlea

axial skeleton
forms the central axis of the body and includes the bones of the skull, the ossicles of the middle ear, the hyoid bone of the throat, the vertebral column, and the thoracic cage (ribcage)

carpus
eight bones that comprise the wrist

clavicle
S-shaped bone that positions the arms laterally

coxal bone
hip bone

cranial bone
one of eight bones that form the cranial cavity that encloses the brain and serves as an attachment site for the muscles of the head and neck

endoskeleton
skeleton of living cells that produce a hard, mineralized tissue located within the soft tissue of organisms

exoskeleton
a secreted cellular product external skeleton that consists of a hard encasement on the surface of an organism

facial bone
one of the 14 bones that form the face; provides cavities for the sense organs (eyes, mouth, and nose) and attachment points for facial muscles

femur
(also, thighbone) longest, heaviest, and strongest bone in the body

fibula
(also, calf bone) parallels and articulates with the tibia

forearm
extends from the elbow to the wrist and consists of two bones: the ulna and the radius

humerus
only bone of the arm

hydrostatic skeleton
skeleton that consists of aqueous fluid held under pressure in a closed body compartment

hyoid bone
lies below the mandible in the front of the neck

intervertebral disc
composed of fibrous cartilage; lies between adjacent vertebrae from the second cervical vertebra to the sacrum

lower limb

consists of the thigh, the leg, and the foot

metacarpus
five bones that comprise the palm

metatarsal
one of the five bones of the foot

patella
(also, kneecap) triangular bone that lies anterior to the knee joint

pectoral girdle
bones that transmit the force generated by the upper limbs to the axial skeleton

phalange
one of the bones of the fingers or toes

pelvic girdle
bones that transmit the force generated by the lower limbs to the axial skeleton

radius
bone located along the lateral (thumb) side of the forearm; articulates with the humerus at the elbow

rib
one of 12 pairs of long, curved bones that attach to the thoracic vertebrae and curve toward the front of the body to form the ribcage

scapula
flat, triangular bone located at the posterior pectoral girdle

skull
bone that supports the structures of the face and protects the brain

sternum
(also, breastbone) long, flat bone located at the front of the chest

tarsal
one of the seven bones of the ankle

thoracic cage
(also, ribcage) skeleton of the chest, which consists of the ribs, thoracic vertebrae, sternum, and costal cartilages

tibia
(also, shinbone) large bone of the leg that is located directly below the knee

ulna
bone located on the medial aspect (pinky-finger side) of the forearm

vertebral column
(also, spine) surrounds and protects the spinal cord, supports the head, and acts as an attachment point for ribs and muscles of the back and neck

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CHAPTER OVERVIEW

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46.1: Types of Digestive Systems

Skills to Develop

- Explain the processes of digestion and absorption
- Compare and contrast different types of digestive systems
- Explain the specialized functions of the organs involved in processing food in the body
- Describe the ways in which organs work together to digest food and absorb nutrients

Animals obtain their nutrition from the consumption of other organisms. Depending on their diet, animals can be classified into the following categories: plant eaters (herbivores), meat eaters (carnivores), and those that eat both plants and animals (omnivores). The nutrients and macromolecules present in food are not immediately accessible to the cells. There are a number of processes that modify food within the animal body in order to make the nutrients and organic molecules accessible for cellular function. As animals evolved in complexity of form and function, their digestive systems have also evolved to accommodate their various dietary needs.

Herbivores, Omnivores, and Carnivores

Herbivores are animals whose primary food source is plant-based. Examples of herbivores, as shown in Figure **46.1.1** include vertebrates like deer, koalas, and some bird species, as well as invertebrates such as crickets and caterpillars. These animals have evolved digestive systems capable of handling large amounts of plant material. Herbivores can be further classified into frugivores (fruit-eaters), granivores (seed eaters), nectivores (nectar feeders), and folivores (leaf eaters).



(a) (b)

Figure 46.1.1: Herbivores, like this (a) mule deer and (b) monarch caterpillar, eat primarily plant material. (credit a: modification of work by Bill Ebbesen; credit b: modification of work by Doug Bowman)

Carnivores are animals that eat other animals. The word carnivore is derived from Latin and literally means “meat eater.” Wild cats such as lions, shown in Figure 46.1.2a and tigers are examples of vertebrate carnivores, as are snakes and sharks, while invertebrate carnivores include sea stars, spiders, and ladybugs, shown in Figure 46.1.2b. Obligate carnivores are those that rely entirely on animal flesh to obtain their nutrients; examples of obligate carnivores are members of the cat family, such as lions and cheetahs. Facultative carnivores are those that also eat non-animal food in addition to animal food. Note that there is no clear line that differentiates facultative carnivores from omnivores; dogs would be considered facultative carnivores.



(a)



(b)

Figure 46.1.2: Carnivores like the (a) lion eat primarily meat. The (b) ladybug is also a carnivore that consumes small insects called aphids. (credit a: modification of work by Kevin Pluck; credit b: modification of work by Jon Sullivan)

Omnivores are animals that eat both plant- and animal-derived food. In Latin, omnivore means to eat everything. Humans, bears (shown in Figure 46.1.3a), and chickens are example of vertebrate omnivores; invertebrate omnivores include cockroaches and crayfish (shown in Figure 46.1.3b).



(a)



(b)

Figure 46.1.3: Omnivores like the (a) bear and (b) crayfish eat both plant and animal based food. (credit a: modification of work by Dave Menke; credit b: modification of work by Jon Sullivan)

Invertebrate Digestive Systems

Animals have evolved different types of digestive systems to aid in the digestion of the different foods they consume. The simplest example is that of a gastrovascular cavity and is found in organisms with only one opening for digestion. Platyhelminthes (flatworms), Ctenophora (comb jellies), and Cnidaria (coral, jelly fish, and sea anemones) use this type of digestion. Gastrovascular cavities, as shown in Figure 46.1.4a, are typically a blind tube or cavity with only one opening, the “mouth”, which also serves as an “anus”. Ingested material enters the mouth and passes through a hollow, tubular cavity. Cells within the cavity secrete digestive enzymes that break down the food. The food particles are engulfed by the cells lining the gastrovascular cavity.

The alimentary canal, shown in Figure 46.1.4b, is a more advanced system: it consists of one tube with a mouth at one end and an anus at the other. Earthworms are an example of an animal with an alimentary canal. Once the food is ingested through the mouth, it passes through the esophagus and is stored in an organ called the crop; then it passes into the gizzard where it is churned and

digested. From the gizzard, the food passes through the intestine, the nutrients are absorbed, and the waste is eliminated as feces, called castings, through the anus.

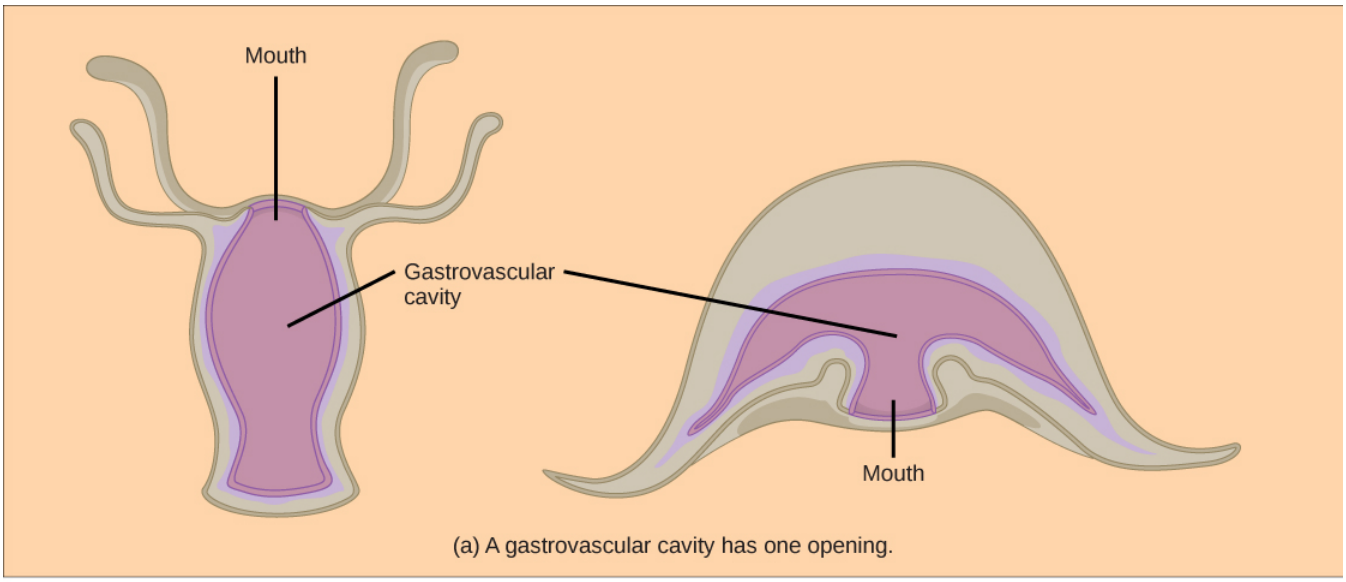


Figure **46.1.4**: (a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food, and an anus for eliminating waste, as shown in this nematode.

Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating unmasticated food.

Monogastric: Single-chambered Stomach

As the word monogastric suggests, this type of digestive system consists of one (“mono”) stomach chamber (“gastric”). Humans and many animals have a monogastric digestive system as illustrated in Figure **46.1.5**. The process of digestion begins with the mouth and the intake of food. The teeth play an important role in masticating (chewing) or physically breaking down food into smaller particles. The enzymes present in saliva also begin to chemically break down food. The esophagus is a long tube that connects the mouth to the stomach. Using peristalsis, or wave-like smooth muscle contractions, the muscles of the esophagus push the food towards the stomach. In order to speed up the actions of enzymes in the stomach, the stomach is an extremely acidic environment, with a pH between 1.5 and 2.5. The gastric juices, which include enzymes in the stomach, act on the food particles and continue the process of digestion. Further breakdown of food takes place in the small intestine where enzymes produced by the liver, the small intestine, and the pancreas continue the process of digestion. The nutrients are absorbed into the blood stream across the epithelial cells lining the walls of the small intestines. The waste material travels on to the large intestine where water is absorbed and the drier waste material is compacted into feces; it is stored until it is excreted through the rectum.

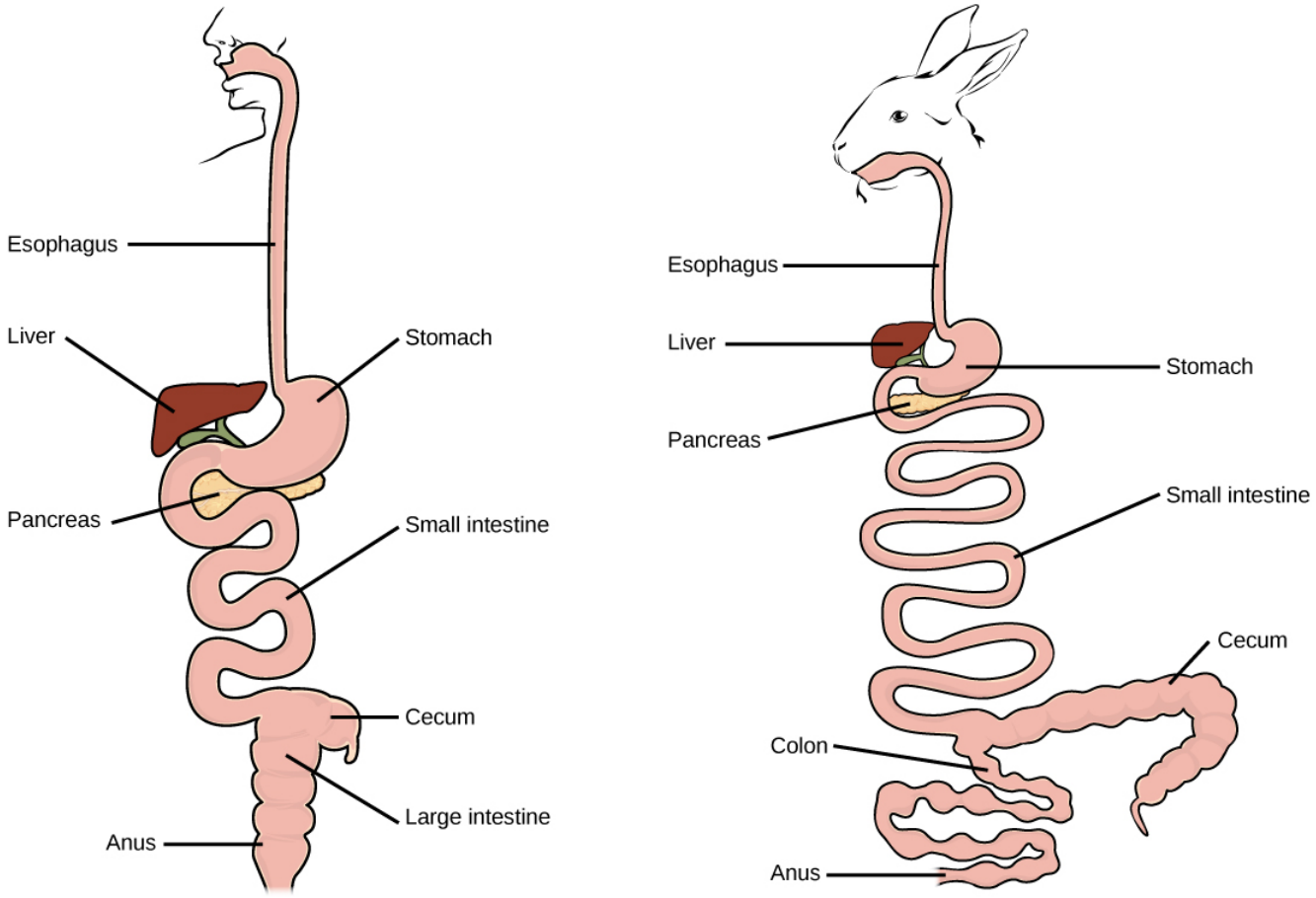


Figure **46.1.5**: (a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients. Rabbits digest their food twice: the first time food passes through the digestive system, it collects in the cecum, and then it passes as soft feces called cecotrophes. The rabbit re-ingests these cecotrophes to further digest them.

Avian

Birds face special challenges when it comes to obtaining nutrition from food. They do not have teeth and so their digestive system, shown in Figure **46.1.6**, must be able to process un-masticated food. Birds have evolved a variety of beak types that reflect the vast variety in their diet, ranging from seeds and insects to fruits and nuts. Because most birds fly, their metabolic rates are high in order to efficiently process food and keep their body weight low. The stomach of birds has two chambers: the proventriculus, where gastric juices are produced to digest the food before it enters the stomach, and the gizzard, where the food is stored, soaked, and mechanically ground. The undigested material forms food pellets that are sometimes regurgitated. Most of the chemical digestion and absorption happens in the intestine and the waste is excreted through the cloaca.

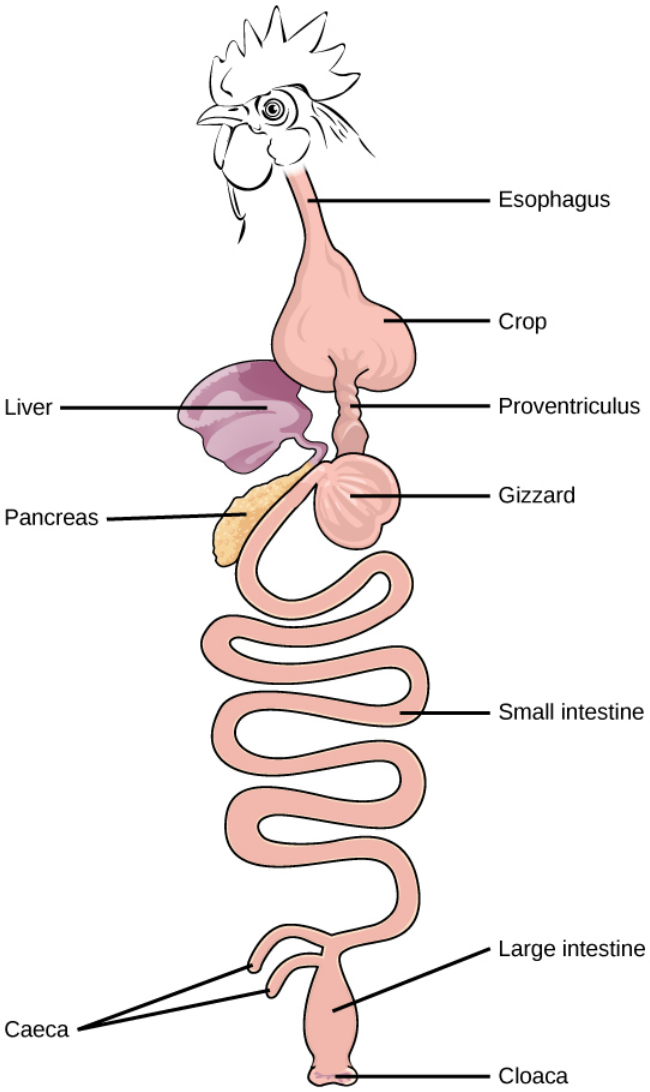


Figure **46.1.6**: The avian esophagus has a pouch, called a crop, which stores food. Food passes from the crop to the first of two stomachs, called the proventriculus, which contains digestive juices that break down food. From the proventriculus, the food enters the second stomach, called the gizzard, which grinds food. Some birds swallow stones or grit, which are stored in the gizzard, to aid the grinding process. Birds do not have separate openings to excrete urine and feces. Instead, uric acid from the kidneys is secreted into the large intestine and combined with waste from the digestive process. This waste is excreted through an opening called the cloaca.

Evolution Connection: Avian Adaptations

Birds have a highly efficient, simplified digestive system. Recent fossil evidence has shown that the evolutionary divergence of birds from other land animals was characterized by streamlining and simplifying the digestive system. Unlike many other animals, birds do not have teeth to chew their food. In place of lips, they have sharp pointy beaks. The horny beak, lack of jaws, and the smaller tongue of the birds can be traced back to their dinosaur ancestors. The emergence of these changes seems to coincide with the inclusion of seeds in the bird diet. Seed-eating birds have beaks that are shaped for grabbing seeds and the two-compartment stomach allows for delegation of tasks. Since birds need to remain light in order to fly, their metabolic rates are very high, which means they digest their food very quickly and need to eat often. Contrast this with the ruminants, where the digestion of plant matter takes a very long time.

Ruminants

Ruminants are mainly herbivores like cows, sheep, and goats, whose entire diet consists of eating large amounts of roughage or fiber. They have evolved digestive systems that help them digest vast amounts of cellulose. An interesting feature of the ruminants' mouth is that they do not have upper incisor teeth. They use their lower teeth, tongue and lips to tear and chew their food. From the mouth, the food travels to the esophagus and on to the stomach.

To help digest the large amount of plant material, the stomach of the ruminants is a multi-chambered organ, as illustrated in Figure **46.1.7**. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that break down cellulose and ferment ingested food. The abomasum is the "true" stomach and is the equivalent of the monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary to digest plant material in ruminants. The fermentation process produces large amounts of gas in the stomach chamber, which must be eliminated. As in other animals, the small intestine plays an important role in nutrient absorption, and the large intestine helps in the elimination of waste.

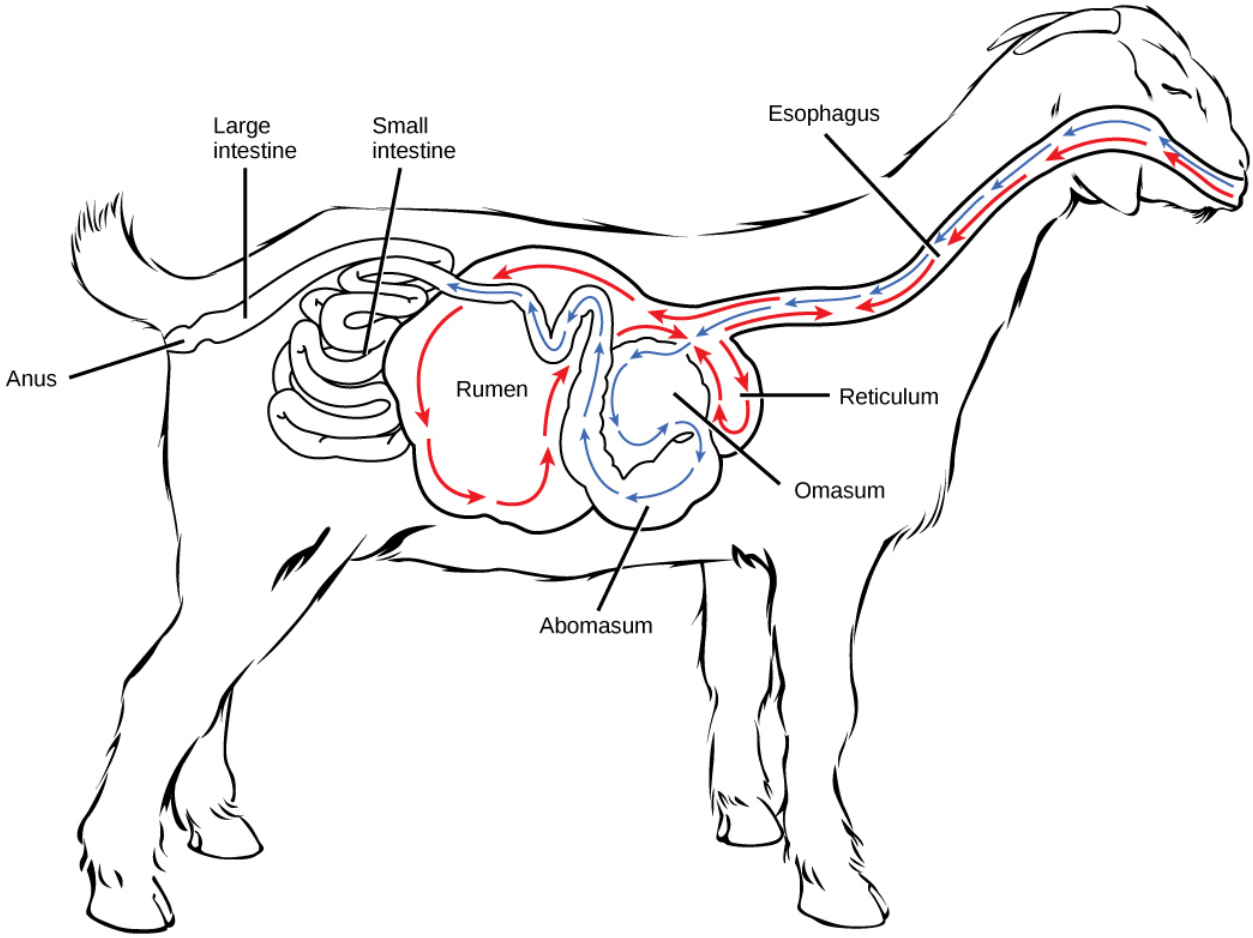


Figure **46.1.7**: Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the omasum, which removes water. The cud then passes onto the fourth stomach, the abomasum, where it is digested by enzymes produced by the ruminant.

Pseudo-ruminants

Some animals, such as camels and alpacas, are pseudo-ruminants. They eat a lot of plant material and roughage. Digesting plant material is not easy because plant cell walls contain the polymeric sugar molecule cellulose. The digestive enzymes of these animals cannot break down cellulose, but microorganisms present in the digestive system can. Therefore, the digestive system must be able to handle large amounts of roughage and break down the cellulose. Pseudo-ruminants have a three-chamber stomach in the digestive system. However, their cecum—a pouched organ at the beginning of the large intestine containing many microorganisms that are necessary for the digestion of plant materials—is large and is the site where the roughage is fermented and digested. These animals do not have a rumen but have an omasum, abomasum, and reticulum.

Parts of the Digestive System

The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms.

Oral Cavity

The oral cavity, or mouth, is the point of entry of food into the digestive system, illustrated in Figure 46.1.8. The food consumed is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

The extensive chemical process of digestion begins in the mouth. As food is being chewed, saliva, produced by the salivary glands, mixes with the food. Saliva is a watery substance produced in the mouths of many animals. There are three major glands that secrete saliva—the parotid, the submandibular, and the sublingual. Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains immunoglobulins and lysozymes, which have antibacterial action to reduce tooth decay by inhibiting growth of some bacteria. Saliva also contains an enzyme called salivary amylase that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme called lipase is produced by the cells in the tongue. Lipases are a class of enzymes that can break down triglycerides. The lingual lipase begins the breakdown of fat components in the food. The chewing and wetting action provided by the teeth and saliva prepare the food into a mass called the bolus for swallowing. The tongue helps in swallowing—moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the trachea, which leads to the lungs, and the esophagus, which leads to the stomach. The trachea has an opening called the glottis, which is covered by a cartilaginous flap called the epiglottis. When swallowing, the epiglottis closes the glottis and food passes into the esophagus and not the trachea. This arrangement allows food to be kept out of the trachea.

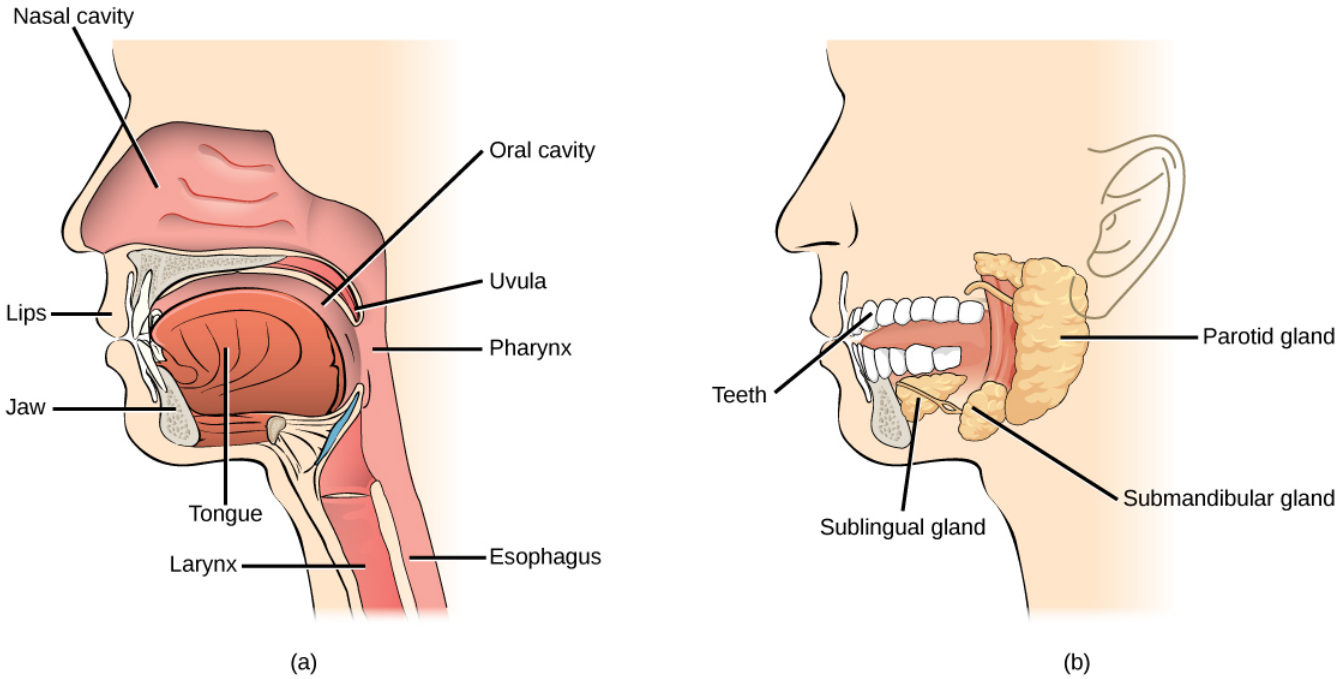


Figure 46.1.8: Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by the National Cancer Institute)

Esophagus

The esophagus is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave like movements called peristalsis that push the food toward the stomach, as illustrated in Figure 46.1.9. The peristalsis wave is unidirectional—it moves food from the mouth to the stomach, and reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.

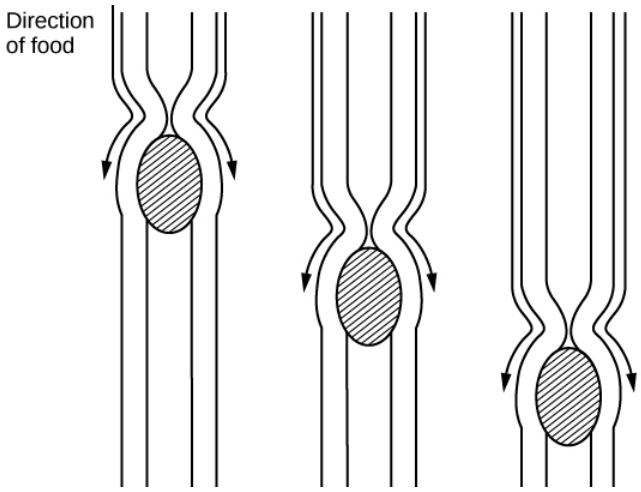


Figure 46.1.9: The esophagus transfers food from the mouth to the stomach through peristaltic movements.

A ring-like muscle called a sphincter forms valves in the digestive system. The gastro-esophageal sphincter is located at the stomach end of the esophagus. In response to swallowing and the pressure exerted by the bolus of food, this sphincter opens, and the bolus enters the stomach. When there is no swallowing action, this sphincter is shut and prevents the contents of the stomach from traveling up the esophagus. Many animals have a true sphincter; however, in humans, there is no true sphincter, but the esophagus remains closed when there is no swallowing action. Acid reflux or "heartburn" occurs when the acidic digestive juices escape into the esophagus.

Stomach

A large part of digestion occurs in the stomach, shown in Figure 46.1.10. The stomach is a saclike organ that secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

Art Connection

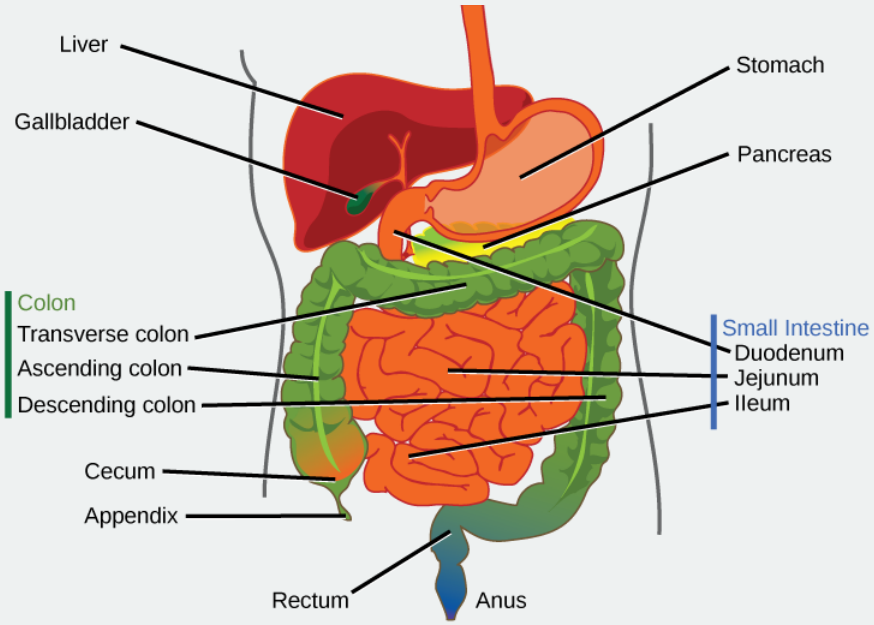


Figure 46.1.10: The human stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)

Which of the following statements about the digestive system is false?

A. Chyme is a mixture of food and digestive juices that is produced in the stomach.
B. Food enters the large intestine before the small intestine.
C. In the small intestine, chyme mixes with bile, which emulsifies fats.
D. The stomach is separated from the small intestine by the pyloric sphincter.

The stomach is also the major site for protein digestion in animals other than ruminants. Protein digestion is mediated by an enzyme called pepsin in the stomach chamber. Pepsin is secreted by the chief cells in the stomach in an inactive form called pepsinogen. Pepsin breaks peptide bonds and cleaves proteins into smaller polypeptides; it also helps activate more pepsinogen, starting a positive feedback mechanism that generates more pepsin. Another cell type—parietal cells—secrete hydrogen and chloride ions, which combine in the lumen to form hydrochloric acid, the primary acidic component of the stomach juices. Hydrochloric acid helps to convert the inactive pepsinogen to pepsin. The highly acidic environment also kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the hydrolysis of protein in the food. Chemical digestion is facilitated by the churning action of the stomach. Contraction and relaxation of smooth muscles mixes the stomach contents about every 20 minutes. The partially digested food and gastric juice mixture is called chyme. Chyme passes from the stomach to the small intestine. Further protein digestion takes place in the small intestine. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by the pyloric sphincter.

When digesting protein and some fats, the stomach lining must be protected from getting digested by pepsin. There are two points to consider when describing how the stomach lining is protected. First, as previously mentioned, the enzyme pepsin is synthesized in the inactive form. This protects the chief cells, because pepsinogen does not have the same enzyme functionality of pepsin. Second, the stomach has a thick mucus lining that protects the underlying tissue from the action of the digestive juices. When this mucus lining is ruptured, ulcers can form in the stomach. Ulcers are open wounds in or on an organ caused by bacteria (*Helicobacter pylori*) when the mucus lining is ruptured and fails to reform.

Small Intestine

Chyme moves from the stomach to the small intestine. The small intestine is the organ where the digestion of protein, fats, and carbohydrates is completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the villi. The apical surface of each villus has many microscopic projections called microvilli. These structures, illustrated in Figure **46.1.11**, are lined with epithelial cells on the luminal side and allow for the nutrients to be absorbed from the digested food and absorbed into the blood stream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients. Absorbed nutrients in the blood are carried into the hepatic portal vein, which leads to the liver. There, the liver regulates the distribution of nutrients to the rest of the body and removes toxic substances, including drugs, alcohol, and some pathogens.

Art Connection

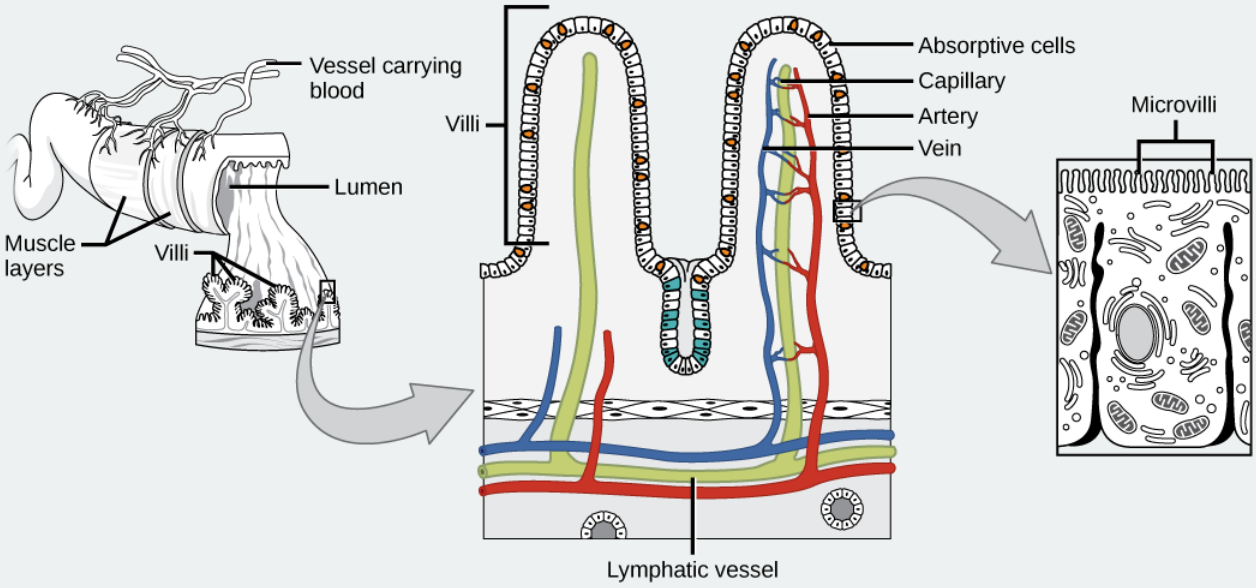


Figure 46.1.11: Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nutrients.

Which of the following statements about the small intestine is false?

A. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
B. The inside of the small intestine has many folds, called villi.
C. Microvilli are lined with blood vessels as well as lymphatic vessels.
D. The inside of the small intestine is called the lumen.

The human small intestine is over 6m long and is divided into three parts: the duodenum, the jejunum, and the ileum. The "C-shaped," fixed part of the small intestine is called the duodenum and is shown in Figure 46.1.11. The duodenum is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum. In the duodenum, chyme is mixed with pancreatic juices in an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Pancreatic juices also contain several digestive enzymes. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. Bile is produced in the liver and stored and concentrated in the gallbladder. Bile contains bile salts which emulsify lipids while the pancreas produces enzymes that catabolize starches, disaccharides, proteins, and fats. These digestive juices break down the food particles in the chyme into glucose, triglycerides, and amino acids. Some chemical digestion of food takes place in the duodenum. Absorption of fatty acids also takes place in the duodenum.

The second part of the small intestine is called the jejunum, shown in Figure 46.1.11. Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. The bulk of chemical digestion and nutrient absorption occurs in the jejunum.

The ileum, also illustrated in Figure 46.1.11 is the last part of the small intestine and here the bile salts and vitamins are absorbed into blood stream. The undigested food is sent to the colon from the ileum via peristaltic movements of the muscle. The ileum ends and the large intestine begins at the ileocecal valve. The vermiform, "worm-like," appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

The large intestine, illustrated in Figure 46.1.12, reabsorbs the water from the undigested food material and processes the waste material. The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or "intestinal flora" that aid in the digestive processes. The colon can be divided into four regions, the ascending colon, the transverse colon, the descending colon and the sigmoid colon. The main functions of the colon are

to extract the water and mineral salts from undigested food, and to store waste material. Carnivorous mammals have a shorter large intestine compared to herbivorous mammals due to their diet.

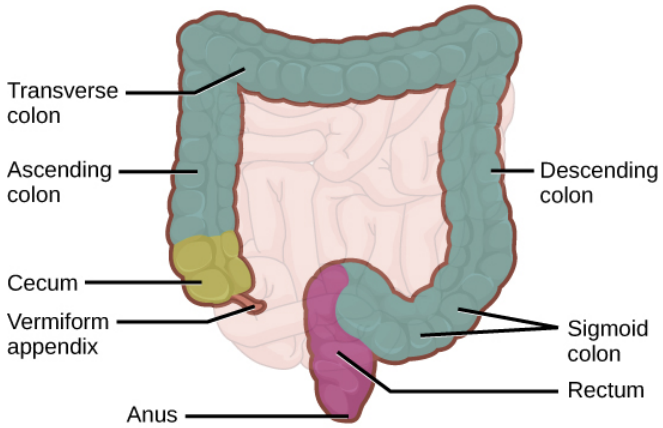


Figure 46.1.12: The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

Rectum and Anus

The rectum is the terminal end of the large intestine, as shown in Figure 46.1.12. The primary role of the rectum is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The anus is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

The organs discussed above are the organs of the digestive tract through which food passes. Accessory organs are organs that add secretions (enzymes) that catabolize food into nutrients. Accessory organs include salivary glands, the liver, the pancreas, and the gallbladder. The liver, pancreas, and gallbladder are regulated by hormones in response to the food consumed.

The liver is the largest internal organ in humans and it plays a very important role in digestion of fats and detoxifying blood. The liver produces bile, a digestive juice that is required for the breakdown of fatty components of the food in the duodenum. The liver also processes the vitamins and fats and synthesizes many plasma proteins.

The pancreas is another important gland that secretes digestive juices. The chyme produced from the stomach is highly acidic in nature; the pancreatic juices contain high levels of bicarbonate, an alkali that neutralizes the acidic chyme. Additionally, the pancreatic juices contain a large variety of enzymes that are required for the digestion of protein and carbohydrates.

The gallbladder is a small organ that aids the liver by storing bile and concentrating bile salts. When chyme containing fatty acids enters the duodenum, the bile is secreted from the gallbladder into the duodenum.

Summary

Different animals have evolved different types of digestive systems specialized to meet their dietary needs. Humans and many other animals have monogastric digestive systems with a single-chambered stomach. Birds have evolved a digestive system that includes a gizzard where the food is crushed into smaller pieces. This compensates for their inability to masticate. Ruminants that consume large amounts of plant material have a multi-chambered stomach that digests roughage. Pseudo-ruminants have similar digestive processes as ruminants but do not have the four-compartment stomach. Processing food involves ingestion (eating), digestion (mechanical and enzymatic breakdown of large molecules), absorption (cellular uptake of nutrients), and elimination (removal of undigested waste as feces).

Many organs work together to digest food and absorb nutrients. The mouth is the point of ingestion and the location where both mechanical and chemical breakdown of food begins. Saliva contains an enzyme called amylase that breaks down carbohydrates. The food bolus travels through the esophagus by peristaltic movements to the stomach. The stomach has an extremely acidic environment. An enzyme called pepsin digests protein in the stomach. Further digestion and absorption take place in the small intestine. The large intestine reabsorbs water from the undigested food and stores waste until elimination.

Art Connections

Figure 46.1.10: Which of the following statements about the digestive system is false?

A. Chyme is a mixture of food and digestive juices that is produced in the stomach.
B. Food enters the large intestine before the small intestine.
C. In the small intestine, chyme mixes with bile, which emulsifies fats.
D. The stomach is separated from the small intestine by the pyloric sphincter.

Answer

B

Figure 46.1.11: Which of the following statements about the small intestine is false?

A. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
B. The inside of the small intestine has many folds, called villi.
C. Microvilli are lined with blood vessels as well as lymphatic vessels.
D. The inside of the small intestine is called the lumen.

Answer

C

Glossary

alimentary canal
tubular digestive system with a mouth and anus

anus
exit point for waste material

bile
digestive juice produced by the liver; important for digestion of lipids

bolus
mass of food resulting from chewing action and wetting by saliva

carnivore
animal that consumes animal flesh

chyme
mixture of partially digested food and stomach juices

duodenum
first part of the small intestine where a large part of digestion of carbohydrates and fats occurs

esophagus
tubular organ that connects the mouth to the stomach

gallbladder
organ that stores and concentrates bile

gastrovascular cavity

digestive system consisting of a single opening

gizzard
muscular organ that grinds food

herbivore
animal that consumes strictly plant diet

ileum
last part of the small intestine; connects the small intestine to the large intestine; important for absorption of B-12

jejunum
second part of the small intestine

large intestine
digestive system organ that reabsorbs water from undigested material and processes waste matter

lipase
enzyme that chemically breaks down lipids

liver
organ that produces bile for digestion and processes vitamins and lipids

monogastric
digestive system that consists of a single-chambered stomach

omnivore
animal that consumes both plants and animals

pancreas
gland that secretes digestive juices

pepsin
enzyme found in the stomach whose main role is protein digestion

pepsinogen
inactive form of pepsin

peristalsis
wave-like movements of muscle tissue

proventriculus
glandular part of a bird’s stomach

rectum
area of the body where feces is stored until elimination

roughage
component of food that is low in energy and high in fiber

ruminant
animal with a stomach divided into four compartments

salivary amylase

enzyme found in saliva, which converts carbohydrates to maltose

small intestine
organ where digestion of protein, fats, and carbohydrates is completed

sphincter
band of muscle that controls movement of materials throughout the digestive tract

stomach
saclike organ containing acidic digestive juices

villi
folds on the inner surface of the small intestine whose role is to increase absorption area

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46.2: The Mouth and Teeth- Food Capture and Bulk Processing

Skills to Develop

- Explain the processes of digestion and absorption
- Compare and contrast different types of digestive systems
- Explain the specialized functions of the organs involved in processing food in the body
- Describe the ways in which organs work together to digest food and absorb nutrients

Animals obtain their nutrition from the consumption of other organisms. Depending on their diet, animals can be classified into the following categories: plant eaters (herbivores), meat eaters (carnivores), and those that eat both plants and animals (omnivores). The nutrients and macromolecules present in food are not immediately accessible to the cells. There are a number of processes that modify food within the animal body in order to make the nutrients and organic molecules accessible for cellular function. As animals evolved in complexity of form and function, their digestive systems have also evolved to accommodate their various dietary needs.

Herbivores, Omnivores, and Carnivores

Herbivores are animals whose primary food source is plant-based. Examples of herbivores, as shown in Figure **46.2.1** include vertebrates like deer, koalas, and some bird species, as well as invertebrates such as crickets and caterpillars. These animals have evolved digestive systems capable of handling large amounts of plant material. Herbivores can be further classified into frugivores (fruit-eaters), granivores (seed eaters), nectivores (nectar feeders), and folivores (leaf eaters).



(a) (b)

Figure 46.2.1: Herbivores, like this (a) mule deer and (b) monarch caterpillar, eat primarily plant material. (credit a: modification of work by Bill Ebbesen; credit b: modification of work by Doug Bowman)

Carnivores are animals that eat other animals. The word carnivore is derived from Latin and literally means “meat eater.” Wild cats such as lions, shown in Figure 46.2.2a and tigers are examples of vertebrate carnivores, as are snakes and sharks, while invertebrate carnivores include sea stars, spiders, and ladybugs, shown in Figure 46.2.2b. Obligate carnivores are those that rely entirely on animal flesh to obtain their nutrients; examples of obligate carnivores are members of the cat family, such as lions and cheetahs. Facultative carnivores are those that also eat non-animal food in addition to animal food. Note that there is no clear line that differentiates facultative carnivores from omnivores; dogs would be considered facultative carnivores.



(a)



(b)

Figure 46.2.2: Carnivores like the (a) lion eat primarily meat. The (b) ladybug is also a carnivore that consumes small insects called aphids. (credit a: modification of work by Kevin Pluck; credit b: modification of work by Jon Sullivan)

Omnivores are animals that eat both plant- and animal-derived food. In Latin, omnivore means to eat everything. Humans, bears (shown in Figure 46.2.3a), and chickens are example of vertebrate omnivores; invertebrate omnivores include cockroaches and crayfish (shown in Figure 46.2.3b).



(a)



(b)

Figure 46.2.3: Omnivores like the (a) bear and (b) crayfish eat both plant and animal based food. (credit a: modification of work by Dave Menke; credit b: modification of work by Jon Sullivan)

Invertebrate Digestive Systems

Animals have evolved different types of digestive systems to aid in the digestion of the different foods they consume. The simplest example is that of a gastrovascular cavity and is found in organisms with only one opening for digestion. Platyhelminthes (flatworms), Ctenophora (comb jellies), and Cnidaria (coral, jelly fish, and sea anemones) use this type of digestion. Gastrovascular cavities, as shown in Figure 46.2.4a, are typically a blind tube or cavity with only one opening, the “mouth”, which also serves as an “anus”. Ingested material enters the mouth and passes through a hollow, tubular cavity. Cells within the cavity secrete digestive enzymes that break down the food. The food particles are engulfed by the cells lining the gastrovascular cavity.

The alimentary canal, shown in Figure 46.2.4b, is a more advanced system: it consists of one tube with a mouth at one end and an anus at the other. Earthworms are an example of an animal with an alimentary canal. Once the food is ingested through the mouth, it passes through the esophagus and is stored in an organ called the crop; then it passes into the gizzard where it is churned and

digested. From the gizzard, the food passes through the intestine, the nutrients are absorbed, and the waste is eliminated as feces, called castings, through the anus.

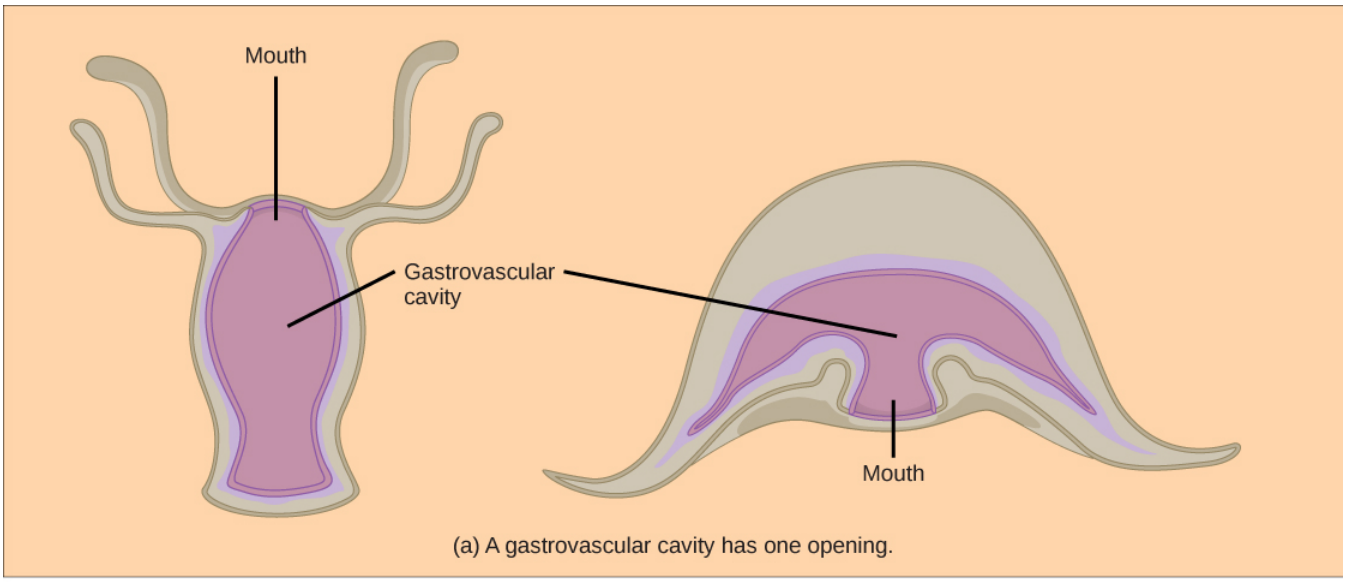


Figure **46.2.4**: (a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food, and an anus for eliminating waste, as shown in this nematode.

Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating unmasticated food.

Monogastric: Single-chambered Stomach

As the word monogastric suggests, this type of digestive system consists of one (“mono”) stomach chamber (“gastric”). Humans and many animals have a monogastric digestive system as illustrated in Figure **46.2.5**. The process of digestion begins with the mouth and the intake of food. The teeth play an important role in masticating (chewing) or physically breaking down food into smaller particles. The enzymes present in saliva also begin to chemically break down food. The esophagus is a long tube that connects the mouth to the stomach. Using peristalsis, or wave-like smooth muscle contractions, the muscles of the esophagus push the food towards the stomach. In order to speed up the actions of enzymes in the stomach, the stomach is an extremely acidic environment, with a pH between 1.5 and 2.5. The gastric juices, which include enzymes in the stomach, act on the food particles and continue the process of digestion. Further breakdown of food takes place in the small intestine where enzymes produced by the liver, the small intestine, and the pancreas continue the process of digestion. The nutrients are absorbed into the blood stream across the epithelial cells lining the walls of the small intestines. The waste material travels on to the large intestine where water is absorbed and the drier waste material is compacted into feces; it is stored until it is excreted through the rectum.

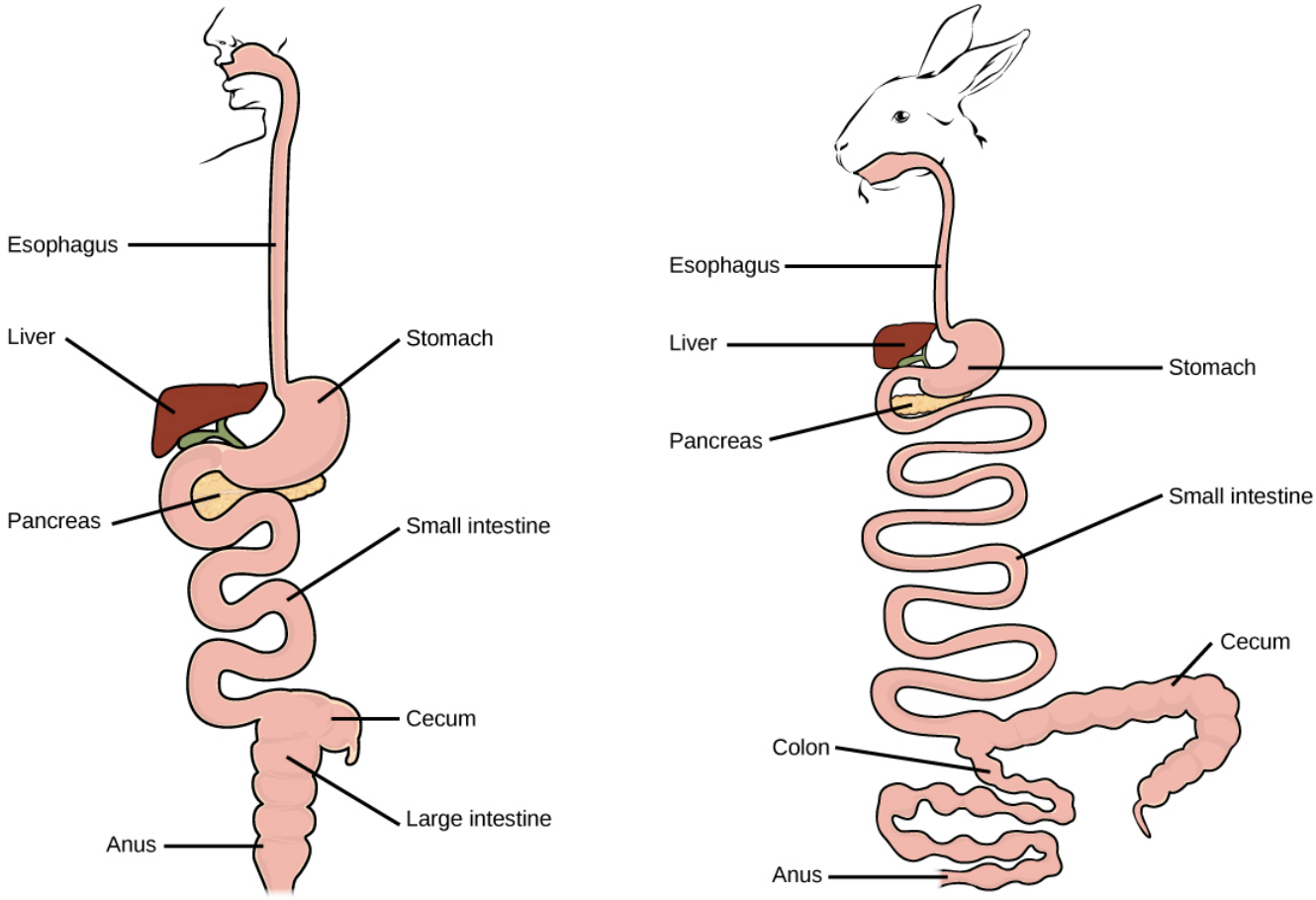


Figure **46.2.5**: (a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients. Rabbits digest their food twice: the first time food passes through the digestive system, it collects in the cecum, and then it passes as soft feces called cecotrophes. The rabbit re-ingests these cecotrophes to further digest them.

Avian

Birds face special challenges when it comes to obtaining nutrition from food. They do not have teeth and so their digestive system, shown in Figure **46.2.6**, must be able to process un-masticated food. Birds have evolved a variety of beak types that reflect the vast variety in their diet, ranging from seeds and insects to fruits and nuts. Because most birds fly, their metabolic rates are high in order to efficiently process food and keep their body weight low. The stomach of birds has two chambers: the proventriculus, where gastric juices are produced to digest the food before it enters the stomach, and the gizzard, where the food is stored, soaked, and mechanically ground. The undigested material forms food pellets that are sometimes regurgitated. Most of the chemical digestion and absorption happens in the intestine and the waste is excreted through the cloaca.

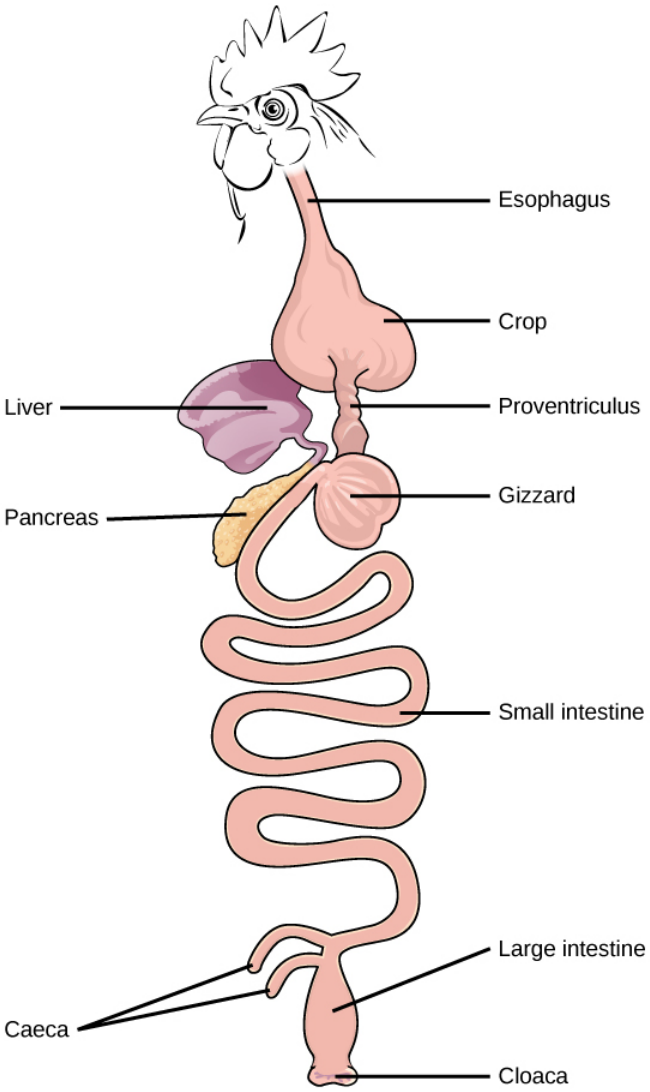


Figure **46.2.6**: The avian esophagus has a pouch, called a crop, which stores food. Food passes from the crop to the first of two stomachs, called the proventriculus, which contains digestive juices that break down food. From the proventriculus, the food enters the second stomach, called the gizzard, which grinds food. Some birds swallow stones or grit, which are stored in the gizzard, to aid the grinding process. Birds do not have separate openings to excrete urine and feces. Instead, uric acid from the kidneys is secreted into the large intestine and combined with waste from the digestive process. This waste is excreted through an opening called the cloaca.

Evolution Connection: Avian Adaptations

Birds have a highly efficient, simplified digestive system. Recent fossil evidence has shown that the evolutionary divergence of birds from other land animals was characterized by streamlining and simplifying the digestive system. Unlike many other animals, birds do not have teeth to chew their food. In place of lips, they have sharp pointy beaks. The horny beak, lack of jaws, and the smaller tongue of the birds can be traced back to their dinosaur ancestors. The emergence of these changes seems to coincide with the inclusion of seeds in the bird diet. Seed-eating birds have beaks that are shaped for grabbing seeds and the two-compartment stomach allows for delegation of tasks. Since birds need to remain light in order to fly, their metabolic rates are very high, which means they digest their food very quickly and need to eat often. Contrast this with the ruminants, where the digestion of plant matter takes a very long time.

Ruminants

Ruminants are mainly herbivores like cows, sheep, and goats, whose entire diet consists of eating large amounts of roughage or fiber. They have evolved digestive systems that help them digest vast amounts of cellulose. An interesting feature of the ruminants' mouth is that they do not have upper incisor teeth. They use their lower teeth, tongue and lips to tear and chew their food. From the mouth, the food travels to the esophagus and on to the stomach.

To help digest the large amount of plant material, the stomach of the ruminants is a multi-chambered organ, as illustrated in Figure **46.2.7**. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that break down cellulose and ferment ingested food. The abomasum is the "true" stomach and is the equivalent of the monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary to digest plant material in ruminants. The fermentation process produces large amounts of gas in the stomach chamber, which must be eliminated. As in other animals, the small intestine plays an important role in nutrient absorption, and the large intestine helps in the elimination of waste.

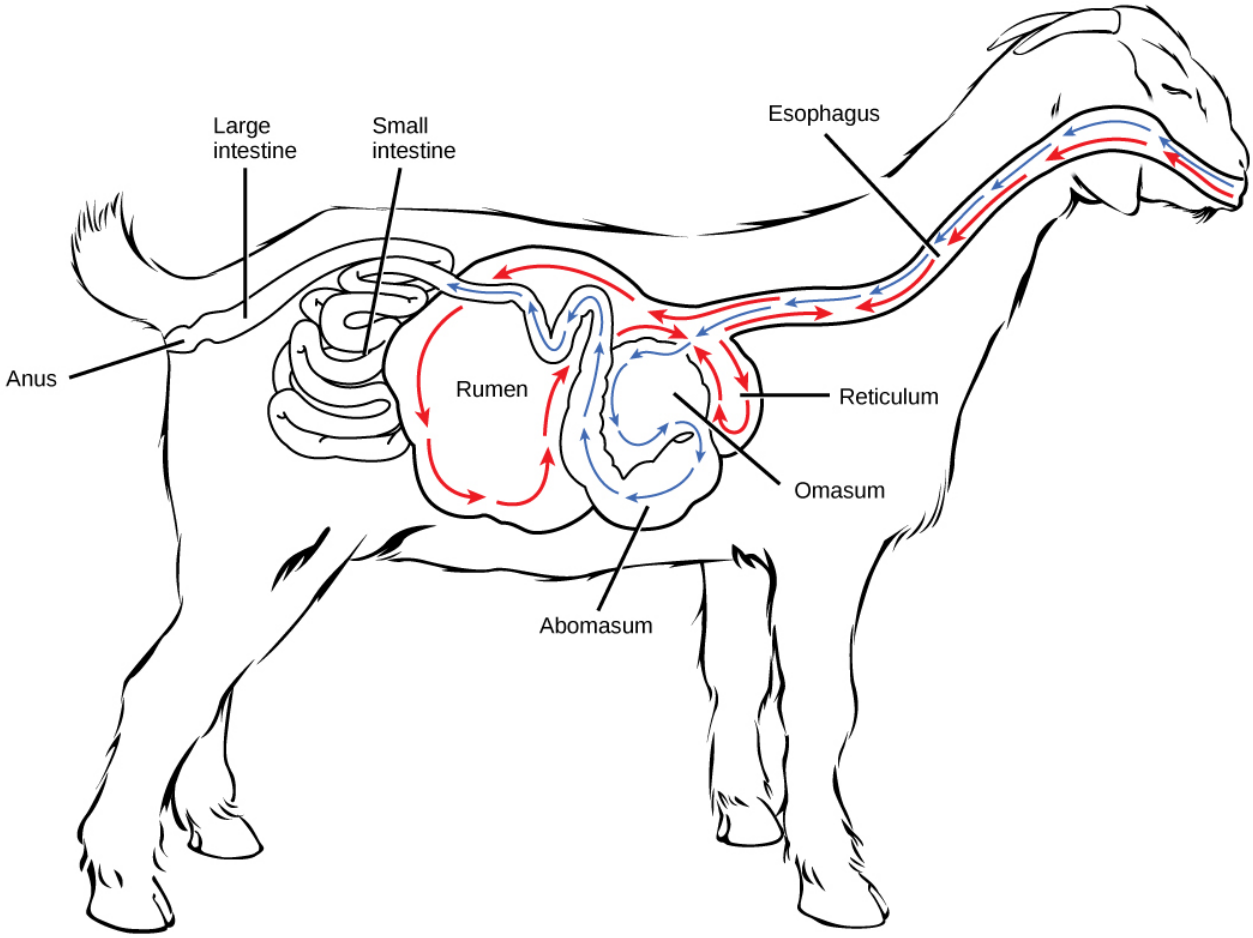


Figure **46.2.7**: Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the omasum, which removes water. The cud then passes onto the fourth stomach, the abomasum, where it is digested by enzymes produced by the ruminant.

Pseudo-ruminants

Some animals, such as camels and alpacas, are pseudo-ruminants. They eat a lot of plant material and roughage. Digesting plant material is not easy because plant cell walls contain the polymeric sugar molecule cellulose. The digestive enzymes of these animals cannot break down cellulose, but microorganisms present in the digestive system can. Therefore, the digestive system must be able to handle large amounts of roughage and break down the cellulose. Pseudo-ruminants have a three-chamber stomach in the digestive system. However, their cecum—a pouched organ at the beginning of the large intestine containing many microorganisms that are necessary for the digestion of plant materials—is large and is the site where the roughage is fermented and digested. These animals do not have a rumen but have an omasum, abomasum, and reticulum.

Parts of the Digestive System

The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms.

Oral Cavity

The oral cavity, or mouth, is the point of entry of food into the digestive system, illustrated in Figure **46.2.8**. The food consumed is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

The extensive chemical process of digestion begins in the mouth. As food is being chewed, saliva, produced by the salivary glands, mixes with the food. Saliva is a watery substance produced in the mouths of many animals. There are three major glands that secrete saliva—the parotid, the submandibular, and the sublingual. Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains immunoglobulins and lysozymes, which have antibacterial action to reduce tooth decay by inhibiting growth of some bacteria. Saliva also contains an enzyme called salivary amylase that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme called lipase is produced by the cells in the tongue. Lipases are a class of enzymes that can break down triglycerides. The lingual lipase begins the breakdown of fat components in the food. The chewing and wetting action provided by the teeth and saliva prepare the food into a mass called the bolus for swallowing. The tongue helps in swallowing—moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the trachea, which leads to the lungs, and the esophagus, which leads to the stomach. The trachea has an opening called the glottis, which is covered by a cartilaginous flap called the epiglottis. When swallowing, the epiglottis closes the glottis and food passes into the esophagus and not the trachea. This arrangement allows food to be kept out of the trachea.

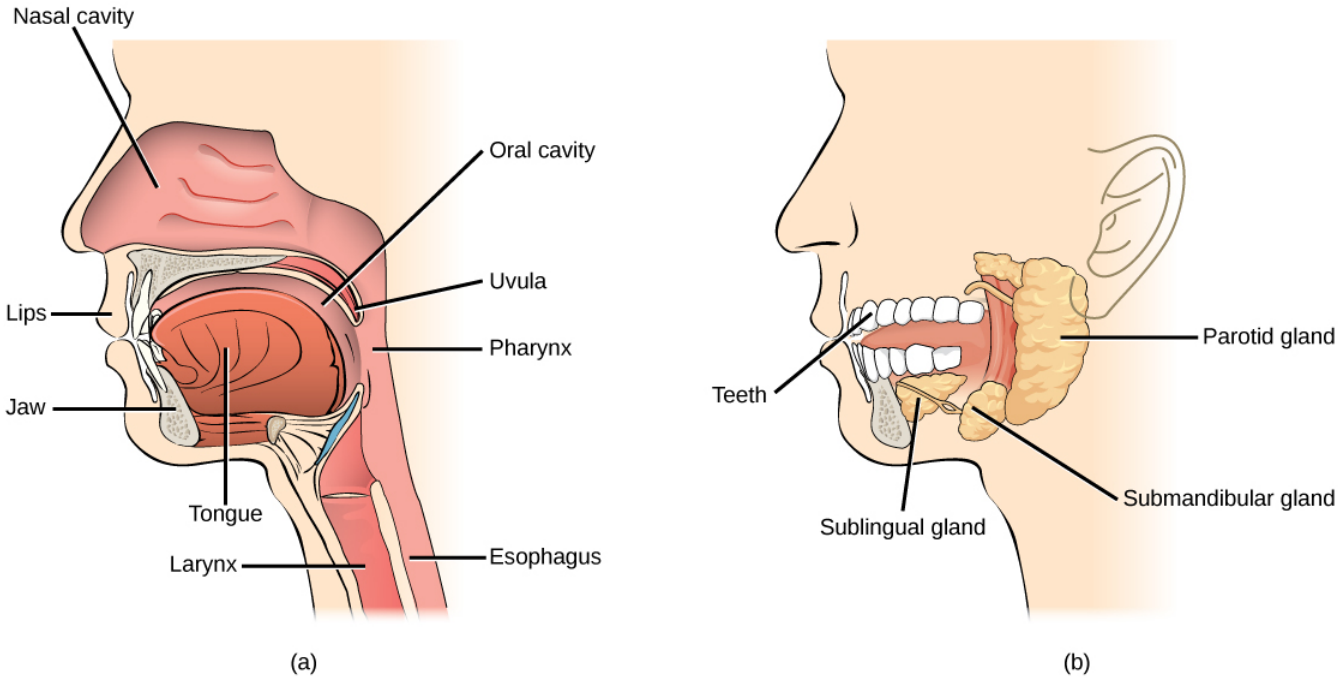


Figure **46.2.8**: Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by the National Cancer Institute)

Esophagus

The esophagus is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave like movements called peristalsis that push the food toward the stomach, as illustrated in Figure **46.2.9**. The peristalsis wave is unidirectional—it moves food from the mouth to the stomach, and reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.

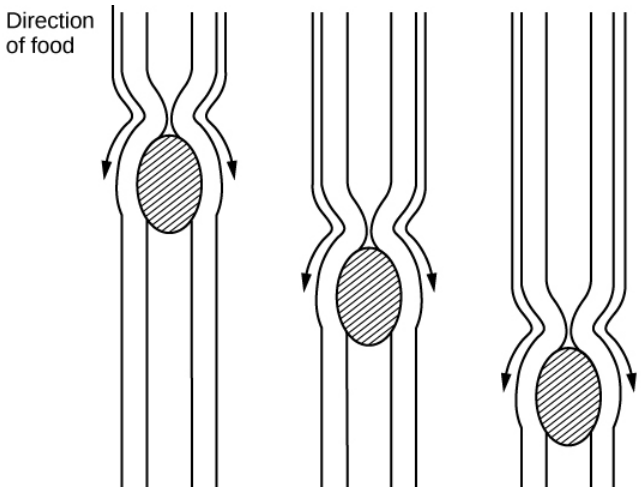


Figure 46.2.9: The esophagus transfers food from the mouth to the stomach through peristaltic movements.

A ring-like muscle called a sphincter forms valves in the digestive system. The gastro-esophageal sphincter is located at the stomach end of the esophagus. In response to swallowing and the pressure exerted by the bolus of food, this sphincter opens, and the bolus enters the stomach. When there is no swallowing action, this sphincter is shut and prevents the contents of the stomach from traveling up the esophagus. Many animals have a true sphincter; however, in humans, there is no true sphincter, but the esophagus remains closed when there is no swallowing action. Acid reflux or "heartburn" occurs when the acidic digestive juices escape into the esophagus.

Stomach

A large part of digestion occurs in the stomach, shown in Figure 46.2.10. The stomach is a saclike organ that secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

Art Connection

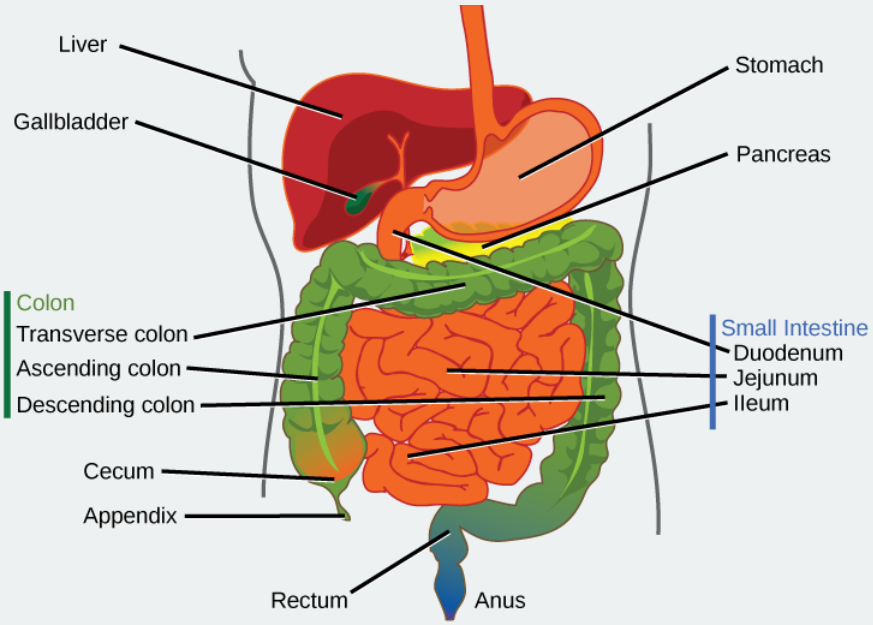


Figure 46.2.10: The human stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)

Which of the following statements about the digestive system is false?

A. Chyme is a mixture of food and digestive juices that is produced in the stomach.
B. Food enters the large intestine before the small intestine.
C. In the small intestine, chyme mixes with bile, which emulsifies fats.
D. The stomach is separated from the small intestine by the pyloric sphincter.

The stomach is also the major site for protein digestion in animals other than ruminants. Protein digestion is mediated by an enzyme called pepsin in the stomach chamber. Pepsin is secreted by the chief cells in the stomach in an inactive form called pepsinogen. Pepsin breaks peptide bonds and cleaves proteins into smaller polypeptides; it also helps activate more pepsinogen, starting a positive feedback mechanism that generates more pepsin. Another cell type—parietal cells—secrete hydrogen and chloride ions, which combine in the lumen to form hydrochloric acid, the primary acidic component of the stomach juices. Hydrochloric acid helps to convert the inactive pepsinogen to pepsin. The highly acidic environment also kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the hydrolysis of protein in the food. Chemical digestion is facilitated by the churning action of the stomach. Contraction and relaxation of smooth muscles mixes the stomach contents about every 20 minutes. The partially digested food and gastric juice mixture is called chyme. Chyme passes from the stomach to the small intestine. Further protein digestion takes place in the small intestine. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by the pyloric sphincter.

When digesting protein and some fats, the stomach lining must be protected from getting digested by pepsin. There are two points to consider when describing how the stomach lining is protected. First, as previously mentioned, the enzyme pepsin is synthesized in the inactive form. This protects the chief cells, because pepsinogen does not have the same enzyme functionality of pepsin. Second, the stomach has a thick mucus lining that protects the underlying tissue from the action of the digestive juices. When this mucus lining is ruptured, ulcers can form in the stomach. Ulcers are open wounds in or on an organ caused by bacteria (*Helicobacter pylori*) when the mucus lining is ruptured and fails to reform.

Small Intestine

Chyme moves from the stomach to the small intestine. The small intestine is the organ where the digestion of protein, fats, and carbohydrates is completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the villi. The apical surface of each villus has many microscopic projections called microvilli. These structures, illustrated in Figure **46.2.11**, are lined with epithelial cells on the luminal side and allow for the nutrients to be absorbed from the digested food and absorbed into the blood stream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients. Absorbed nutrients in the blood are carried into the hepatic portal vein, which leads to the liver. There, the liver regulates the distribution of nutrients to the rest of the body and removes toxic substances, including drugs, alcohol, and some pathogens.

Art Connection

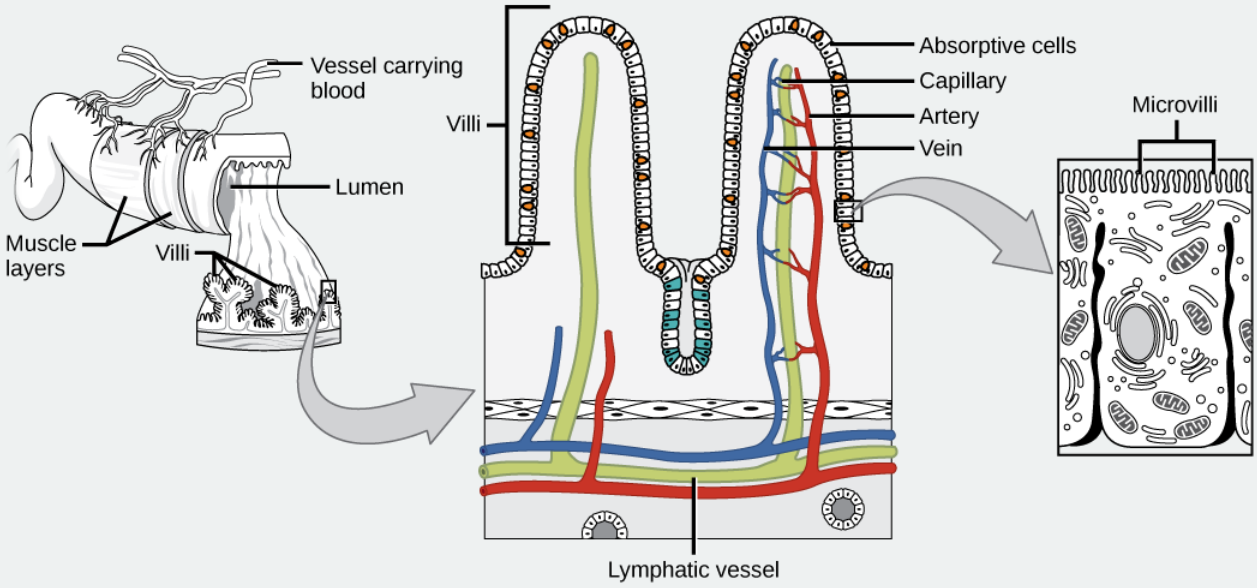


Figure 46.2.11: Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nutrients.

Which of the following statements about the small intestine is false?

A. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
B. The inside of the small intestine has many folds, called villi.
C. Microvilli are lined with blood vessels as well as lymphatic vessels.
D. The inside of the small intestine is called the lumen.

The human small intestine is over 6m long and is divided into three parts: the duodenum, the jejunum, and the ileum. The "C-shaped," fixed part of the small intestine is called the duodenum and is shown in Figure 46.2.11. The duodenum is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum. In the duodenum, chyme is mixed with pancreatic juices in an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Pancreatic juices also contain several digestive enzymes. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. Bile is produced in the liver and stored and concentrated in the gallbladder. Bile contains bile salts which emulsify lipids while the pancreas produces enzymes that catabolize starches, disaccharides, proteins, and fats. These digestive juices break down the food particles in the chyme into glucose, triglycerides, and amino acids. Some chemical digestion of food takes place in the duodenum. Absorption of fatty acids also takes place in the duodenum.

The second part of the small intestine is called the jejunum, shown in Figure 46.2.11. Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. The bulk of chemical digestion and nutrient absorption occurs in the jejunum.

The ileum, also illustrated in Figure 46.2.11 is the last part of the small intestine and here the bile salts and vitamins are absorbed into blood stream. The undigested food is sent to the colon from the ileum via peristaltic movements of the muscle. The ileum ends and the large intestine begins at the ileocecal valve. The vermiform, "worm-like," appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

The large intestine, illustrated in Figure 46.2.12, reabsorbs the water from the undigested food material and processes the waste material. The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or "intestinal flora" that aid in the digestive processes. The colon can be divided into four regions, the ascending colon, the transverse colon, the descending colon and the sigmoid colon. The main functions of the colon are

to extract the water and mineral salts from undigested food, and to store waste material. Carnivorous mammals have a shorter large intestine compared to herbivorous mammals due to their diet.

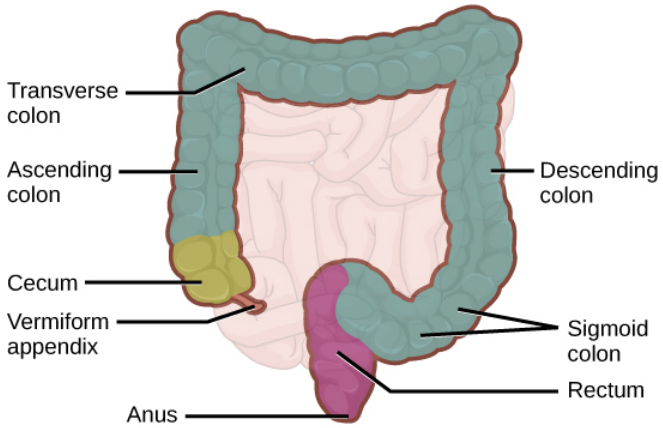


Figure 46.2.12: The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

Rectum and Anus

The rectum is the terminal end of the large intestine, as shown in Figure 46.2.12. The primary role of the rectum is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The anus is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

The organs discussed above are the organs of the digestive tract through which food passes. Accessory organs are organs that add secretions (enzymes) that catabolize food into nutrients. Accessory organs include salivary glands, the liver, the pancreas, and the gallbladder. The liver, pancreas, and gallbladder are regulated by hormones in response to the food consumed.

The liver is the largest internal organ in humans and it plays a very important role in digestion of fats and detoxifying blood. The liver produces bile, a digestive juice that is required for the breakdown of fatty components of the food in the duodenum. The liver also processes the vitamins and fats and synthesizes many plasma proteins.

The pancreas is another important gland that secretes digestive juices. The chyme produced from the stomach is highly acidic in nature; the pancreatic juices contain high levels of bicarbonate, an alkali that neutralizes the acidic chyme. Additionally, the pancreatic juices contain a large variety of enzymes that are required for the digestion of protein and carbohydrates.

The gallbladder is a small organ that aids the liver by storing bile and concentrating bile salts. When chyme containing fatty acids enters the duodenum, the bile is secreted from the gallbladder into the duodenum.

Summary

Different animals have evolved different types of digestive systems specialized to meet their dietary needs. Humans and many other animals have monogastric digestive systems with a single-chambered stomach. Birds have evolved a digestive system that includes a gizzard where the food is crushed into smaller pieces. This compensates for their inability to masticate. Ruminants that consume large amounts of plant material have a multi-chambered stomach that digests roughage. Pseudo-ruminants have similar digestive processes as ruminants but do not have the four-compartment stomach. Processing food involves ingestion (eating), digestion (mechanical and enzymatic breakdown of large molecules), absorption (cellular uptake of nutrients), and elimination (removal of undigested waste as feces).

Many organs work together to digest food and absorb nutrients. The mouth is the point of ingestion and the location where both mechanical and chemical breakdown of food begins. Saliva contains an enzyme called amylase that breaks down carbohydrates. The food bolus travels through the esophagus by peristaltic movements to the stomach. The stomach has an extremely acidic environment. An enzyme called pepsin digests protein in the stomach. Further digestion and absorption take place in the small intestine. The large intestine reabsorbs water from the undigested food and stores waste until elimination.

Art Connections

Figure 46.2.10: Which of the following statements about the digestive system is false?

A. Chyme is a mixture of food and digestive juices that is produced in the stomach.
B. Food enters the large intestine before the small intestine.
C. In the small intestine, chyme mixes with bile, which emulsifies fats.
D. The stomach is separated from the small intestine by the pyloric sphincter.

Answer

B

Figure 46.2.11: Which of the following statements about the small intestine is false?

A. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
B. The inside of the small intestine has many folds, called villi.
C. Microvilli are lined with blood vessels as well as lymphatic vessels.
D. The inside of the small intestine is called the lumen.

Answer

C

Glossary

alimentary canal
tubular digestive system with a mouth and anus

anus
exit point for waste material

bile
digestive juice produced by the liver; important for digestion of lipids

bolus
mass of food resulting from chewing action and wetting by saliva

carnivore
animal that consumes animal flesh

chyme
mixture of partially digested food and stomach juices

duodenum
first part of the small intestine where a large part of digestion of carbohydrates and fats occurs

esophagus
tubular organ that connects the mouth to the stomach

gallbladder
organ that stores and concentrates bile

gastrovascular cavity

digestive system consisting of a single opening

gizzard
muscular organ that grinds food

herbivore
animal that consumes strictly plant diet

ileum
last part of the small intestine; connects the small intestine to the large intestine; important for absorption of B-12

jejunum
second part of the small intestine

large intestine
digestive system organ that reabsorbs water from undigested material and processes waste matter

lipase
enzyme that chemically breaks down lipids

liver
organ that produces bile for digestion and processes vitamins and lipids

monogastric
digestive system that consists of a single-chambered stomach

omnivore
animal that consumes both plants and animals

pancreas
gland that secretes digestive juices

pepsin
enzyme found in the stomach whose main role is protein digestion

pepsinogen
inactive form of pepsin

peristalsis
wave-like movements of muscle tissue

proventriculus
glandular part of a bird’s stomach

rectum
area of the body where feces is stored until elimination

roughage
component of food that is low in energy and high in fiber

ruminant
animal with a stomach divided into four compartments

salivary amylase

enzyme found in saliva, which converts carbohydrates to maltose

small intestine

organ where digestion of protein, fats, and carbohydrates is completed

sphincter

band of muscle that controls movement of materials throughout the digestive tract

stomach

saclike organ containing acidic digestive juices

villi

folds on the inner surface of the small intestine whose role is to increase absorption area

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46.3: The Esophagus and Stomach- The Early Stages of Digestion

Skills to Develop

- Describe the process of digestion
- Detail the steps involved in digestion and absorption
- Define elimination
- Explain the role of both the small and large intestines in absorption

Obtaining nutrition and energy from food is a multi-step process. For true animals, the first step is ingestion, the act of taking in food. This is followed by digestion, absorption, and elimination. In the following sections, each of these steps will be discussed in detail.

Ingestion

The large molecules found in intact food cannot pass through the cell membranes. Food needs to be broken into smaller particles so that animals can harness the nutrients and organic molecules. The first step in this process is ingestion. Ingestion is the process of taking in food through the mouth. In vertebrates, the teeth, saliva, and tongue play important roles in mastication (preparing the food into bolus). While the food is being mechanically broken down, the enzymes in saliva begin to chemically process the food as well. The combined action of these processes modifies the food from large particles to a soft mass that can be swallowed and can travel the length of the esophagus.

Digestion and Absorption

Digestion is the mechanical and chemical break down of food into small organic fragments. It is important to break down macromolecules into smaller fragments that are of suitable size for absorption across the digestive epithelium. Large, complex molecules of proteins, polysaccharides, and lipids must be reduced to simpler particles such as simple sugar before they can be absorbed by the digestive epithelial cells. Different organs play specific roles in the digestive process. The animal diet needs carbohydrates, protein, and fat, as well as vitamins and inorganic components for nutritional balance. How each of these components is digested is discussed in the following sections.

Carbohydrates

The digestion of carbohydrates begins in the mouth. The salivary enzyme amylase begins the breakdown of food starches into maltose, a disaccharide. As the bolus of food travels through the esophagus to the stomach, no significant digestion of carbohydrates takes place. The esophagus produces no digestive enzymes but does produce mucous for lubrication. The acidic environment in the stomach stops the action of the amylase enzyme.

The next step of carbohydrate digestion takes place in the duodenum. Recall that the chyme from the stomach enters the duodenum and mixes with the digestive secretion from the pancreas, liver, and gallbladder. Pancreatic juices also contain amylase, which continues the breakdown of starch and glycogen into maltose, a disaccharide. The disaccharides are broken down into monosaccharides by enzymes called maltases, sucrases, and lactases, which are also present in the brush border of the small intestinal wall. Maltase breaks down maltose into glucose. Other disaccharides, such as sucrose and lactose are broken down by sucrase and lactase, respectively. Sucrase breaks down sucrose (or “table sugar”) into glucose and fructose, and lactase breaks down lactose (or “milk sugar”) into glucose and galactose. The monosaccharides (glucose) thus produced are absorbed and then can be used in metabolic pathways to harness energy. The monosaccharides are transported across the intestinal epithelium into the bloodstream to be transported to the different cells in the body. The steps in carbohydrate digestion are summarized in Figure **46.3.1**.

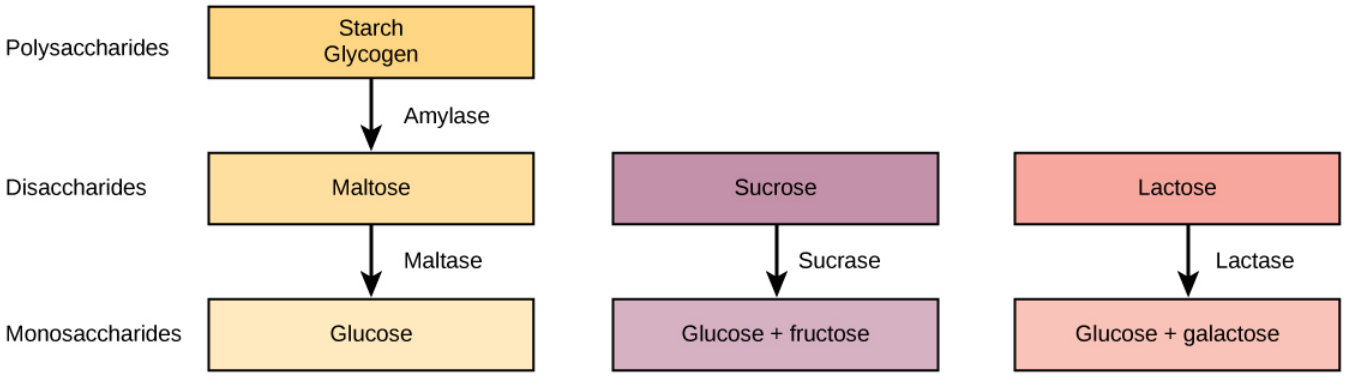


Figure **46.3.1**: Digestion of carbohydrates is performed by several enzymes. Starch and glycogen are broken down into glucose by amylase and maltase. Sucrose (table sugar) and lactose (milk sugar) are broken down by sucrase and lactase, respectively.

Table 46.3.1: Digestion of Carbohydrates

Enzyme	Produced By	Site of Action	Substrate Acting On	End Products
Salivary amylase	Salivary glands	Mouth	Polysaccharides (Starch)	Disaccharides (maltose), oligosaccharides
Pancreatic amylase	Pancreas	Small intestine	Polysaccharides (starch)	Disaccharides (maltose), monosaccharides
Oligosaccharidases	Lining of the intestine; brush border membrane	Small intestine	Disaccharides	Monosaccharides (e.g., glucose, fructose, galactose)

Protein

A large part of protein digestion takes place in the stomach. The enzyme pepsin plays an important role in the digestion of proteins by breaking down the intact protein to peptides, which are short chains of four to nine amino acids. In the duodenum, other enzymes—trypsin, elastase, and chymotrypsin—act on the peptides reducing them to smaller peptides. Trypsin elastase, carboxypeptidase, and chymotrypsin are produced by the pancreas and released into the duodenum where they act on the chyme. Further breakdown of peptides to single amino acids is aided by enzymes called peptidases (those that break down peptides). Specifically, carboxypeptidase, dipeptidase, and aminopeptidase play important roles in reducing the peptides to free amino acids. The amino acids are absorbed into the bloodstream through the small intestines. The steps in protein digestion are summarized in Figure **46.3.2**.

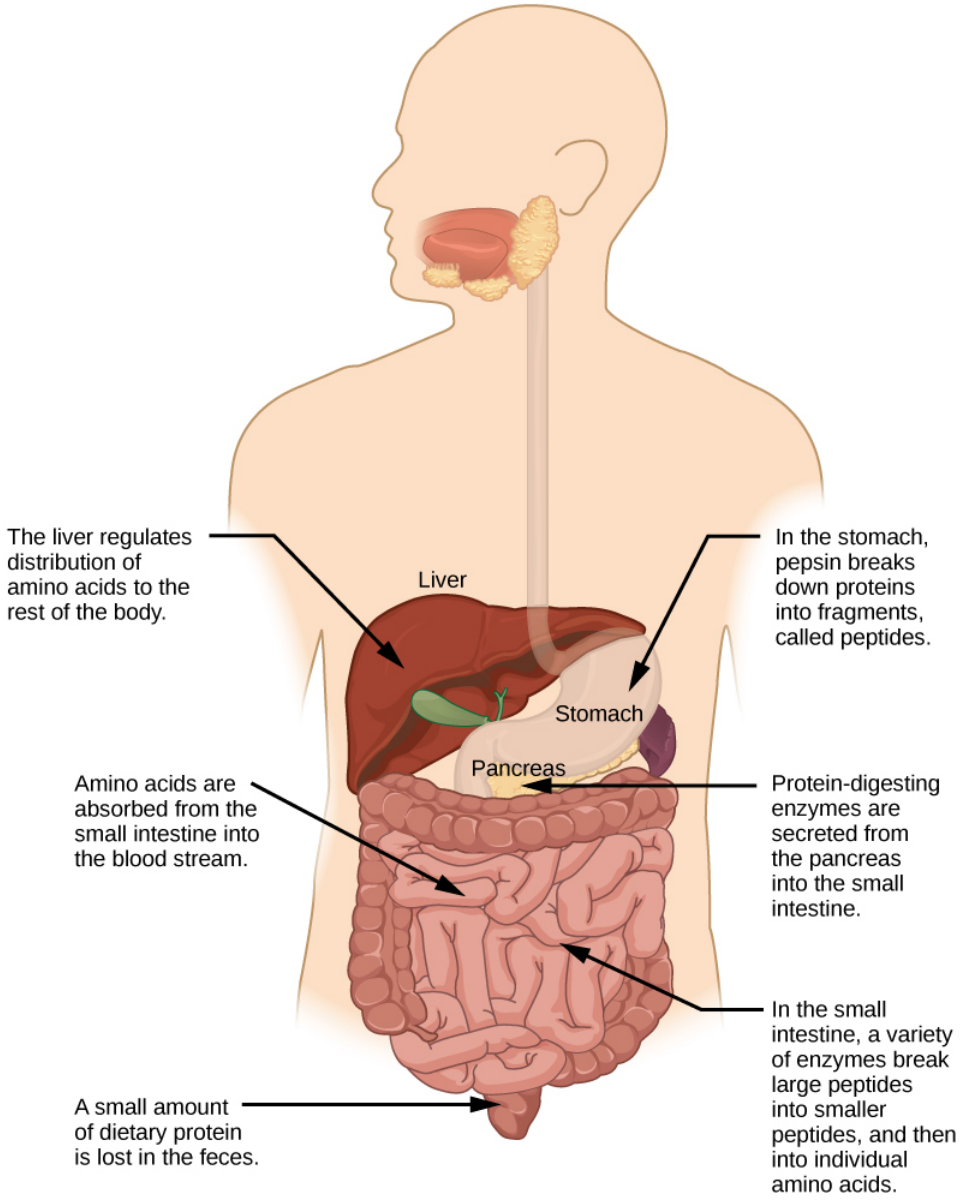


Figure **46.3.2**: Protein digestion is a multistep process that begins in the stomach and continues through the intestines.

Table 46.3.2: Digestion of Protein

Enzyme	Produced By	Site of Action	Substrate Acting On	End Products
Pepsin	Stomach chief cells	Stomach	Proteins	Peptides
Trypsin Elastase Chymotrypsin	Pancreas	Small intestine	Proteins	Peptides
Carboxypeptidase	Pancreas	Small intestine	Peptides	Amino acids and peptides
Aminopeptidase Dipeptidase	Lining of intestine	Small intestine	Peptides	Amino acids

Lipids

Lipid digestion begins in the stomach with the aid of lingual lipase and gastric lipase. However, the bulk of lipid digestion occurs in the small intestine due to pancreatic lipase. When chyme enters the duodenum, the hormonal responses trigger the release of bile,

which is produced in the liver and stored in the gallbladder. Bile aids in the digestion of lipids, primarily triglycerides by emulsification. Emulsification is a process in which large lipid globules are broken down into several small lipid globules. These small globules are more widely distributed in the chyme rather than forming large aggregates. Lipids are hydrophobic substances: in the presence of water, they will aggregate to form globules to minimize exposure to water. Bile contains bile salts, which are amphipathic, meaning they contain hydrophobic and hydrophilic parts. Thus, the bile salts hydrophilic side can interface with water on one side and the hydrophobic side interfaces with lipids on the other. By doing so, bile salts emulsify large lipid globules into small lipid globules.

Why is emulsification important for digestion of lipids? Pancreatic juices contain enzymes called lipases (enzymes that break down lipids). If the lipid in the chyme aggregates into large globules, very little surface area of the lipids is available for the lipases to act on, leaving lipid digestion incomplete. By forming an emulsion, bile salts increase the available surface area of the lipids many fold. The pancreatic lipases can then act on the lipids more efficiently and digest them, as detailed in Figure **46.3.3**. Lipases break down the lipids into fatty acids and glycerides. These molecules can pass through the plasma membrane of the cell and enter the epithelial cells of the intestinal lining. The bile salts surround long-chain fatty acids and monoglycerides forming tiny spheres called micelles. The micelles move into the brush border of the small intestine absorptive cells where the long-chain fatty acids and monoglycerides diffuse out of the micelles into the absorptive cells leaving the micelles behind in the chyme. The long-chain fatty acids and monoglycerides recombine in the absorptive cells to form triglycerides, which aggregate into globules and become coated with proteins. These large spheres are called chylomicrons. Chylomicrons contain triglycerides, cholesterol, and other lipids and have proteins on their surface. The surface is also composed of the hydrophilic phosphate "heads" of phospholipids. Together, they enable the chylomicron to move in an aqueous environment without exposing the lipids to water. Chylomicrons leave the absorptive cells via exocytosis. Chylomicrons enter the lymphatic vessels, and then enter the blood in the subclavian vein.

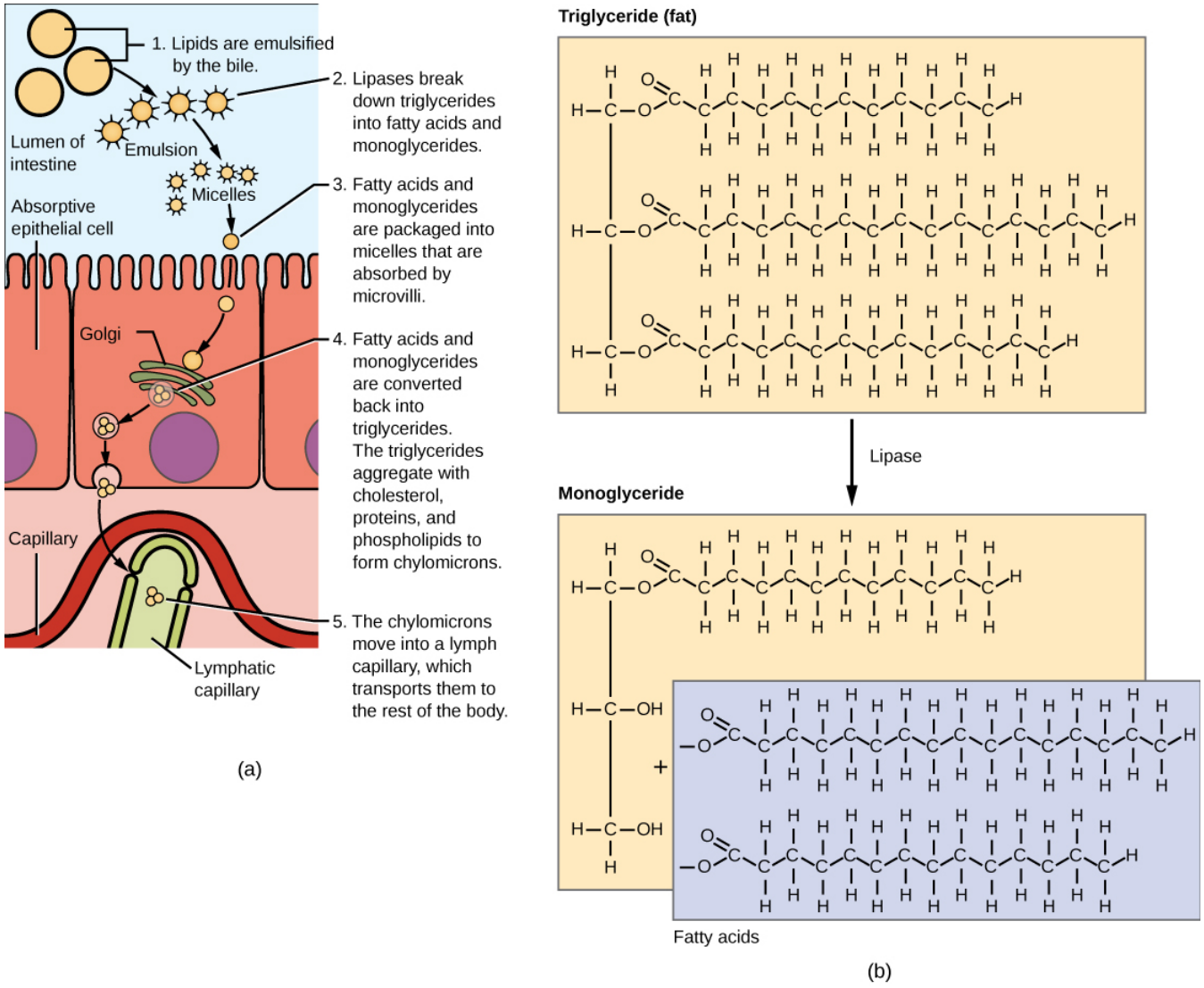


Figure **46.3.3**: Lipids are digested and absorbed in the small intestine.

Vitamins

Vitamins can be either water-soluble or lipid-soluble. Fat soluble vitamins are absorbed in the same manner as lipids. It is important to consume some amount of dietary lipid to aid the absorption of lipid-soluble vitamins. Water-soluble vitamins can be directly absorbed into the bloodstream from the intestine.

Art Connection

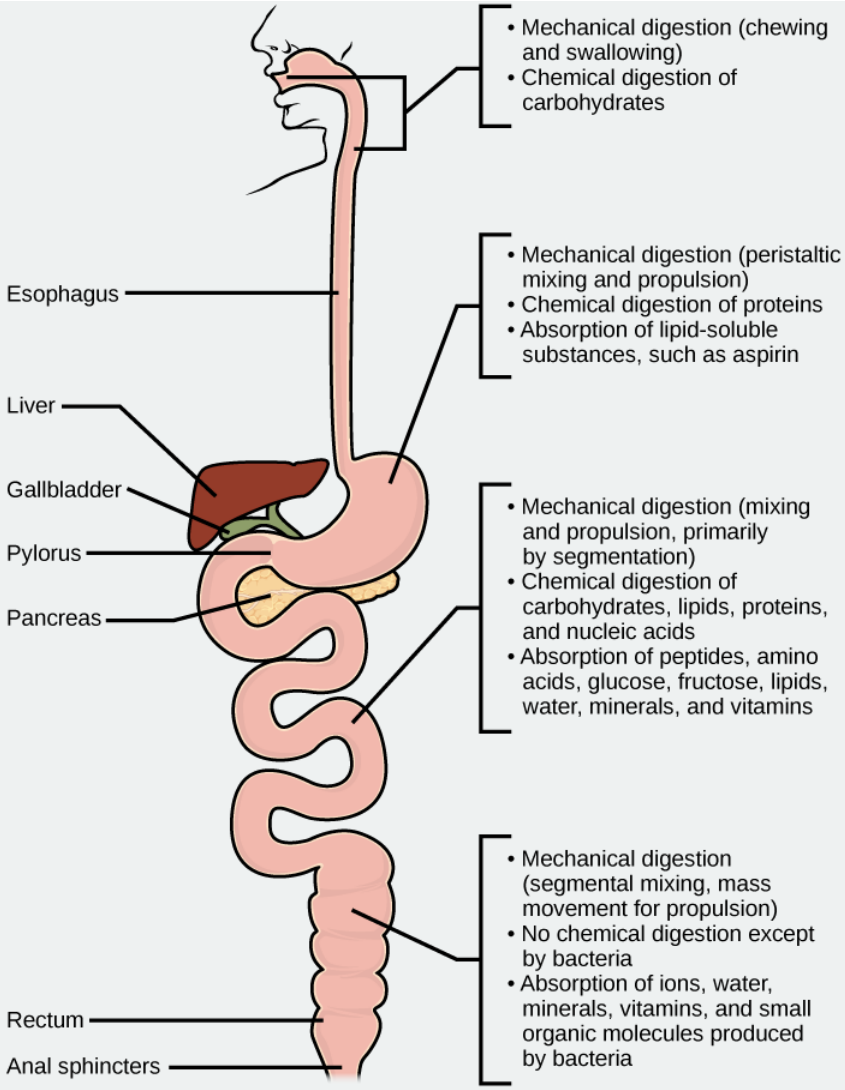


Figure **46.3.4**: Mechanical and chemical digestion of food takes place in many steps, beginning in the mouth and ending in the rectum.

Which of the following statements about digestive processes is true?

A. Amylase, maltase, and lactase in the mouth digest carbohydrates.
B. Trypsin and lipase in the stomach digest protein.
C. Bile emulsifies lipids in the small intestine.
D. No food is absorbed until the small intestine.

Elimination

The final step in digestion is the elimination of undigested food content and waste products. The undigested food material enters the colon, where most of the water is reabsorbed. Recall that the colon is also home to the microflora called “intestinal flora” that aid in the digestion process. The semi-solid waste is moved through the colon by peristaltic movements of the muscle and is stored in the rectum. As the rectum expands in response to storage of fecal matter, it triggers the neural signals required to set up the urge to eliminate. The solid waste is eliminated through the anus using peristaltic movements of the rectum.

Common Problems with Elimination

Diarrhea and constipation are some of the most common health concerns that affect digestion. Constipation is a condition where the feces are hardened because of excess water removal in the colon. In contrast, if enough water is not removed from the feces, it

results in diarrhea. Many bacteria, including the ones that cause cholera, affect the proteins involved in water reabsorption in the colon and result in excessive diarrhea.

Emesis

Emesis, or vomiting, is elimination of food by forceful expulsion through the mouth. It is often in response to an irritant that affects the digestive tract, including but not limited to viruses, bacteria, emotions, sights, and food poisoning. This forceful expulsion of the food is due to the strong contractions produced by the stomach muscles. The process of emesis is regulated by the medulla.

Summary

Digestion begins with ingestion, where the food is taken in the mouth. Digestion and absorption take place in a series of steps with special enzymes playing important roles in digesting carbohydrates, proteins, and lipids. Elimination describes removal of undigested food contents and waste products from the body. While most absorption occurs in the small intestines, the large intestine is responsible for the final removal of water that remains after the absorptive process of the small intestines. The cells that line the large intestine absorb some vitamins as well as any leftover salts and water. The large intestine (colon) is also where feces is formed.

Art Connections

Figure **46.3.4**: Which of the following statements about digestive processes is true?

A. Amylase, maltase and lactase in the mouth digest carbohydrates.
B. Trypsin and lipase in the stomach digest protein.
C. Bile emulsifies lipids in the small intestine.
D. No food is absorbed until the small intestine.

Answer

C

Glossary

aminopeptidase
protease that breaks down peptides to single amino acids; secreted by the brush border of small intestine

carboxypeptidase
protease that breaks down peptides to single amino acids; secreted by the brush border of the small intestine

chylomicron
small lipid globule

chymotrypsin
pancreatic protease

digestion
mechanical and chemical break down of food into small organic fragments

dipeptidase
protease that breaks down peptides to single amino acids; secreted by the brush border of small intestine

elastase
pancreatic protease

ingestion

act of taking in food

lactase
enzyme that breaks down lactose into glucose and galactose

maltase
enzyme that breaks down maltose into glucose

sucrase
enzyme that breaks down sucrose into glucose and fructose

trypsin
pancreatic protease that breaks down protein

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46.4: The Intestines- Breakdown, Absorption, and Elimination

Skills to Develop

- Describe the process of digestion
- Detail the steps involved in digestion and absorption
- Define elimination
- Explain the role of both the small and large intestines in absorption

Obtaining nutrition and energy from food is a multi-step process. For true animals, the first step is ingestion, the act of taking in food. This is followed by digestion, absorption, and elimination. In the following sections, each of these steps will be discussed in detail.

Ingestion

The large molecules found in intact food cannot pass through the cell membranes. Food needs to be broken into smaller particles so that animals can harness the nutrients and organic molecules. The first step in this process is ingestion. Ingestion is the process of taking in food through the mouth. In vertebrates, the teeth, saliva, and tongue play important roles in mastication (preparing the food into bolus). While the food is being mechanically broken down, the enzymes in saliva begin to chemically process the food as well. The combined action of these processes modifies the food from large particles to a soft mass that can be swallowed and can travel the length of the esophagus.

Digestion and Absorption

Digestion is the mechanical and chemical break down of food into small organic fragments. It is important to break down macromolecules into smaller fragments that are of suitable size for absorption across the digestive epithelium. Large, complex molecules of proteins, polysaccharides, and lipids must be reduced to simpler particles such as simple sugar before they can be absorbed by the digestive epithelial cells. Different organs play specific roles in the digestive process. The animal diet needs carbohydrates, protein, and fat, as well as vitamins and inorganic components for nutritional balance. How each of these components is digested is discussed in the following sections.

Carbohydrates

The digestion of carbohydrates begins in the mouth. The salivary enzyme amylase begins the breakdown of food starches into maltose, a disaccharide. As the bolus of food travels through the esophagus to the stomach, no significant digestion of carbohydrates takes place. The esophagus produces no digestive enzymes but does produce mucous for lubrication. The acidic environment in the stomach stops the action of the amylase enzyme.

The next step of carbohydrate digestion takes place in the duodenum. Recall that the chyme from the stomach enters the duodenum and mixes with the digestive secretion from the pancreas, liver, and gallbladder. Pancreatic juices also contain amylase, which continues the breakdown of starch and glycogen into maltose, a disaccharide. The disaccharides are broken down into monosaccharides by enzymes called maltases, sucrases, and lactases, which are also present in the brush border of the small intestinal wall. Maltase breaks down maltose into glucose. Other disaccharides, such as sucrose and lactose are broken down by sucrase and lactase, respectively. Sucrase breaks down sucrose (or “table sugar”) into glucose and fructose, and lactase breaks down lactose (or “milk sugar”) into glucose and galactose. The monosaccharides (glucose) thus produced are absorbed and then can be used in metabolic pathways to harness energy. The monosaccharides are transported across the intestinal epithelium into the bloodstream to be transported to the different cells in the body. The steps in carbohydrate digestion are summarized in Figure 46.4.1.

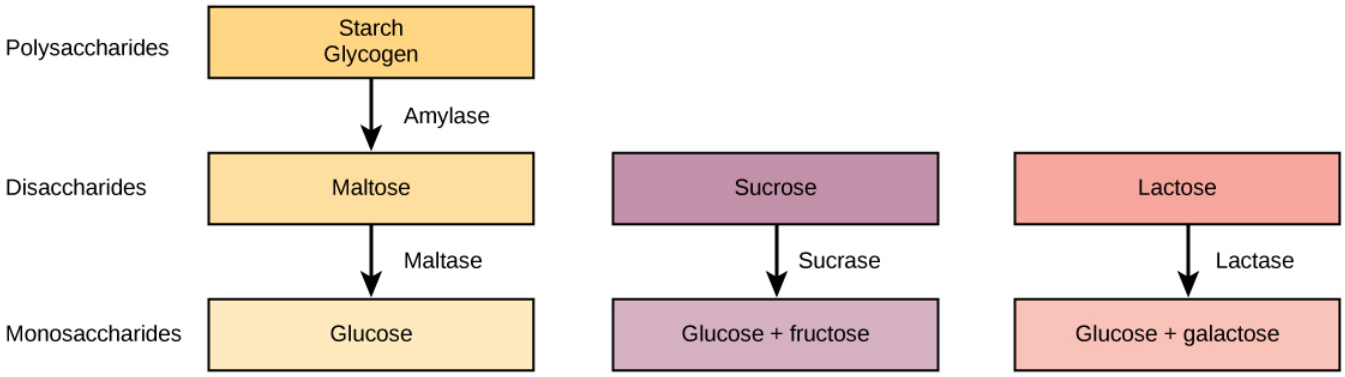


Figure **46.4.1**: Digestion of carbohydrates is performed by several enzymes. Starch and glycogen are broken down into glucose by amylase and maltase. Sucrose (table sugar) and lactose (milk sugar) are broken down by sucrase and lactase, respectively.

Table 46.4.1: Digestion of Carbohydrates

Enzyme	Produced By	Site of Action	Substrate Acting On	End Products
Salivary amylase	Salivary glands	Mouth	Polysaccharides (Starch)	Disaccharides (maltose), oligosaccharides
Pancreatic amylase	Pancreas	Small intestine	Polysaccharides (starch)	Disaccharides (maltose), monosaccharides
Oligosaccharidases	Lining of the intestine; brush border membrane	Small intestine	Disaccharides	Monosaccharides (e.g., glucose, fructose, galactose)

Protein

A large part of protein digestion takes place in the stomach. The enzyme pepsin plays an important role in the digestion of proteins by breaking down the intact protein to peptides, which are short chains of four to nine amino acids. In the duodenum, other enzymes—trypsin, elastase, and chymotrypsin—act on the peptides reducing them to smaller peptides. Trypsin elastase, carboxypeptidase, and chymotrypsin are produced by the pancreas and released into the duodenum where they act on the chyme. Further breakdown of peptides to single amino acids is aided by enzymes called peptidases (those that break down peptides). Specifically, carboxypeptidase, dipeptidase, and aminopeptidase play important roles in reducing the peptides to free amino acids. The amino acids are absorbed into the bloodstream through the small intestines. The steps in protein digestion are summarized in Figure **46.4.2**.

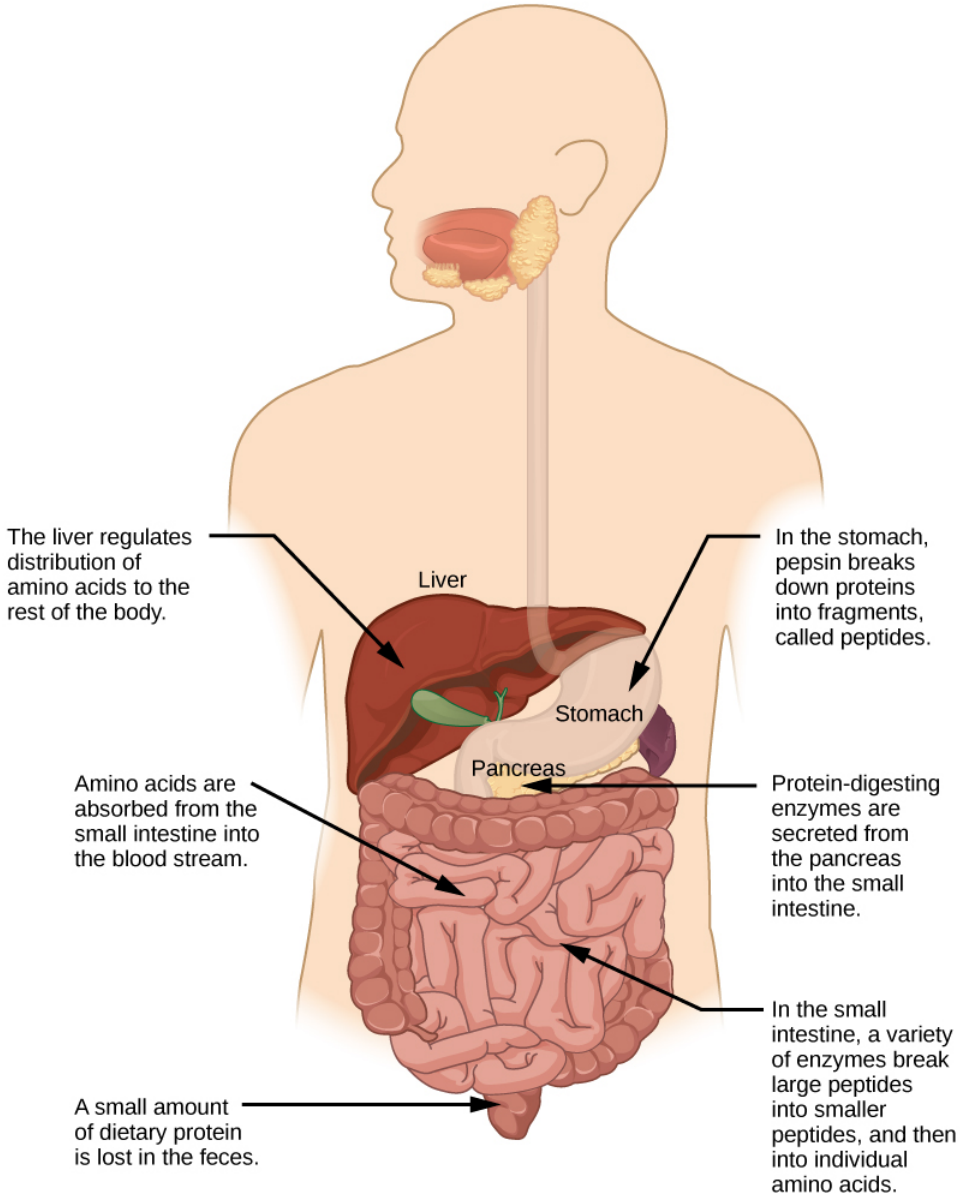


Figure **46.4.2**: Protein digestion is a multistep process that begins in the stomach and continues through the intestines.

Table 46.4.2: Digestion of Protein

Enzyme	Produced By	Site of Action	Substrate Acting On	End Products
Pepsin	Stomach chief cells	Stomach	Proteins	Peptides
Trypsin Elastase Chymotrypsin	Pancreas	Small intestine	Proteins	Peptides
Carboxypeptidase	Pancreas	Small intestine	Peptides	Amino acids and peptides
Aminopeptidase Dipeptidase	Lining of intestine	Small intestine	Peptides	Amino acids

Lipids

Lipid digestion begins in the stomach with the aid of lingual lipase and gastric lipase. However, the bulk of lipid digestion occurs in the small intestine due to pancreatic lipase. When chyme enters the duodenum, the hormonal responses trigger the release of bile,

which is produced in the liver and stored in the gallbladder. Bile aids in the digestion of lipids, primarily triglycerides by emulsification. Emulsification is a process in which large lipid globules are broken down into several small lipid globules. These small globules are more widely distributed in the chyme rather than forming large aggregates. Lipids are hydrophobic substances: in the presence of water, they will aggregate to form globules to minimize exposure to water. Bile contains bile salts, which are amphipathic, meaning they contain hydrophobic and hydrophilic parts. Thus, the bile salts hydrophilic side can interface with water on one side and the hydrophobic side interfaces with lipids on the other. By doing so, bile salts emulsify large lipid globules into small lipid globules.

Why is emulsification important for digestion of lipids? Pancreatic juices contain enzymes called lipases (enzymes that break down lipids). If the lipid in the chyme aggregates into large globules, very little surface area of the lipids is available for the lipases to act on, leaving lipid digestion incomplete. By forming an emulsion, bile salts increase the available surface area of the lipids many fold. The pancreatic lipases can then act on the lipids more efficiently and digest them, as detailed in Figure **46.4.3**. Lipases break down the lipids into fatty acids and glycerides. These molecules can pass through the plasma membrane of the cell and enter the epithelial cells of the intestinal lining. The bile salts surround long-chain fatty acids and monoglycerides forming tiny spheres called micelles. The micelles move into the brush border of the small intestine absorptive cells where the long-chain fatty acids and monoglycerides diffuse out of the micelles into the absorptive cells leaving the micelles behind in the chyme. The long-chain fatty acids and monoglycerides recombine in the absorptive cells to form triglycerides, which aggregate into globules and become coated with proteins. These large spheres are called chylomicrons. Chylomicrons contain triglycerides, cholesterol, and other lipids and have proteins on their surface. The surface is also composed of the hydrophilic phosphate "heads" of phospholipids. Together, they enable the chylomicron to move in an aqueous environment without exposing the lipids to water. Chylomicrons leave the absorptive cells via exocytosis. Chylomicrons enter the lymphatic vessels, and then enter the blood in the subclavian vein.

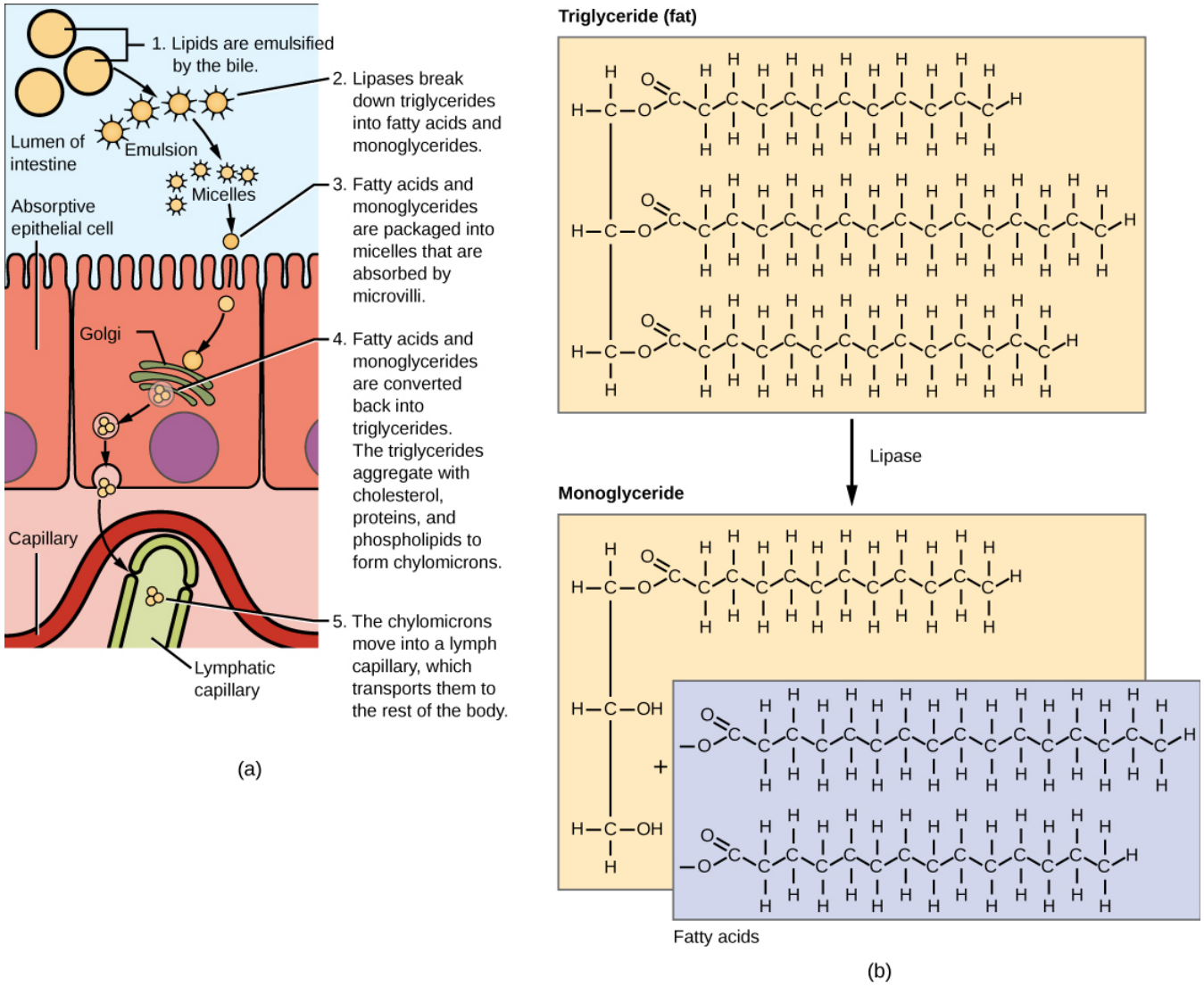


Figure **46.4.3**: Lipids are digested and absorbed in the small intestine.

Vitamins

Vitamins can be either water-soluble or lipid-soluble. Fat soluble vitamins are absorbed in the same manner as lipids. It is important to consume some amount of dietary lipid to aid the absorption of lipid-soluble vitamins. Water-soluble vitamins can be directly absorbed into the bloodstream from the intestine.

Art Connection

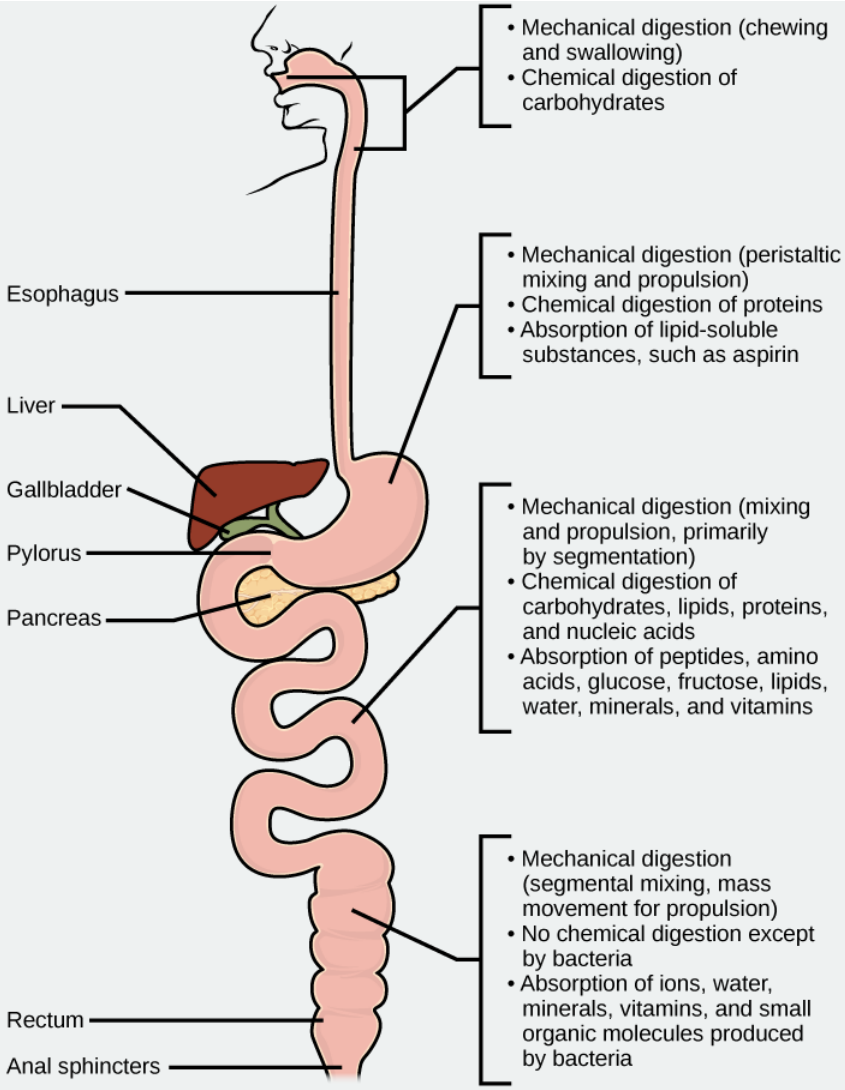


Figure **46.4.4**: Mechanical and chemical digestion of food takes place in many steps, beginning in the mouth and ending in the rectum.

Which of the following statements about digestive processes is true?

A. Amylase, maltase, and lactase in the mouth digest carbohydrates.
B. Trypsin and lipase in the stomach digest protein.
C. Bile emulsifies lipids in the small intestine.
D. No food is absorbed until the small intestine.

Elimination

The final step in digestion is the elimination of undigested food content and waste products. The undigested food material enters the colon, where most of the water is reabsorbed. Recall that the colon is also home to the microflora called “intestinal flora” that aid in the digestion process. The semi-solid waste is moved through the colon by peristaltic movements of the muscle and is stored in the rectum. As the rectum expands in response to storage of fecal matter, it triggers the neural signals required to set up the urge to eliminate. The solid waste is eliminated through the anus using peristaltic movements of the rectum.

Common Problems with Elimination

Diarrhea and constipation are some of the most common health concerns that affect digestion. Constipation is a condition where the feces are hardened because of excess water removal in the colon. In contrast, if enough water is not removed from the feces, it

results in diarrhea. Many bacteria, including the ones that cause cholera, affect the proteins involved in water reabsorption in the colon and result in excessive diarrhea.

Emesis

Emesis, or vomiting, is elimination of food by forceful expulsion through the mouth. It is often in response to an irritant that affects the digestive tract, including but not limited to viruses, bacteria, emotions, sights, and food poisoning. This forceful expulsion of the food is due to the strong contractions produced by the stomach muscles. The process of emesis is regulated by the medulla.

Summary

Digestion begins with ingestion, where the food is taken in the mouth. Digestion and absorption take place in a series of steps with special enzymes playing important roles in digesting carbohydrates, proteins, and lipids. Elimination describes removal of undigested food contents and waste products from the body. While most absorption occurs in the small intestines, the large intestine is responsible for the final removal of water that remains after the absorptive process of the small intestines. The cells that line the large intestine absorb some vitamins as well as any leftover salts and water. The large intestine (colon) is also where feces is formed.

Art Connections

Figure **46.4.4**: Which of the following statements about digestive processes is true?

A. Amylase, maltase and lactase in the mouth digest carbohydrates.
B. Trypsin and lipase in the stomach digest protein.
C. Bile emulsifies lipids in the small intestine.
D. No food is absorbed until the small intestine.

Answer

C

Glossary

aminopeptidase
protease that breaks down peptides to single amino acids; secreted by the brush border of small intestine

carboxypeptidase
protease that breaks down peptides to single amino acids; secreted by the brush border of the small intestine

chylomicron
small lipid globule

chymotrypsin
pancreatic protease

digestion
mechanical and chemical break down of food into small organic fragments

dipeptidase
protease that breaks down peptides to single amino acids; secreted by the brush border of small intestine

elastase
pancreatic protease

ingestion

act of taking in food

lactase
enzyme that breaks down lactose into glucose and galactose

maltase
enzyme that breaks down maltose into glucose

sucrase
enzyme that breaks down sucrose into glucose and fructose

trypsin
pancreatic protease that breaks down protein

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46.5: Accessory Organ Functions

By the end of the section, you will be able to:

- State the main digestive roles of the liver, pancreas, and gallbladder
- Identify three main features of liver histology that are critical to its function
- Discuss the composition and function of bile
- Identify the major types of enzymes and buffers present in pancreatic juice

Chemical digestion in the small intestine relies on the activities of three accessory digestive organs: the liver, pancreas, and gallbladder (Figure 21.7.1). The digestive role of the liver is to produce bile and export it to the duodenum. The gallbladder primarily stores, concentrates, and releases bile. The pancreas produces pancreatic juice, which contains digestive enzymes and bicarbonate ions, and delivers it to the duodenum.

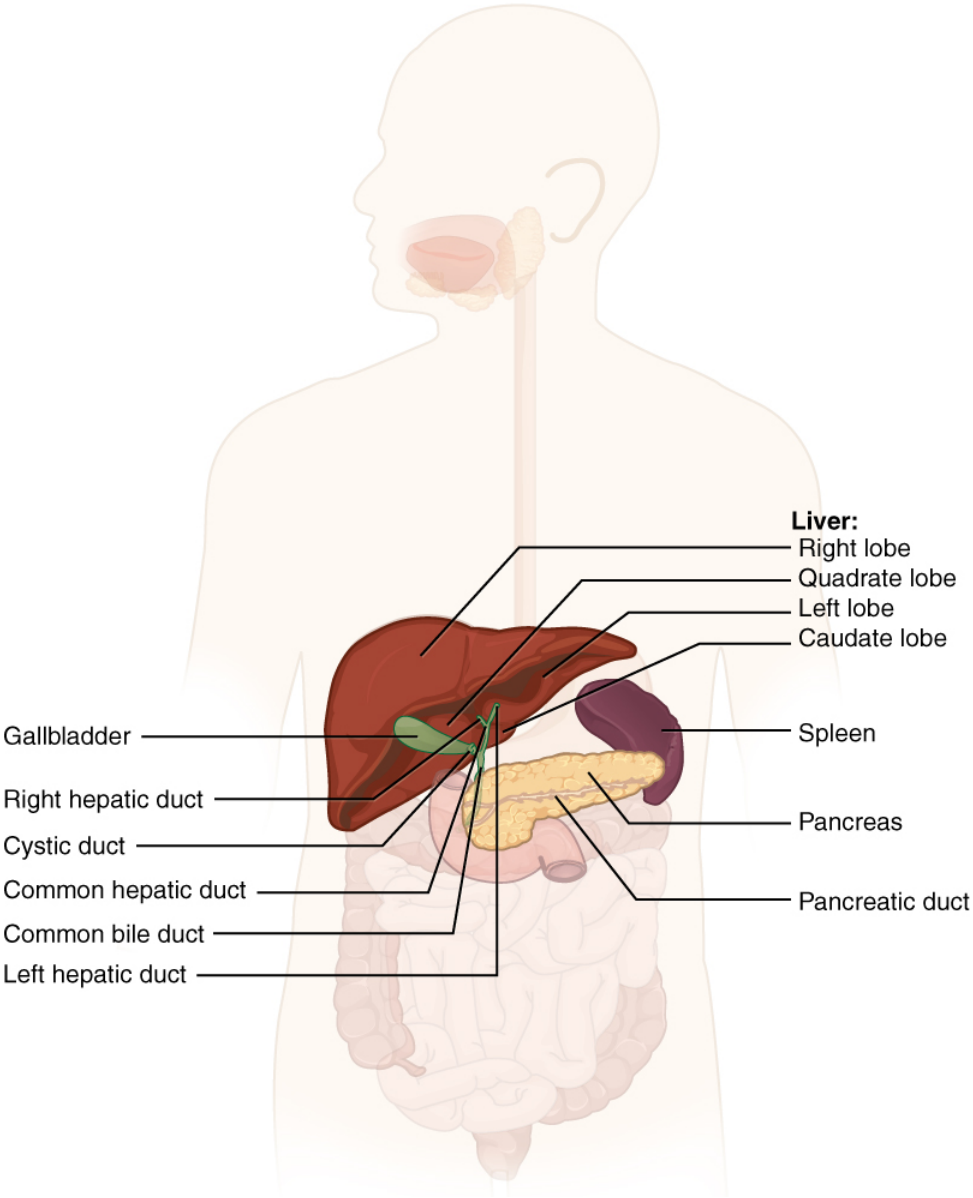


Figure 21.7.1: Accessory Organs.
The liver, pancreas, and gallbladder are considered accessory digestive organs, but their roles in the digestive system are vital.
(Image credit: "Accessory Organs" by OpenStax is licensed under CC BY 3.0)

Liver

The **liver** is the largest gland in the body, weighing about three pounds in an adult. It is also one of the most important organs. In addition to being an accessory digestive organ, it plays a number of roles in metabolism and regulation. The liver lies inferior to the diaphragm in the right upper quadrant of the abdominal cavity and receives protection from the surrounding ribs.

The liver is divided into two primary lobes: a large **right lobe** and a much smaller **left lobe**. In the right lobe, some anatomists also identify an inferior **quadrate lobe** and a posterior **caudate lobe**, which are defined by internal features. The liver is connected to the abdominal wall and diaphragm by five peritoneal folds referred to as ligaments. These are the **falciform ligament**, the **coronary ligament**, two **lateral ligaments**, and the **ligamentum teres hepatis**. The falciform ligament and ligamentum teres hepatis are actually remnants of the umbilical vein, and separate the right and left lobes anteriorly. The lesser omentum tethers the liver to the lesser curvature of the stomach.

The **porta hepatis** (“gate to the liver”) is where the **hepatic artery** and **hepatic portal vein** enter the liver. These two vessels, along with the common hepatic duct, run behind the lateral border of the lesser omentum on the way to their destinations. As shown in Figure 21.7.2, the hepatic artery delivers oxygenated blood from the heart to the liver. The hepatic portal vein delivers partially deoxygenated blood containing nutrients absorbed from the small intestine and actually supplies more oxygen to the liver than do the much smaller hepatic arteries. In addition to nutrients, drugs and toxins are also absorbed. After processing the bloodborne nutrients and toxins, the liver releases nutrients needed by other cells back into the blood, which drains into the central vein and then through the hepatic vein to the inferior vena cava. With this hepatic portal circulation, all blood from the alimentary canal passes through the liver. This largely explains why the liver is the most common site for the metastasis of cancers that originate in the alimentary canal.

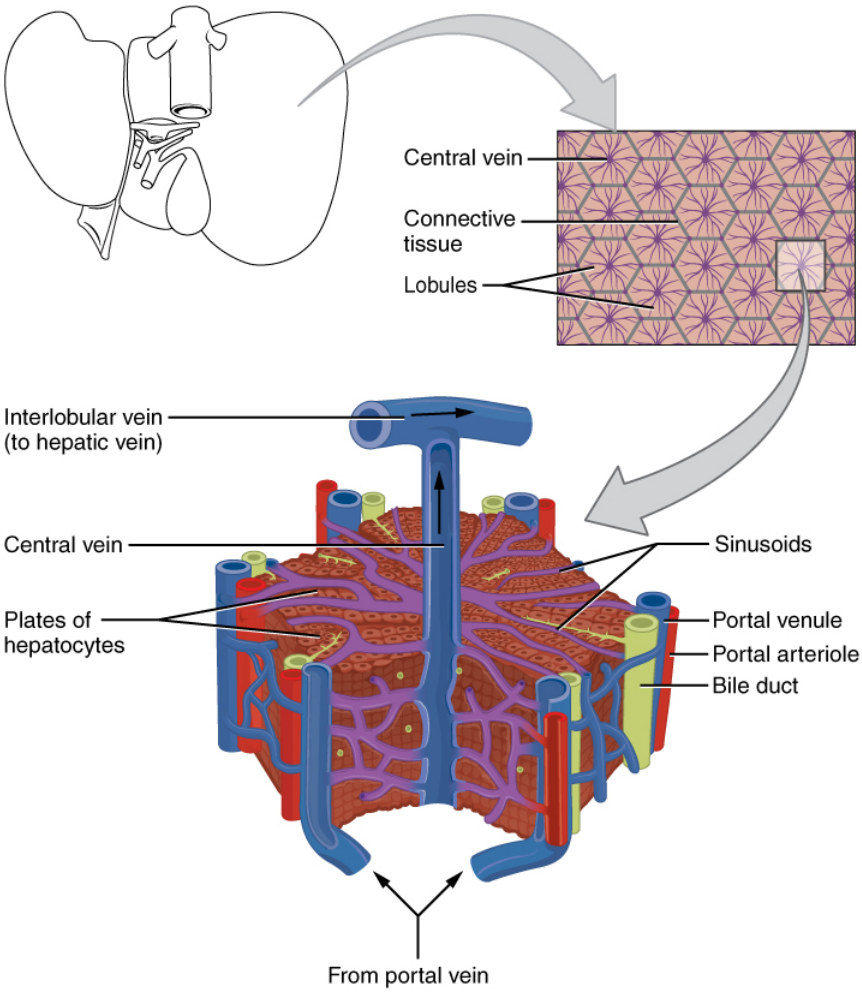


Figure 21.7.2: Microscopic Anatomy of the Liver. The liver receives oxygenated blood from the hepatic artery and nutrient-rich deoxygenated blood from the hepatic portal vein. (Image credit: “Microscopic Anatomy of Liver” by OpenStax is licensed under CC BY 3.0)

Histology

The liver has three main components: hepatocytes, bile canaliculi, and hepatic sinusoids. A **hepatocyte** is the liver's main cell type, accounting for around 80 percent of the liver's volume. These cells play a role in a wide variety of secretory, metabolic, and endocrine functions. Plates of hepatocytes called hepatic laminae radiate outward from the central vein in each **hepatic lobule**. The liver lobule is a hexagon shape with **portal triads** on each corner at the perimeter of the hexagon. The portal triad is a distinctive arrangement consisting of three basic structures: a bile duct, a small branch of the hepatic artery (portal arteriole) bringing in oxygenated blood and a branch of the hepatic portal vein (portal venule) delivering nutrient rich blood. The bile duct carries freshly made bile away from hepatocytes toward the gallbladder and duodenum.

Between adjacent hepatocytes, grooves in the cell membranes provide room for each **bile canaliculus** (plural = canaliculi). These small ducts accumulate the bile produced by hepatocytes. From the hepatocyes, bile flows first into bile ductules and then into bile ducts. The bile ducts unite to form the larger right and left hepatic ducts, which themselves merge and exit the liver as the **common hepatic duct** (Figure 21.7.4). This duct then joins with the cystic duct from the gallbladder, forming the **common bile duct** through which bile flows into the small intestine.

A **hepatic sinusoid** is an open, porous blood space formed by fenestrated capillaries from nutrient-rich hepatic portal veins and oxygen-rich hepatic arteries. Hepatocytes are tightly packed around the fenestrated endothelium of these spaces, giving them easy access to the blood. From their central position, hepatocytes process the nutrients, toxins, and waste materials carried by the blood. Materials such as bilirubin are processed and excreted into the bile canaliculi. Other materials including proteins, lipids, and carbohydrates are processed and secreted into the sinusoids or just stored in the cells until called upon. The hepatic sinusoids combine and send blood to a **central vein**. Blood then flows through a **hepatic vein** into the inferior vena cava. This means that blood and bile flow in opposite directions. The hepatic sinusoids also contain star-shaped **reticuloendothelial cells** (Kupffer cells), phagocytes that remove dead red and white blood cells, bacteria, and other foreign material that enter the sinusoids.

Bile

Recall that lipids are hydrophobic, that is, they do not dissolve in water. Thus, before they can be digested in the watery environment of the small intestine, large lipid globules must be broken down into smaller lipid globules, a process called emulsification. **Bile** is a mixture secreted by the liver to accomplish the emulsification of lipids in the small intestine.

Hepatocytes secrete about one liter of bile each day. A yellow-brown or yellow-green alkaline solution (pH 7.6 to 8.6), bile is a mixture of water, bile salts, bile pigments (including bilirubin), phospholipids (such as lecithin), electrolytes, cholesterol, and triglycerides. Some molecules in bile have regions attracted to water molecules and regions attracted to lipids. This results in the large lipid globules being pulled apart into many tiny lipid fragments of about 1 μm in diameter. This change dramatically increases the surface area available for lipid-digesting enzyme activity. This is the same way dish soap works on fats mixed with water.

Bile salts act as emulsifying agents, explained above, so they are also important for the absorption of digested lipids. While most constituents of bile are eliminated in feces, bile salts are reclaimed by the **enterohepatic circulation**. Once bile salts reach the ileum, they are absorbed and returned to the liver in the hepatic portal blood. The hepatocytes then excrete the bile salts into newly formed bile. Thus, this precious resource is recycled.

Bilirubin, the main bile pigment, is a waste product produced when the spleen removes old or damaged red blood cells from the circulation. These breakdown products, including proteins, iron, and toxic bilirubin, are transported to the liver via the splenic vein of the hepatic portal system. In the liver, proteins and iron are recycled, whereas bilirubin is excreted in the bile. It accounts for the green color of bile. Bilirubin is eventually transformed by intestinal bacteria into stercobilin, a brown pigment that gives your stool its characteristic color! In some disease states, bile does not enter the intestine, resulting in white ('acholic') stool with a high fat content, since virtually no fats are broken down or absorbed.

Hepatocytes work non-stop, but bile production increases when fatty chyme enters the duodenum and stimulates the secretion of the gut hormone secretin. Between meals, bile is produced but conserved. The valve-like hepatopancreatic ampulla closes, allowing bile to divert to the gallbladder, where it is concentrated and stored until the next meal.

Pancreas

The soft, oblong, glandular **pancreas** lies transversely in the retroperitoneum behind the stomach. Its head is nestled into the "c-shaped" curvature of the duodenum with the body extending to the left about 15.2 cm (6 in) and ending as a tapering tail in the hilum of the spleen. It performs a curious mix of exocrine (secreting digestive enzymes) and endocrine (releasing hormones into the blood) functions (Figure 21.7.3). Histology of the pancreas reveals round clusters of acinar cells connected to the pancreatic duct and the bigger clusters of pancreatic islets.

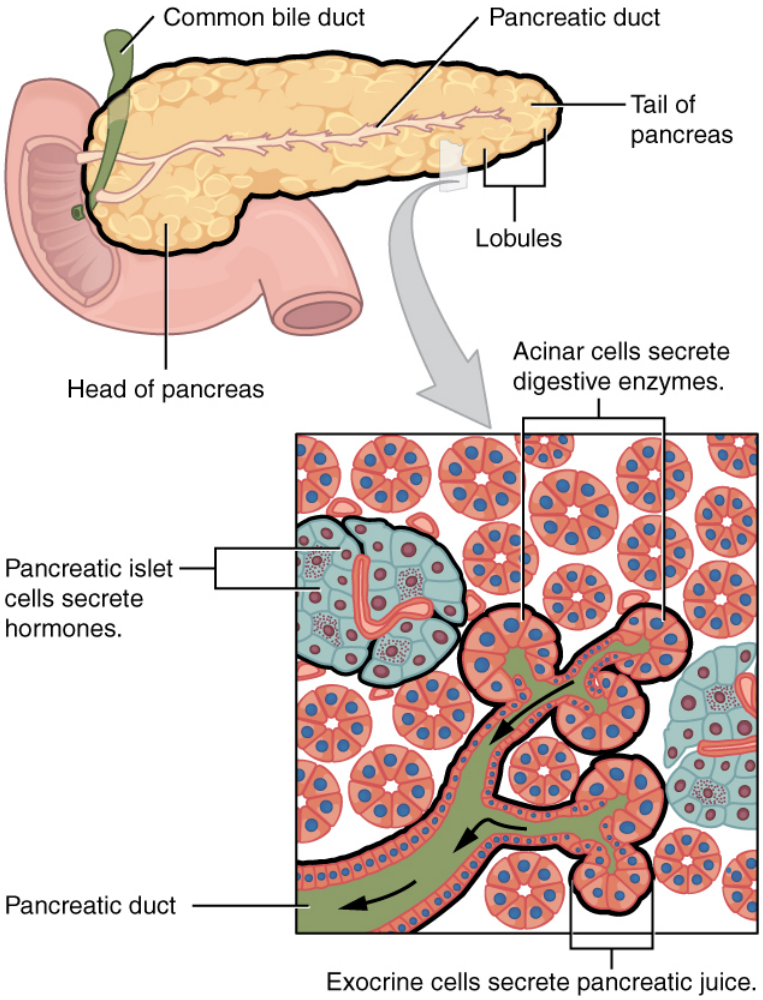


Figure 21.7.3: Exocrine and Endocrine Pancreas. The pancreas has a head, a body, and a tail. It delivers pancreatic juice to the duodenum through the pancreatic duct. (Image credit: "Exocrine and Endocrine Pancreas" by OpenStax is licensed under CC BY 3.0)

The exocrine part of the pancreas arises as little grape-like cell clusters, each called an **acinus** (plural = acini), located at the terminal ends of pancreatic ducts. These acinar cells secrete enzyme-rich **pancreatic juice** into tiny merging ducts that form two dominant ducts. The larger duct fuses with the common bile duct (carrying bile from the liver and gallbladder) just before entering the duodenum via a common opening (the hepatopancreatic ampulla). The smooth muscle sphincter of the hepatopancreatic ampulla controls the release of pancreatic juice and bile into the small intestine. The second and smaller pancreatic duct, the **accessory duct** (duct of Santorini), present in approximately 30% of the population, runs from the pancreas directly into the duodenum, approximately 1 inch above the hepatopancreatic ampulla. When present, it is a persistent remnant of pancreatic development.

Scattered through the sea of exocrine acini are small islands of endocrine cells, the islets of Langerhans. These vital cells produce the hormones pancreatic polypeptide, insulin, glucagon, and somatostatin. These hormones play roles in regulating several metabolic functions.

Pancreatic Juice

The pancreas produces over a liter of pancreatic juice each day. Unlike bile, it is clear and composed mostly of water along with some salts, sodium bicarbonate, and several digestive enzymes. Sodium bicarbonate is responsible for the slight alkalinity of pancreatic juice (pH 7.1 to 8.2), which serves to buffer the acidic gastric juice in chyme, inactivate pepsin from the stomach, and create an optimal environment for the activity of pH-sensitive digestive enzymes in the small intestine. Pancreatic enzymes are active in the digestion of sugars, proteins, and fats.

The pancreas produces protein-digesting enzymes in their inactive forms. These enzymes are activated in the duodenum. If produced in an active form, they would digest the pancreas (which is exactly what occurs in the disease, pancreatitis). The intestinal brush border enzyme **enteropeptidase** stimulates the activation of an enzyme that starts the cascade of other enzymes to digest proteins.

The enzymes that digest starch (amylase), fat (lipase), and nucleic acids (nuclease) are secreted in their active forms, since they do not attack the pancreas as do the protein-digesting enzymes.

Pancreatic Secretion

Regulation of pancreatic secretion is the job of hormones and the parasympathetic nervous system. The entry of acidic chyme into the duodenum and the presence of proteins and fats in the duodenum stimulates the release of multiple hormones of digestion. Parasympathetic regulation occurs through the vagus nerve, cranial nerve X, mainly during the cephalic and gastric phases of gastric secretion. Usually, the pancreas secretes just enough bicarbonate to counterbalance the amount of HCl produced in the stomach.

Gallbladder

Figure 21.7.4 is a drawing showing the anterior view of the gallbladder, part of the liver superior to the gallbladder, and the duct connecting the liver to gallbladder, eventually becoming the common bile duct. The **gallbladder** is 8–10 cm (~3–4 in) long and is nested in a shallow area on the posterior aspect of the right lobe of the liver. This muscular sac stores, concentrates, and, when stimulated, propels the bile into the duodenum via the common bile duct. The gallblader can accumulate gall stones over time, resulting in removal of the gallbladder with the gall stones in some people. It is divided into three regions. The fundus is the widest portion and tapers medially into the body, which in turn narrows to become the neck. The neck angles slightly superiorly as it approaches the hepatic duct. The cystic duct is 1–2 cm (less than 1 in) long and turns inferiorly as it bridges the neck and hepatic duct.

The simple columnar epithelium of the gallbladder mucosa is organized in rugae, similar to those of the stomach. There is no submucosa in the gallbladder wall. The wall’s middle, muscular coat is made of smooth muscle fibers. When these fibers contract, the gallbladder’s contents are ejected through the **cystic duct** and into the bile duct (Figure 21.7.4). Visceral peritoneum reflected from the liver capsule holds the gallbladder against the liver and forms the outer coat of the gallbladder. The gallbladder's mucosa absorbs water and ions from bile, concentrating it by up to 10-fold.

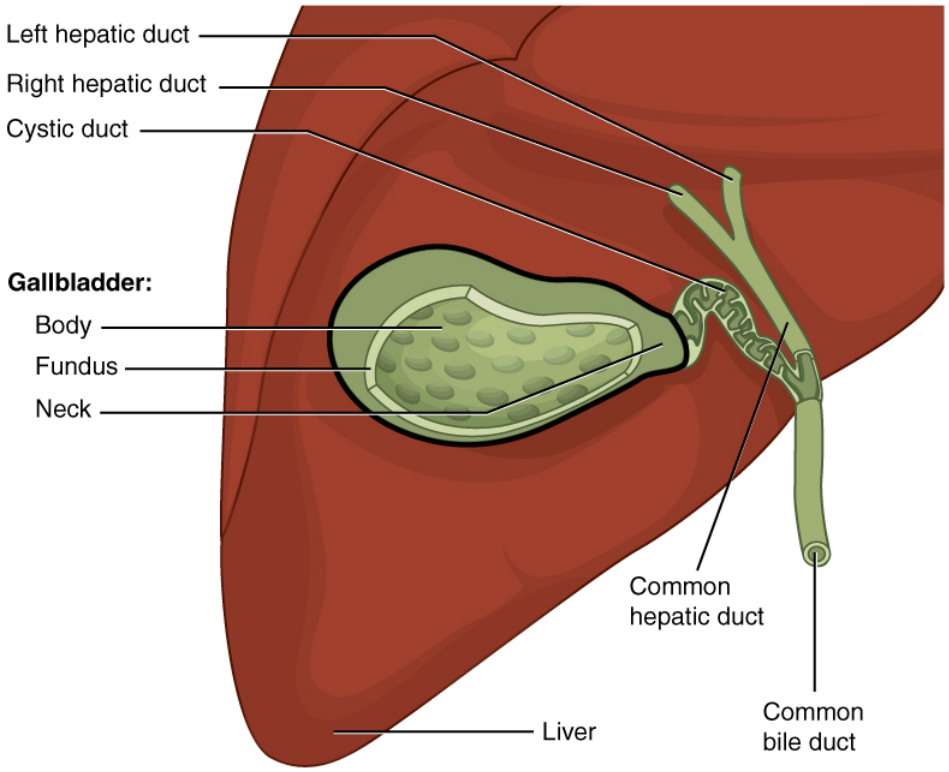


Figure 21.7.4: Gallbladder. The gallbladder stores and concentrates bile, and releases it into the two-way cystic duct when it is needed by the small intestine. (Image credit: "Gallbladder" by OpenStax is licensed under CC BY 3.0)

Concept Review

Chemical digestion in the small intestine cannot occur without the help of the liver and pancreas. The liver produces bile and delivers it to the common hepatic duct. Bile contains bile salts and phospholipids, which emulsify large lipid globules into tiny lipid droplets, a necessary step in lipid digestion and absorption. The gallbladder stores and concentrates bile, releasing it when it is needed by the small intestine.

The pancreas produces the enzyme- and bicarbonate-rich pancreatic juice and delivers it to the small intestine through ducts. Pancreatic juice buffers the acidic gastric juice in chyme, inactivates pepsin from the stomach, and enables the optimal functioning of digestive enzymes in the small intestine.

Review Questions

Q. Which of these statements about bile is true?

A. It is brown.

B. It is stored in the liver.

C. It is synthesized in the gallbladder.

D. Bile salts are recycled.

Answer

Answer: D

Q. Pancreas _____.

A. is anterior to the stomach.

B. has only a body and tail.

C. has a pancreatic duct to carry pancreatic juice to duodenum.

D. merges with the cystic duct.

Answer

Answer: C

Critical Thinking Questions

Q. When will gall stones be dangerous?

Answer

A. The pancreas secretes protein-digesting enzymes and empties them into the duodenum via the pancreatic duct. The pancreatic duct merges with the common bile duct prior to entering into the duodenum. A gall stone blocking this merging point can be dangerous because it leads to pancreatitis since the pancreatic enzymes are not emptied into the duodenum.

Q. Describe the location of hepatocytes in the liver and how this arrangement enhances their function.

Answer

A. The hepatocytes are the main cell type of the liver. They process, store, and release nutrients into the blood. Radiating out from the central vein, they are tightly packed around the hepatic sinusoids, allowing the hepatocytes easy access to the blood flowing through the sinusoids.

Glossary

accessory duct
(also, duct of Santorini) duct that runs from the pancreas into the duodenum

acinus
cluster of glandular epithelial cells in the pancreas that secretes pancreatic juice in the pancreas

bile
alkaline solution produced by the liver and important for the emulsification of lipids

bile canaliculus
small duct between hepatocytes that collects bile

bilirubin
main bile pigment, which is responsible for the brown color of feces

central vein
vein that receives blood from hepatic sinusoids

common bile duct
structure formed by the union of the common hepatic duct and the gallbladder’s cystic duct

common hepatic duct
duct formed by the merger of the two hepatic ducts

cystic duct
duct through which bile drains and enters the gallbladder

enterohepatic circulation
recycling mechanism that conserves bile salts

enteropeptidase

intestinal brush-border enzyme that activates trypsinogen to trypsin

gallbladder
accessory digestive organ that stores and concentrates bile

hepatic artery
artery that supplies oxygenated blood to the liver

hepatic lobule
hexagonal-shaped structure composed of hepatocytes that radiate outward from a central vein

hepatic portal vein
vein that supplies deoxygenated nutrient-rich blood to the liver

hepatic sinusoid
blood capillaries between rows of hepatocytes that receive blood from the hepatic portal vein and the branches of the hepatic artery

hepatic vein
vein that drains into the inferior vena cava

hepatocytes
major functional cells of the liver

liver
largest gland in the body whose main digestive function is the production of bile

pancreas
accessory digestive organ that secretes pancreatic juice

pancreatic juice
secretion of the pancreas containing digestive enzymes and bicarbonate

porta hepatis
“gateway to the liver” where the hepatic artery and hepatic portal vein enter the liver

portal triad
bile duct, hepatic artery branch, and hepatic portal vein branch

reticuloendothelial cell
(also, Kupffer cell) phagocyte in hepatic sinusoids that filters out material from venous blood from the alimentary canal

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46.6: Neural and Hormonal Regulation of the Digestive Tract

Skills to Develop

- Discuss the role of neural regulation in digestive processes
- Explain how hormones regulate digestion

The brain is the control center for the sensation of hunger and satiety. The functions of the digestive system are regulated through neural and hormonal responses.

Neural Responses to Food

In reaction to the smell, sight, or thought of food, like that shown in Figure **46.6.1**, the first hormonal response is that of salivation. The salivary glands secrete more saliva in response to the stimulus presented by food in preparation for digestion. Simultaneously, the stomach begins to produce hydrochloric acid to digest the food. Recall that the peristaltic movements of the esophagus and other organs of the digestive tract are under the control of the brain. The brain prepares these muscles for movement as well. When the stomach is full, the part of the brain that detects satiety signals fullness. There are three overlapping phases of gastric control—the cephalic phase, the gastric phase, and the intestinal phase—each requires many enzymes and is under neural control as well.



Figure **46.6.1**: Seeing a plate of food triggers the secretion of saliva in the mouth and the production of HCL in the stomach. (credit: Kelly Bailey)

Digestive Phases

The response to food begins even before food enters the mouth. The first phase of ingestion, called the cephalic phase, is controlled by the neural response to the stimulus provided by food. All aspects—such as sight, sense, and smell—trigger the neural responses resulting in salivation and secretion of gastric juices. The gastric and salivary secretion in the cephalic phase can also take place due to the thought of food. Right now, if you think about a piece of chocolate or a crispy potato chip, the increase in salivation is a cephalic phase response to the thought. The central nervous system prepares the stomach to receive food.

The gastric phase begins once the food arrives in the stomach. It builds on the stimulation provided during the cephalic phase. Gastric acids and enzymes process the ingested materials. The gastric phase is stimulated by (1) distension of the stomach, (2) a decrease in the pH of the gastric contents, and (3) the presence of undigested material. This phase consists of local, hormonal, and neural responses. These responses stimulate secretions and powerful contractions.

The intestinal phase begins when chyme enters the small intestine triggering digestive secretions. This phase controls the rate of gastric emptying. In addition to gastrin emptying, when chyme enters the small intestine, it triggers other hormonal and neural events that coordinate the activities of the intestinal tract, pancreas, liver, and gallbladder.

Hormonal Responses to Food

The endocrine system controls the response of the various glands in the body and the release of hormones at the appropriate times.

One of the important factors under hormonal control is the stomach acid environment. During the gastric phase, the hormone gastrin is secreted by G cells in the stomach in response to the presence of proteins. Gastrin stimulates the release of stomach acid, or hydrochloric acid (HCl) which aids in the digestion of the proteins. However, when the stomach is emptied, the acidic environment need not be maintained and a hormone called somatostatin stops the release of hydrochloric acid. This is controlled by a negative feedback mechanism.

In the duodenum, digestive secretions from the liver, pancreas, and gallbladder play an important role in digesting chyme during the intestinal phase. In order to neutralize the acidic chyme, a hormone called secretin stimulates the pancreas to produce alkaline bicarbonate solution and deliver it to the duodenum. Secretin acts in tandem with another hormone called cholecystokinin (CCK). Not only does CCK stimulate the pancreas to produce the requisite pancreatic juices, it also stimulates the gallbladder to release bile into the duodenum.

Another level of hormonal control occurs in response to the composition of food. Foods high in lipids take a long time to digest. A hormone called gastric inhibitory peptide is secreted by the small intestine to slow down the peristaltic movements of the intestine to allow fatty foods more time to be digested and absorbed.

Understanding the hormonal control of the digestive system is an important area of ongoing research. Scientists are exploring the role of each hormone in the digestive process and developing ways to target these hormones. Advances could lead to knowledge that may help to battle the obesity epidemic.

Summary

The brain and the endocrine system control digestive processes. The brain controls the responses of hunger and satiety. The endocrine system controls the release of hormones and enzymes required for digestion of food in the digestive tract.

Glossary

cephalic phase
: first phase of digestion, controlled by the neural response to the stimulus provided by food

cholecystokinin
: hormone that stimulates the contraction of the gallbladder to release bile

endocrine system
: system that controls the response of the various glands in the body and the release of hormones at the appropriate times

gastric inhibitory peptide

hormone secreted by the small intestine in the presence of fatty acids and sugars; it also inhibits acid production and peristalsis in order to slow down the rate at which food enters the small intestine

gastric phase

digestive phase beginning once food enters the stomach; gastric acids and enzymes process the ingested materials

gastrin

hormone which stimulates hydrochloric acid secretion in the stomach

intestinal phase

third digestive phase; begins when chyme enters the small intestine triggering digestive secretions and controlling the rate of gastric emptying

secretin

hormone which stimulates sodium bicarbonate secretion in the small intestine

somatostatin

hormone released to stop acid secretion when the stomach is empty

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46.7: Food Energy, Energy Expenditure, and Essential Nutrients

Diet versus Food and Nutrients

There are many popular diets, most often associated with weight loss and popularized in social media. Many of these so-called diets are not based on scientific research and could come with health risks, as well as a big cost to your bank account! In this book, we will use the term **diet** to represent a pattern of eating. There are medically based diets to manage chronic conditions that are based on evidence-based research. Some food patterns, such as the Mediterranean Diet, are based on decades of research on populations and their positive health outcomes. Your personal diet is defined as the foods you choose to eat, impacted by each dimension of wellness discussed earlier in this chapter. Keep these ideas in mind as we discuss how diet relates to food and nutrients.

Diet: A Pattern of Eating



Figure **46.7.1**: The Ketogenic Diet Menu.[1] Each diet represents a pattern of eating, and diets need to be based on research and personal needs.

What is in Food?

The diet of most people contains a variety of foods: fruit, dairy, beans, meats, nuts, seeds, leafy green vegetables, as well as fats, oils, and sweets. The foods we eat contain nutrients. **Nutrients** are substances required by the body to perform its basic functions. Nutrients must be obtained from diet because the human body does not synthesize them or does not synthesize them in large enough amounts for human health. Nutrients are used for many body functions, such as growing, moving your muscles, repairing tissues, and much more! In summary, an **essential nutrient** is a nutrient you must have, a nutrient your body cannot make in adequate amounts, and, therefore, a nutrient you must eat or drink in adequate amounts.

Six classes of essential nutrients are required for the body to function and maintain overall health: carbohydrates, lipids (fats), proteins, water, vitamins, and minerals. Other substances in food appear to be very important for human health, such as colorful plant pigments, whereas others may be harmful to human health, such as preservatives, colorings, flavorings, and pesticide residues.

Essential Nutrients

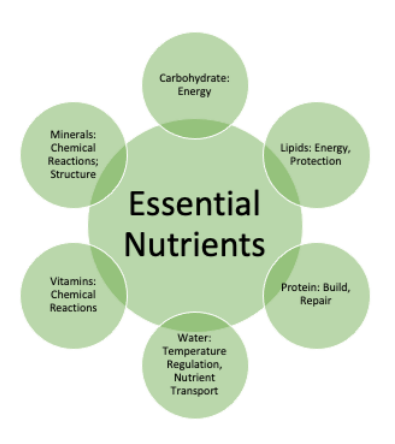


Figure **46.7.2**: The six classes of nutrients.[2]

Macronutrients

Nutrients that are needed in large amounts are called **macronutrients**. There are three major classes of macronutrients: carbohydrates, lipids (fats), and proteins. All three of these nutrients are needed in relatively large amounts, *and* they contain Calories that can be "burned" in your body to create energy for your body cells. The energy from these macronutrients comes from their chemical bonds. This chemical energy is converted into cellular energy that is then utilized to perform work, allowing our bodies to conduct their basic functions. A unit of measurement of food energy is the **Calorie** (note that Calorie with a capital C indicates kcalories, the term used in science research). The next time you are eating a packaged food, look on the "Nutrition Facts" panel to find out how many Calories you are getting when you eat one serving of that food. Water is also a macronutrient because you require a large amount of it, but unlike the other macronutrients, it does not yield Calories. One other possible component of the diet that can provide Calories is alcohol, though it is generally not considered to be a nutrient.

Macronutrients

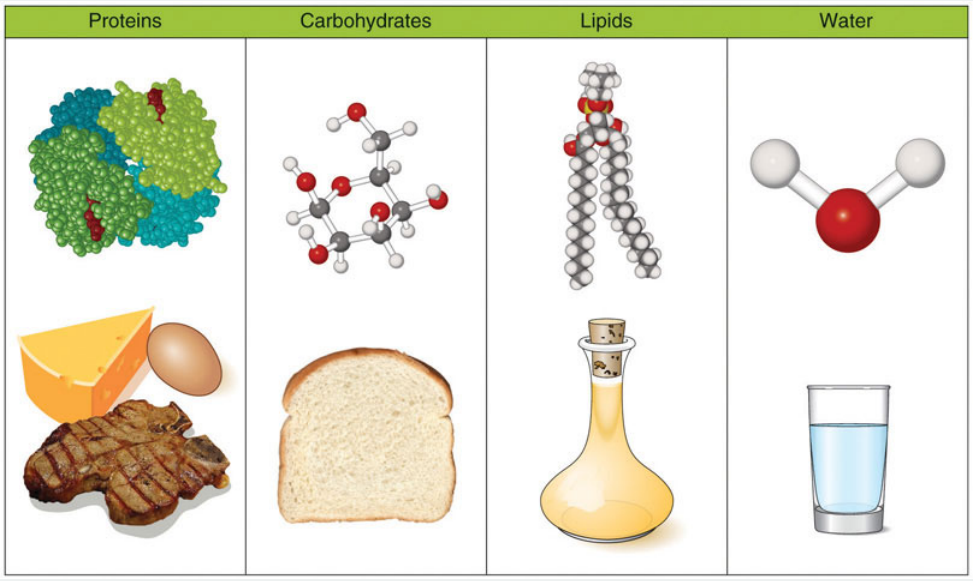


Figure **46.7.3**: The macronutrients: carbohydrates, lipids, protein, and water.[3]

Carbohydrates

When you eat a food that contains carbohydrates, like bread or broccoli, for example, you receive approximately 4 Calories for every gram of carbohydrate you eat. Carbohydrates are molecules composed of carbon, hydrogen, and oxygen. The major whole food sources of carbohydrates are grains, milk, fruits, and starchy vegetables such as potatoes and corn. Non-starchy vegetables, such as spinach and green beans, also contain carbohydrates, but in lesser quantities. Many processed foods contain carbohydrates, providing a Calorie source without many vitamins or minerals.

Carbohydrates are broadly classified into two forms based on their chemical structure: fast-releasing carbohydrates, often called "simple sugars," and slow-releasing carbohydrates, often called "complex carbohydrates." Fast-releasing carbohydrates consist of one or two basic sugar units. They are sometimes called "simple sugars" because their chemical structure is fairly simple, with only one or two sugar units. If the carbohydrate has one sugar unit, we call it a **monosaccharide**. Mono means one, and saccharide means sugar. Examples of monosaccharides include glucose (the sugar that is in your blood); fructose (a sugar commonly found in fruit); and galactose (a sugar that is found as part of milk sugar). If the carbohydrate has two sugar units, we call it a **disaccharide**. Di means two, and saccharide means sugar. Examples of disaccharides include: sucrose (table sugar); lactose (milk sugar) and maltose (sugar in grains). **Sucrose** is made of a glucose linked together with a fructose. **Lactose** is made of a glucose linked together with galactose. **Maltose** is made of two glucose molecules bonded together. To digest a disaccharide, your body has to break the two sugars apart. We will talk more about this when we discuss lactose intolerance in a later chapter.

Slow-releasing carbohydrates are long chains of simple sugars (**polysaccharides**) that can be branched or unbranched. Some polysaccharides that you have probably heard of are starch and fiber. During digestion, the body does its best to break down all slow-releasing carbohydrates like starch into simple sugars, mostly glucose. Glucose is then transported to all our cells, where it is stored, used to make energy, or used to build macromolecules. Fiber is also a slow-releasing carbohydrate, but it cannot be fully broken down in the human body and passes through the digestive tract undigested unless the bacteria that live in the large intestine break it down for us. Therefore, starch is considered a Calorie source, but fiber is not considered a Calorie source.

In addition to providing energy and serving as building blocks for bigger macromolecules, carbohydrates are essential for the proper functioning of the nervous system, heart, and kidneys. As mentioned, glucose can be stored in the body for future use. In humans, the storage molecule of carbohydrates is called glycogen, and in plants, it is known as **starch**. Glycogen and starch are slow-releasing carbohydrates.

Lipids

Lipids are also a family of molecules composed of carbon, hydrogen, and oxygen, but unlike carbohydrates, they are insoluble in water. Lipids are predominately found in butter, oils, meats, dairy products, nuts, seeds, and many processed foods. The three main types of lipids are fats in the form of triglycerides (triacylglycerols), phospholipids, and sterols. The main job of fat is to store energy. Fats provide more energy per gram than carbohydrates (nine Calories per gram of fat versus four Calories per gram of carbohydrate). Cholesterol, another form of lipid, does not provide Calories. In addition to energy storage, lipids serve as cell membranes, surround and protect organs, aid in temperature regulation, and regulate many other bodily functions.

Proteins

Proteins are molecules composed of chains of subunits called **amino acids**. Amino acids are composed of carbon, oxygen, hydrogen, and nitrogen. The food sources of proteins are meats, dairy products, seafood, and various plant-based foods, including beans and nuts. The word protein comes from a Greek word meaning “of primary importance,” which is an apt description of these macronutrients; they are also known colloquially as the “workhorses” of life. Proteins provide four Calories of energy per gram; however, providing energy is not protein’s most important function. Proteins provide structure to bones, muscles, and skin and play a role in conducting most of the chemical reactions that take place in the body. Scientists estimate that greater than 100,000 different proteins exist within the human body.

Water

There is one other nutrient that we must have in large quantities: water. Water does not contain carbon but is composed of two hydrogen atoms and one oxygen atom per molecule of water. Water does not provide any Calories. More than 60 percent of your total body weight is water. Without it, nothing could be transported in or out of the body, chemical reactions would not occur,

organs would not be cushioned, and body temperature would fluctuate widely. On average, an adult consumes just over two liters of water daily from food and drink. According to the “rule of threes,” a generalization supported by survival experts, a person can survive three minutes without oxygen, three days without water, and three weeks without food. Since water is so critical for life’s basic processes, the amount of water input and output is supremely important, a topic we will explore in a later chapter.

Alcohol (not a nutrient)

Drinks containing alcohol are a source of Calories even though they are generally not considered nutrients. Alcohol comprises carbon, hydrogen, and oxygen and provides approximately 7 Calories for every gram consumed. In addition to alcohol, many of these drinks contain carbohydrates as well.

Micronutrients

Micronutrients are nutrients the body requires in lesser amounts but are still essential for carrying out bodily functions. Micronutrients include all the essential minerals and vitamins. There are sixteen essential minerals and thirteen vitamins. (Tables 46.7.1 and 46.7.2 provide a complete list and their major functions). In contrast to macronutrients (carbohydrates, fats, and proteins), micronutrients do not contain Calories. This is often confusing because most people have heard how tired a person will feel if they are low in a micronutrient such as iron. The tiredness can be explained by the fact that micronutrients assist in the process of making energy by being part of enzymes (i.e., coenzymes). Enzymes catalyze chemical reactions in the body and are involved in many aspects of body functions, from producing energy to digesting nutrients to building macromolecules. Micronutrients play many roles in the body.

Minerals

Minerals are solid inorganic substances that form crystals and are classified depending on how much of them we need. **Trace minerals**, such as molybdenum, selenium, zinc, iron, and iodine, are only required in a few milligrams or less; and **macrominerals**, such as calcium, magnesium, potassium, sodium, and phosphorus, are required in hundreds of milligrams. Many minerals are critical for enzyme function; others are used to maintain fluid balance, build bone tissue, synthesize hormones, transmit nerve impulses, contract and relax muscles, and protect against harmful free radicals.

Table 46.7.1: : Minerals and Their Major Functions

Minerals	Major Functions
Macrominerals	
Sodium	Fluid balance, nerve transmission, muscle contraction
Chloride	Fluid balance, stomach acid production
Potassium	Fluid balance, nerve transmission, muscle contraction
Calcium	Bone and teeth health maintenance, nerve transmission, muscle contraction, blood clotting
Phosphorus	Bone and teeth health maintenance, acid-base balance
Magnesium	Protein production, nerve transmission, muscle contraction
Sulfur	Protein production
Trace Minerals	
Iron	Carries oxygen, assists in energy production
Zinc	Protein and DNA production, wound healing, growth, immune system function
Iodine	Thyroid hormone production, growth, metabolism
Selenium	Antioxidant
Copper	Coenzyme, iron metabolism
Manganese	Coenzyme
Fluoride	Bone and teeth health maintenance, tooth decay prevention
Chromium	Assists insulin in glucose metabolism
Molybdenum	Coenzyme

Vitamins

The thirteen vitamins are categorized as either water-soluble or fat-soluble. The water-soluble vitamins are vitamin C and all the B vitamins, which include thiamine, riboflavin, niacin, pantothenic acid, pyroxidine, biotin, folate, and cobalamin. The fat-soluble vitamins are A, D, E, and K. Vitamins are required to perform many functions in the body, such as making red blood cells, synthesizing bone tissue, and playing a role in normal vision, nervous system function, and immune system function.

Table 46.7.2: Vitamins and Their Major Functions

Vitamins	Major Functions
Water Soluble Vitamins	
B_1 (thiamine)	Coenzyme, energy metabolism assistance
B_2 (riboflavin)	Coenzyme, energy metabolism assistance
B_3 (niacin)	Coenzyme, energy metabolism assistance
B_5 (pantothenic acid)	Coenzyme, energy metabolism assistance
B_6 (pyroxidine)	Coenzyme, amino acid synthesis assistance
B_7 Biotin	Coenzyme
B_9 Folate	Coenzyme, essential for growth
B_{12} (cobalamin)	Coenzyme, red blood cell synthesis
C	Collagen synthesis, antioxidant
Fat Soluble Vitamins	
A	Vision, reproduction, immune system function
D	Bone and teeth health maintenance, immune system function
E	Antioxidant, cell membrane protection
K	Bone and teeth health maintenance, blood clotting

Vitamin deficiencies can cause severe health problems. For example, a deficiency in niacin causes a disease called pellagra, which was common in the early twentieth century. The common signs and symptoms of pellagra are known as the "4Ds—diarrhea, dermatitis, dementia, and death." Until scientists found out that better diets relieved the signs and symptoms of pellagra, many people with the disease ended up in insane asylums awaiting death (Video **46.7.1**). Other vitamins were also found to prevent certain disorders and diseases such as scurvy (vitamin C), night blindness (vitamin A), and rickets (vitamin D).

The Discovery of Pellagra



Video **46.7.1**: This video provides a brief history of Dr. Joseph Goldberger's discovery that pellagra was a diet-related disease.[4]

Food Quality: Nutrient Density compared with Calorie Density

One way to think about the quality of your food is to consider how many nutrients you receive from a serving of that food compared to the number of Calories you receive from one serving of the food. For example, a candy bar gives you quite a few Calories but not very many of the essential nutrients. We would say that the candy bar has Calorie density but low Nutrient density. An apple on the other hand, has quite a few essential nutrients but not very many Calories. We would say that the apple has high nutrient density but low Calorie density. **Nutrient density** can be defined as a measure of nutrients relative to the amount of Calories they provide. A nutrient-dense food may also be referred to as a nutrient-rich food. Nutrient-dense foods are the opposite of “empty-calorie” foods, such as carbonated sugary soft drinks, which provide many calories and very little, if any, other nutrients.

What's in the Foods You Eat?

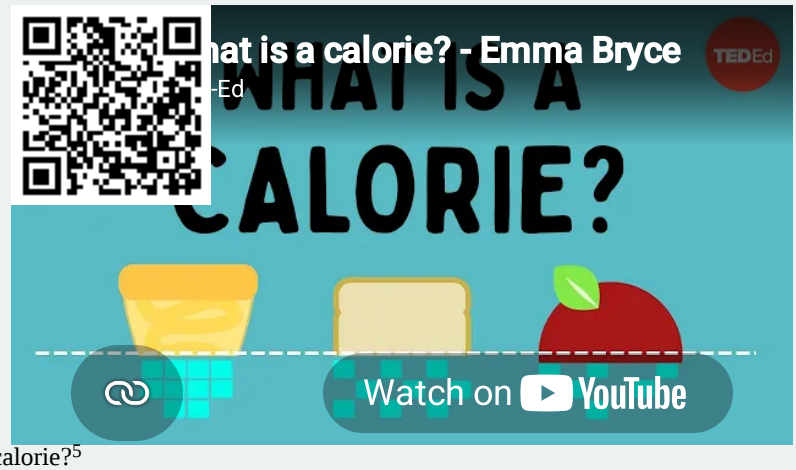
Curious to know if your favorite foods contain essential nutrients? Visit the USDA's search tool “What’s In the Foods You Eat?” (opens in new window)

Food Energy

Although this is only Chapter 1, you have already seen the words "Calories" and "Energy" used several times. In everyday life, you have probably heard people talk about how many Calories they burned on the treadmill or how many Calories are listed on a bag of chips. Calories are a measure of energy. It takes quite a lot of Calories (energy) to keep us alive. Even if a person is in a coma, they still burn approximately 1000 Calories of energy for their heart to beat, their blood to circulate, their lungs to breathe, and similar life-sustaining actions. We burn even more Calories when we exercise. The carbohydrates, fats, and proteins we eat and drink provide Calories for us (and alcohol as well if we choose to consume it). Sometimes people refer to these nutrients as "energy-yielding." As you read above, carbohydrates provide 4 Calories for every gram we consume; proteins provide 4 Calories for every gram we consume; fats provide 9 Calories for every gram we consume, and alcohol provides 7 Calories of energy for every gram we consume. Vitamins, minerals, and water do not provide any Calories, even though they are still essential nutrients.

Please watch the following Ted-Ed video, "What is a Calorie?" It will describe in more detail what a Calorie is and why you may want to know how many Calories you are consuming compared with how many you are burning each day.

Calories



Video **46.7.2**: What is a calorie?[5]

Food: A Better Source of Nutrients

It is better to get all your micronutrients from the foods you eat than from supplements. Supplements contain only what is listed on the label, but foods contain many more macronutrients, micronutrients, and other chemicals, such as antioxidants, that benefit health. Vitamins, multivitamins, and supplements are a $20 billion industry in this country, and more than 50 percent of Americans purchase and use them daily. According to the *British Medical Journal*, randomized clinical trials “have largely

shown no benefit of vitamin, mineral, and fish oil supplements on the risk of major non-communicable diseases in people without clinical nutritional deficiency."[6] Of course, there are exceptions in favor of supplementation, such as those on restrictive diets due to medical conditions.

Attributions

- Zimmerman, "An Introduction to Nutrition (Zimmerman)(opens in new window)," CC BY-NC-SA 3.0(opens in new window). *The original material was reorganized and updated. New figures were added. New references were added.*

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46.7.1: Food Energy Balance

Learning Objectives

- Estimate your daily energy requirement.
- Define basal metabolism and explain the factors that affect basal metabolic rate.
- Summarize why the amount of food we eat (appetite) is not completely under our conscious control.

Energy Intake Balances Energy Output To Maintain Weight

Recall that the macronutrients you consume are either converted to energy, stored, or used to synthesize macromolecules. A nutrient's metabolic path is dependent upon energy balance. When you are in a positive energy balance the excess nutrient energy will be stored or used to grow (e.g., during childhood, pregnancy, and wound healing). When you are in negative energy balance you aren't taking in enough energy to meet your needs, so your body will need to use its stores to provide energy. Energy balance is achieved when intake of energy is equal to energy expended. Weight can be thought of as a whole body estimate of energy balance; body weight is maintained when the body is in energy balance, lost when it is in negative energy balance, and gained when it is in positive energy balance. In general, weight is a good predictor of energy balance, but many other factors play a role in energy intake and energy expenditure. Some of these factors are under your control and others are not. Let us begin with the basics on how to estimate energy intake, energy requirement, and energy output. Then we will consider the other factors that play a role in maintaining energy balance and hence, body weight.

Estimating Energy Requirement

To maintain body weight you have to balance the calories obtained from food and beverages with the calories expended every day. Here, we will discuss how to calculate your energy needs in kilocalories per day so that you can determine whether your caloric intake falls short, meets, or exceeds your energy needs. The Institute of Medicine has devised a formula for calculating your Estimated Energy Requirement (EER). It takes into account your age, sex, weight, height, and physical activity level (PA). The EER is a standardized mathematical prediction of a person's daily energy needs in kilocalories per day required to maintain weight. It is calculated via the following formulas:

- Adult male:

$$\mathbf{EER} = 662 - [9.53 \times age(y)] + PA \times [15.91 \times wt(kg) + 5.39.6 \times ht(m)] \quad (46.7.1.1)$$

- Adult female:

$$\mathbf{EER} = 354 - [6.91 \times age(y)] + PA \times [9.36 \times wt(kg) + 726 \times ht(m) \quad (46.7.1.2)$$

Note: to convert pounds to kilograms, divide weight in pounds by 2.2. To convert feet to meters, divide height in feet by 3.3.

Interactive

To begin your dietary assessment, go to MyPlate, which is available on the US Department of Agriculture (USDA) website: http://www.choosemyplate.gov/.

Table **46.7.1.1**: Physical Activity (PA) Categories and Values

Activity Level	Men PA Value	Women PA Value	Description
Sedentary	1.00	1.00	No physical activity beyond that required for independent living
Low	1.11	1.12	Equivalent to walking 1.5 to 3 miles per day
Moderate	1.25	1.27	Equivalent to walking 3 to 10 miles per day
High	1.48	1.45	Equivalent to walking 10 or more miles per day

These values only apply to normal weight adults and not to children or pregnant or lactating women. Source: Health Canada. "Dietary Reference Intake Tables." Last modified November 29, 2010. http://www.hc-sc.gc.ca/fn-an/nutrition/reference/table/index-eng.php#eeer.

The numbers within the equations for the EER were derived from measurements taken from a group of people of the same sex and age with similar body size and physical activity level. These standardized formulas are then applied to individuals whose measurements have not been taken, but who have similar characteristics in order to estimate their energy requirements. Thus, a person's EER is, as the name suggests, an estimate for an average person of similar characteristics. EER values are different for children, pregnant or lactating women, and for overweight and obese people. Also, remember the EER is calculated based on weight maintenance, not for weight loss or weight gain.

Table **46.7.1.2**: Estimated Daily Calorie Needs

Sex	Age (years)	Sedentary	Moderately Active	Active
Child (female and male)	2–3	1,000–1,200	1,000–1,400	1,000–1,400
Female	4–8	1,200–1,400	1,400–1,600	1,400–1,800
	9–13	1,400–1,600	1,600–2,000	1,800–2,200
	14–18	1,800	2,000	2,400
	19–30	1,800–2,000	2,000–2,200	2,400
	31–50	1,800	2,000	2,200
	51+	1,600	1,800	2,000–2,200
Male	4–8	1,200–1,400	1400–1,600	1,600–2,000
	9–13	1,600–2,000	1,800–2,200	2,000–2,600
	14–18	2,000–2,400	2,400–2,800	2,800–3,200
	19–30	2,400–2,600	2,600–2,800	3,000
	31–50	2,200–2,400	2,400–2,600	2,800–3,000
	51+	2,000–2,200	2,200–2,400	2,400–2,800

Source: US Department of Agriculture. *2010 Dietary Guidelines for Americans.* 2010. http://health.gov/dietaryguidelines/dga2010/DietaryGuidelines2010.pdf.

The *2010 Dietary Guidelines* provides a table (Table **46.7.1.2**) that gives the estimated daily calorie needs for different age groups of males and females with various activity levels. The *2010 Dietary Guidelines* also states that while knowing the number of

calories you need each day is useful, it is also pertinent to obtain your calories from nutrient-dense foods and consume the various macronutrients in their Acceptable Macronutrient Distribution Ranges (AMDRs) (Table **46.7.1.3**).

Table **46.7.1.3**: Acceptable Macronutrient Distribution Ranges

Age	Carbohydrates (% of Calories)	Protein (% of Calories)	Fat (% of Calories)
Young Children (1–3)	45–65	5–20	30–40
Older children/adolescents (4–18)	45–65	10–30	25–35
Adults (19 and older)	45–65	10–35	20–35

Source: Institute of Medicine. "Dietary Reference Intakes: Macronutrients." Dietary Reference Intakes for Energy, Carbohydrate. Fiber, Fat, Fatty Acids, Cholesterol, Protein, and Amino Acids. September 5, 2002. www.iom.edu/~/media/Files/Act...onutrients.pdf

Total Energy Expenditure (Output)

The amount of energy you expend every day includes not only the calories you burn during physical activity, but also the calories you burn while at rest (basal metabolism), and the calories you burn when you digest food. The sum of caloric expenditure is referred to as total energy expenditure (TEE). Basal metabolism refers to those metabolic pathways necessary to support and maintain the body's basic functions (e.g. breathing, heartbeat, liver and kidney function) while at rest. The basal metabolic rate (BMR) is the amount of energy required by the body to conduct its basic functions over a certain time period. The great majority of energy expended (between 50 and 70 percent) daily is from conducting life's basic processes. Of all the organs, the liver requires the most energy (Table **46.7.1.4**). Unfortunately, you cannot tell your liver to ramp up its activity level to expend more energy so you can lose weight. BMR is dependent on body size, body composition, sex, age, nutritional status, and genetics. People with a larger frame size have a higher BMR simply because they have more mass. Muscle tissue burns more calories than fat tissue even while at rest and thus the more muscle mass a person has, the higher their BMR. Since females typically have less muscle mass and a smaller frame size than men, their BMRs are generally lower than men's. As we get older muscle mass declines and thus so does BMR. Nutritional status also affects basal metabolism. Caloric restriction, as occurs while dieting, for example, causes a decline in BMR. This is because the body attempts to maintain homeostasis and will adapt by slowing down its basic functions to offset the decrease in energy intake. Body temperature and thyroid hormone levels are additional determinants of BMR.

Table **46.7.1.4**: Energy Breakdown of Organs

Organ	**Percent of Energy Expended**
Liver	27
Brain	19
Heart	7
Kidneys	10
Skeletal muscle (at rest)	18
Other organs	19

The energy required for all the enzymatic reactions that take place during food digestion and absorption of nutrients is called the "thermic effect of food" and accounts for about 10 percent of total energy expended per day. The other energy required during the day is for physical activity. Depending on lifestyle, the energy required for this ranges between 15 and 30 percent of total energy expended. The main control a person has over TEE is to increase physical activity.

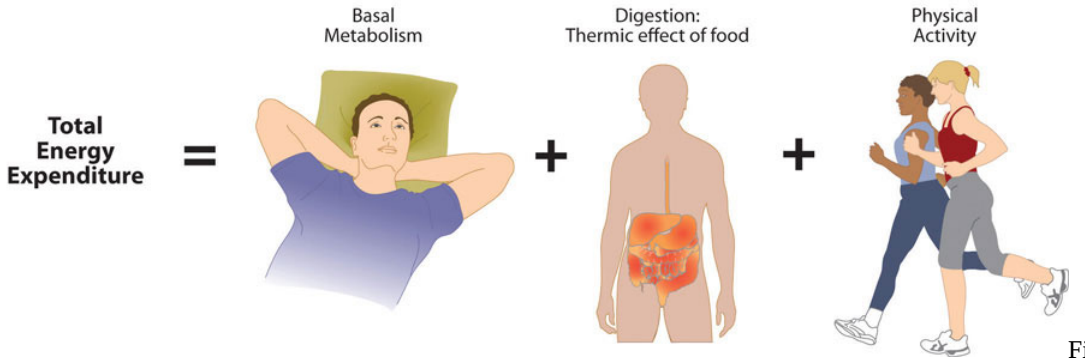


Figure 46.7.1.1: Total energy expenditure is the sum of energy expended at rest, during digestion, and during physical activity.

How to Calculate Total Energy Expenditure

Calculating TEE can be tedious, but has been made easier as there are now calculators available on the Web. TEE is dependent on age, sex, height, weight, and physical activity level. The equations are based on standardized formulas produced from actual measurements on groups of people with similar characteristics. To get accurate results from web-based TEE calculators, it is necessary to record your daily activities and the time spent performing them. A spreadsheet for doing so is available online at http://www.health-calc.com/Calculate_daily_energy_expenditure.pdf.

Interactive 11.4: Health-calc.com offers an interactive TEE calculator.

http://www.health-calc.com/diet/energy-expenditure-advanced

Factors Affecting Energy Intake

Physiology

In the last few decades scientific studies have revealed that how much we eat and what we eat is controlled not only by our own desires, but also is regulated physiologically and influenced by genetics. The hypothalamus in the brain is the main control point of appetite. It receives hormonal and neural signals, which determine if you feel hungry or full. Hunger is an unpleasant sensation of feeling empty that is communicated to the brain by both mechanical and chemical signals from the periphery. Conversely, satiety is the sensation of feeling full and it also is determined by mechanical and chemical signals relayed from the periphery. The hypothalamus contains distinct centers of neural circuits that regulate hunger and satiety (Figure 46.7.1.2).

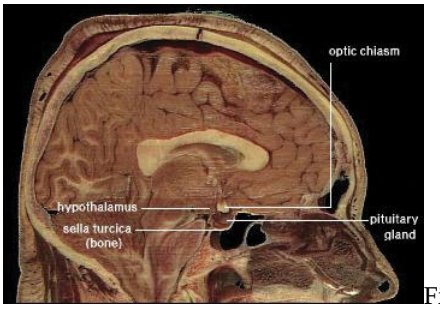


Figure 46.7.1.2: This is a scan of a brain. The hypothalamus contains distinct centers of neural circuits that regulate hunger and satiety. Source: Diabesity, Sixth Framework Programme. “Novel Molecular Targets for Obesity and Type 2 Diabetes.” 2002-2006. www.diabesity.eu/.honours.htm.

Hunger pangs are real and so is a “growling” stomach. When the stomach is empty it contracts, producing the characteristic pang and “growl.” The stomach’s mechanical movements relay neural signals to the hypothalamus, which relays other neural signals to parts of the brain. This results in the conscious feeling of the need to eat. Alternatively, after you eat a meal the stomach stretches and sends a neural signal to the brain stimulating the sensation of satiety and relaying the message to stop eating. The stomach also sends out certain hormones when it is full and others when it is empty. These hormones communicate to the hypothalamus and other areas of the brain either to stop eating or to find some food.

Fat tissue also plays a role in regulating food intake. Fat tissue produces the hormone leptin, which communicates to the satiety center in the hypothalamus that the body is in positive energy balance. The discovery of leptin's functions sparked a craze in the research world and in the diet pill industry as it was hypothesized that if you give leptin to a person who is overweight, they will decrease their food intake. Alas, this is not the case. In several clinical trials it was found that people who are overweight or obese are actually resistant to the hormone, meaning their brain does not respond as well to it.Dardeno, T. A. et al. "Leptin in Human Physiology and Therapeutics." *Front Neuroendocrinol* 31, no. 3 (2010): 377–93. http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2916735/?tool=pubmed. Therefore, when you administer leptin to an overweight or obese person there is no sustained effect on food intake.

Nutrients themselves also play a role in influencing food intake. The hypothalamus senses nutrient levels in the blood. When they are low the hunger center is stimulated, and when they are high the satiety center is stimulated. Furthermore, cravings for salty and sweet foods have an underlying physiological basis. Both undernutrition and overnutrition affect hormone levels and the neural circuitry controlling appetite, which makes losing or gaining weight a substantial physiological hurdle.

Genetic Influences

Genetics certainly play a role in body fatness and weight and also affects food intake. Children who have been adopted typically are similar in weight and body fatness to their biological parents. Moreover, identical twins are twice as likely to be of similar weights as compared to fraternal twins. The scientific search for obesity genes is ongoing and a few have been identified, such as the gene that encodes for leptin. However, overweight and obesity that manifests in millions of people is not likely to be attributed to one or even a few genes, but to rather the interactions of hundreds of genes with the environment. In fact, when an individual has a mutated version of the gene coding for leptin, they are obese, but only a few dozen people around the world have been identified as having a completely defective leptin gene.

Psychological/Behavioral Influences

When your mouth waters in response to the smell of a roasting Thanksgiving turkey and steaming hot pies, you are experiencing a psychological influence on food intake. A person's perception of good-smelling and good-tasting food influences what they eat and how much they eat. Mood and emotions are associated with food intake. Depression, low self-esteem, compulsive disorders, and emotional trauma are sometimes linked with increased food intake and obesity.

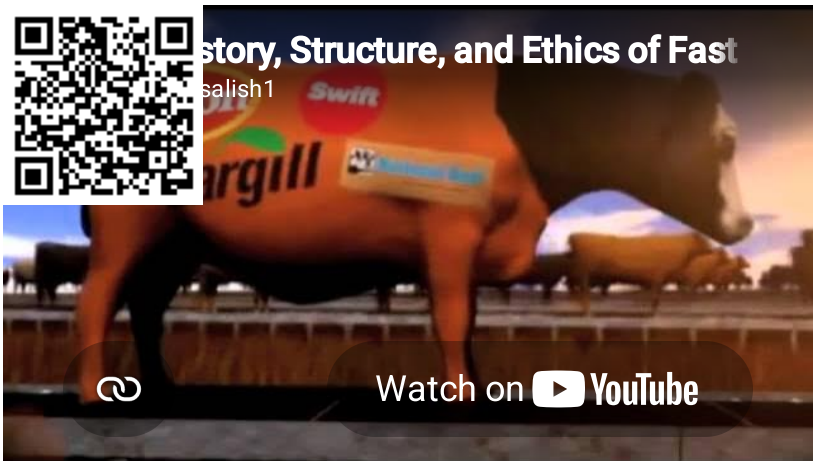
Certain behaviors can be predictive of how much a person eats. Some of these are how much food a person heaps onto their plate, how often they snack on calorie-dense, salty foods, how often they watch television or sit at a computer, and how often they eat out. A study published in a 2008 issue of *Obesity* looked at characteristics of Chinese buffet patrons. The study found that those who chose to immediately eat before browsing the buffet, used larger plates, used a fork rather than chopsticks, and chewed less per bite of food, had higher BMIs than patrons who did not exhibit these behaviors.Levin, B. E. "Developmental Gene X Environment Interactions Affecting Systems Regulating Energy Homeostasis and Obesity." *Front Neuroendocrinol* 3 (2010): 270–83. http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2903638/?tool=pubmed. Of course many behaviors are reflective of what we have easy access to—a concept we will discuss next.

Societal Influences

It is without a doubt that the American society affects what and how much we eat. Portion sizes have increased dramatically in the past few decades. For example, a bagel is now more than twice the size it was in the 1960s. Today, American teenagers have access to a massive amount of calorie-dense foods and beverages, which is a large contributor to the recent rapid increase in overweight and obesity in adolescents in this country. Even different cultures within the United States have different eating habits. For instance, southern Americans, in general, consume more foods high in fat, which is a contributing factor to their higher incidences of overweight and obesity than Americans who live in the northern states. (Alaska is an exception because it also has a high incidence of overweight and obesity, which is also partly attributed to diet.)

The fast food industry in America not only supplies Americans with a large proportion of their diet, but because of its massive presence in society dominates the workings of the entire food system. To generalize, most fast food items have little nutritional merit as they are highly processed and rich in saturated fat, salt, and added sugars. Despite fast foods being a poor source of nourishment, Americans spend over one hundred billion dollars per year on fast food, up from six billion dollars in the early 1970s. The fast food business is likely to continue to grow in North America (and the rest of the world) and greatly affect the diets of

whole populations. Because it is unrealistic to say that Americans should abruptly quit eating fast food to save their health (because they will not) society needs to come up with ideas that push nutrient-dense whole foods into the fast food industry. You may have observed that this largely consumer-driven push is having some effect on the foods the fast food industry serves (just watch a recent Subway commercial, or check the options now available in a McDonald's Happy Meal). Pushing the fast food industry to serve healthier foods is a realistic and positive way to improve the American diet.



***Video* 46.7.1.1:** *History, Structure, and Ethics of the Fast Food Industry (click to see video) A brief clip about the fast food industry and its effect on the United States.*

Tools for Change

Support the consumer movement of pushing the fast food industry and your favorite local restaurants into serving more nutrient-dense foods. You can begin this task by starting simple, such as requesting extra tomatoes and lettuce on your burger and more nutrient-dense choices in the salad bar. Also, choose their low-calorie menu options and help support the emerging market of healthier choices in the fast food industry. In today's fast-paced society, it is difficult for most people to avoid fast food all the time. When you do need a quick bite on the run, choose the fast food restaurants that serve healthier foods. Also, start asking for caloric contents of foods so that the restaurant becomes more aware that their patrons are being calorie conscious.

Factors Affecting Energy Expenditure

Physiological and Genetic Influences

Why is it so difficult for some people to lose weight and for others to gain weight? One theory is that every person has a "set point" of energy balance. This set point can also be called a fat-stat or lipostat, meaning the brain senses body fatness and triggers changes in energy intake or expenditure to maintain body fatness within a target range. Some believe that this theory provides an explanation as to why after dieting, most people return to their original weight not long after stopping the diet. Another theory is referred to as the "settling" point system, which takes into account (more so than the "set-point" theory) the contribution of the obesogenic environment to weight gain. In this model, the reservoir of body fatness responds to energy intake or energy expenditure, such that if a person is exposed to a greater amount of food, body fatness increases, or if a person watches more television body fatness increases. A major problem with these theories is that they overgeneralize and do not take into account that not all individuals respond in the same way to changes in food intake or energy expenditure. This brings up the importance of the interactions of genes and the environment.

Not all individuals who take a weight-loss drug lose weight and not all people who smoke are thin. An explanation for these discrepancies is that each individual's genes respond differently to a specific environment. Alternatively, environmental factors can influence a person's gene profile, which is exemplified by the effects of the prenatal environment on body weight and fatness and disease incidence later in life. One of the first scientific investigations of prenatal control over energy balance was conducted in Germany. In this observational study, scientists found that offspring born to mothers who experienced famine were more likely to be obese in adulthood than offspring born to mothers who were pregnant just after World War II who lived in the same

geographical locations.Matthews, C. E. “Amount of Time Spent in Sedentary Behaviors in the United States, 2003–2004.” *Am J Epidemiol* 167, no. 7 (2008): 875–81. doi: 10.1093/aje/kwm390. Other studies have shown that the offspring of women who were overweight during pregnancy have a greater propensity for being overweight and for developing Type 2 diabetes. Thus, undernutrition and overnutrition during pregnancy influence body weight and disease risk for offspring later in life. They do so by adapting energy metabolism to the early nutrient and hormonal environment in the womb.

Audio Link 11.1: Rethinking Thin - The Myths and Realities of Dieting

Listen to this NPR broadcast for scientific information about why it is so difficult for some people to lose weight.

Psychological/Behavioral Influence

Sedentary behavior is defined as the participation in the pursuits in which energy expenditure is no more than one-and-one-half times the amount of energy expended while at rest and include sitting, reclining, or lying down while awake. Of course, the sedentary lifestyle of many North Americans contributes to their average energy expenditure in daily life. Simply put, the more you sit, the less energy you expend. A study published in a 2008 issue of the *American Journal of Epidemiology* reports that 55 percent of Americans spend 7.7 hours in sedentary behavior daily.Matthews, C. E. “Amount of Time Spent in Sedentary Behaviors in the United States, 2003–2004.” *Am J Epidemiol* 167, no. 7 (2008): 875–81. doi: 10.1093/aje/kwm390. Fortunately, including only a small amount of low-level physical activity benefits weight control. A study published in the June 2001 issue of the *International Journal of Behavioral Nutrition and Physical Activity* reports that even breaking up sitting-time with frequent, but brief increased energy expenditure activities, such as walking for five minutes every hour, helps maintain weight and even aids in weight loss.Wu, Y. “Overweight and Obesity in China.” *Br Med J* 333, no. 7564 (2006): 362. doi: 10.1136/bmj.333.7564.362. Americans partake in an excessive amount of screen time, which is a sedentary behavior that not only reduces energy expenditure, but also contributes to weight gain because of the exposure to aggressive advertising campaigns for unhealthy foods.

Societal Influence

In the United States, many societal factors influence the number of calories burned in a day. Escalators, moving walkways, and elevators (not to mention cars!) are common modes of transportation that reduce average daily energy expenditure. Office work, high-stress jobs, and occupations requiring extended working hours are all societal pressures that reduce the time allotted for exercise of large populations of Americans. Even the remote controls that many have for various electronic devices in their homes contribute to the US society being less active. More “obesogenic” factors were discussed in the opening of this chapter.

Socioeconomic status has been found to be inversely proportional to weight gain. One reason for this relationship is that inhabitants of low-income neighborhoods have reduced access to safe streets and parks for walking. Another is that fitness clubs are expensive and few are found in lower-income neighborhoods. The recent and long-lasting economic crisis in this country is predicted to have profound effects on the average body weight of Americans. The number of homeless in this country is rising with many children and adults living in hotels and cars. As you can imagine neither of these “home spaces” has a kitchen, making it impossible to cook nutritious meals and resulting in increased economically-forced access to cheap, unhealthy foods, such as that at a nearby gas station.

Key Takeaways

Energy balance is achieved when energy intake is equal to energy expended. Energy balance is essential for maintaining weight. Knowing the number of calories you need each day is a useful reference point, but it is also important to obtain your calories from nutrient-dense foods and consume the macronutrients in their AMDRs. The amount of energy you expend every day includes not only the calories you burn during physical activity, but also the calories you burn at rest (basal metabolism), and the calories you burn when you digest food. Basal metabolic rate (BMR) is dependent on body size, body composition, sex, age, nutritional status, genetics, body temperature, and thyroid hormone levels. The great majority of energy expended (between 50 and 70 percent) daily comes from conducting life’s basic processes. The main control a person has over TEE is to increase physical activity. Energy intake is regulated by complex physiological responses and is influenced by genetics, behavior, and society. Energy expenditure is also regulated by complex physiological responses and is influenced by genetics, behavior, and society.

Discussion Starters

1. Some types of transportation are becoming economically unfeasible for obese people. Discuss whether or not it is acceptable that air carriers can enforce that obese people (or what they politely call “passengers of size” or “passengers requiring extra space”) pay more for their seats.
2. Many people have a hard time understanding the difficulties of being too skinny. Discuss with your peers how to empathize with the weight problems of underweight people. Read the article to understand that being skinny does not mean a person necessarily has a lower risk of chronic disease. http://www.msnbc.msn.com/id/18594089/ns/health-fitness/t/thin-people-can-be-fat-inside/

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46.8: Variations in Vertebrate Digestive Systems

Skills to Develop

- Explain the processes of digestion and absorption
- Compare and contrast different types of digestive systems
- Explain the specialized functions of the organs involved in processing food in the body
- Describe the ways in which organs work together to digest food and absorb nutrients

Animals obtain their nutrition from the consumption of other organisms. Depending on their diet, animals can be classified into the following categories: plant eaters (herbivores), meat eaters (carnivores), and those that eat both plants and animals (omnivores). The nutrients and macromolecules present in food are not immediately accessible to the cells. There are a number of processes that modify food within the animal body in order to make the nutrients and organic molecules accessible for cellular function. As animals evolved in complexity of form and function, their digestive systems have also evolved to accommodate their various dietary needs.

Herbivores, Omnivores, and Carnivores

Herbivores are animals whose primary food source is plant-based. Examples of herbivores, as shown in Figure 46.8.1 include vertebrates like deer, koalas, and some bird species, as well as invertebrates such as crickets and caterpillars. These animals have evolved digestive systems capable of handling large amounts of plant material. Herbivores can be further classified into frugivores (fruit-eaters), granivores (seed eaters), nectivores (nectar feeders), and folivores (leaf eaters).



(a) (b)

Figure 46.8.1: Herbivores, like this (a) mule deer and (b) monarch caterpillar, eat primarily plant material. (credit a: modification of work by Bill Ebbesen; credit b: modification of work by Doug Bowman)

Carnivores are animals that eat other animals. The word carnivore is derived from Latin and literally means “meat eater.” Wild cats such as lions, shown in Figure 46.8.2a and tigers are examples of vertebrate carnivores, as are snakes and sharks, while invertebrate carnivores include sea stars, spiders, and ladybugs, shown in Figure 46.8.2b. Obligate carnivores are those that rely entirely on animal flesh to obtain their nutrients; examples of obligate carnivores are members of the cat family, such as lions and cheetahs. Facultative carnivores are those that also eat non-animal food in addition to animal food. Note that there is no clear line that differentiates facultative carnivores from omnivores; dogs would be considered facultative carnivores.



(a)



(b)

Figure 46.8.2: Carnivores like the (a) lion eat primarily meat. The (b) ladybug is also a carnivore that consumes small insects called aphids. (credit a: modification of work by Kevin Pluck; credit b: modification of work by Jon Sullivan)

Omnivores are animals that eat both plant- and animal-derived food. In Latin, omnivore means to eat everything. Humans, bears (shown in Figure 46.8.3a), and chickens are example of vertebrate omnivores; invertebrate omnivores include cockroaches and crayfish (shown in Figure 46.8.3b).



(a)



(b)

Figure 46.8.3: Omnivores like the (a) bear and (b) crayfish eat both plant and animal based food. (credit a: modification of work by Dave Menke; credit b: modification of work by Jon Sullivan)

Invertebrate Digestive Systems

Animals have evolved different types of digestive systems to aid in the digestion of the different foods they consume. The simplest example is that of a gastrovascular cavity and is found in organisms with only one opening for digestion. Platyhelminthes (flatworms), Ctenophora (comb jellies), and Cnidaria (coral, jelly fish, and sea anemones) use this type of digestion. Gastrovascular cavities, as shown in Figure 46.8.4a, are typically a blind tube or cavity with only one opening, the “mouth”, which also serves as an “anus”. Ingested material enters the mouth and passes through a hollow, tubular cavity. Cells within the cavity secrete digestive enzymes that break down the food. The food particles are engulfed by the cells lining the gastrovascular cavity.

The alimentary canal, shown in Figure 46.8.4b, is a more advanced system: it consists of one tube with a mouth at one end and an anus at the other. Earthworms are an example of an animal with an alimentary canal. Once the food is ingested through the mouth, it passes through the esophagus and is stored in an organ called the crop; then it passes into the gizzard where it is churned and

digested. From the gizzard, the food passes through the intestine, the nutrients are absorbed, and the waste is eliminated as feces, called castings, through the anus.

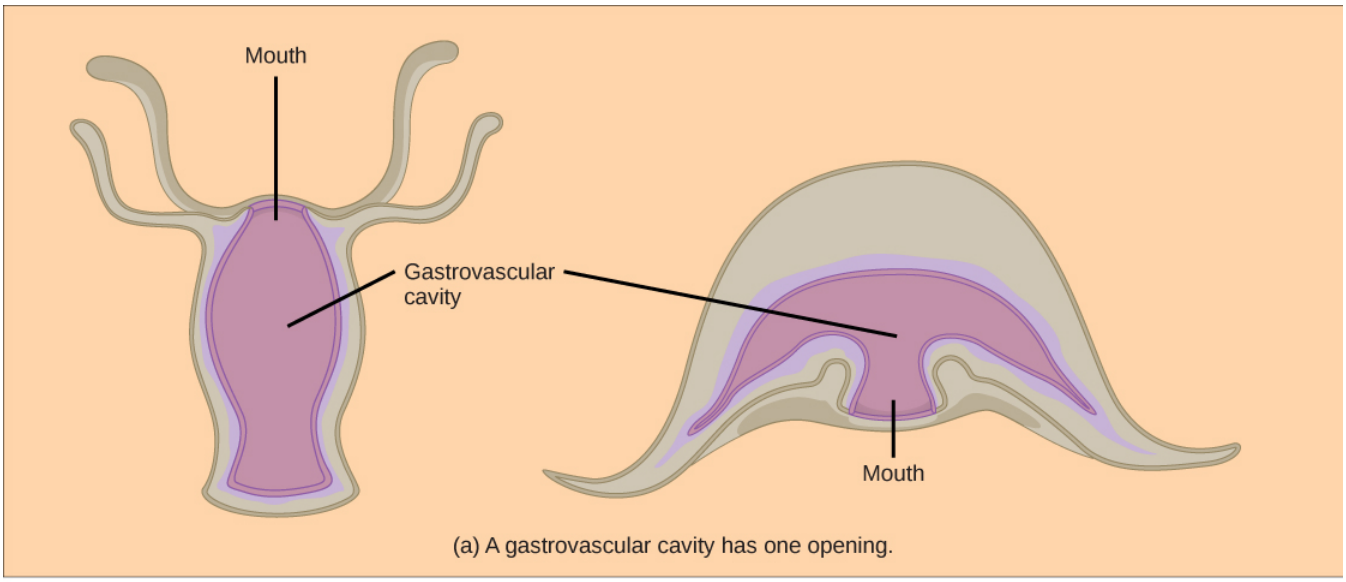


Figure 46.8.4: (a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food, and an anus for eliminating waste, as shown in this nematode.

Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating unmasticated food.

Monogastric: Single-chambered Stomach

As the word monogastric suggests, this type of digestive system consists of one (“mono”) stomach chamber (“gastric”). Humans and many animals have a monogastric digestive system as illustrated in Figure 46.8.5. The process of digestion begins with the mouth and the intake of food. The teeth play an important role in masticating (chewing) or physically breaking down food into smaller particles. The enzymes present in saliva also begin to chemically break down food. The esophagus is a long tube that connects the mouth to the stomach. Using peristalsis, or wave-like smooth muscle contractions, the muscles of the esophagus push the food towards the stomach. In order to speed up the actions of enzymes in the stomach, the stomach is an extremely acidic environment, with a pH between 1.5 and 2.5. The gastric juices, which include enzymes in the stomach, act on the food particles and continue the process of digestion. Further breakdown of food takes place in the small intestine where enzymes produced by the liver, the small intestine, and the pancreas continue the process of digestion. The nutrients are absorbed into the blood stream across the epithelial cells lining the walls of the small intestines. The waste material travels on to the large intestine where water is absorbed and the drier waste material is compacted into feces; it is stored until it is excreted through the rectum.

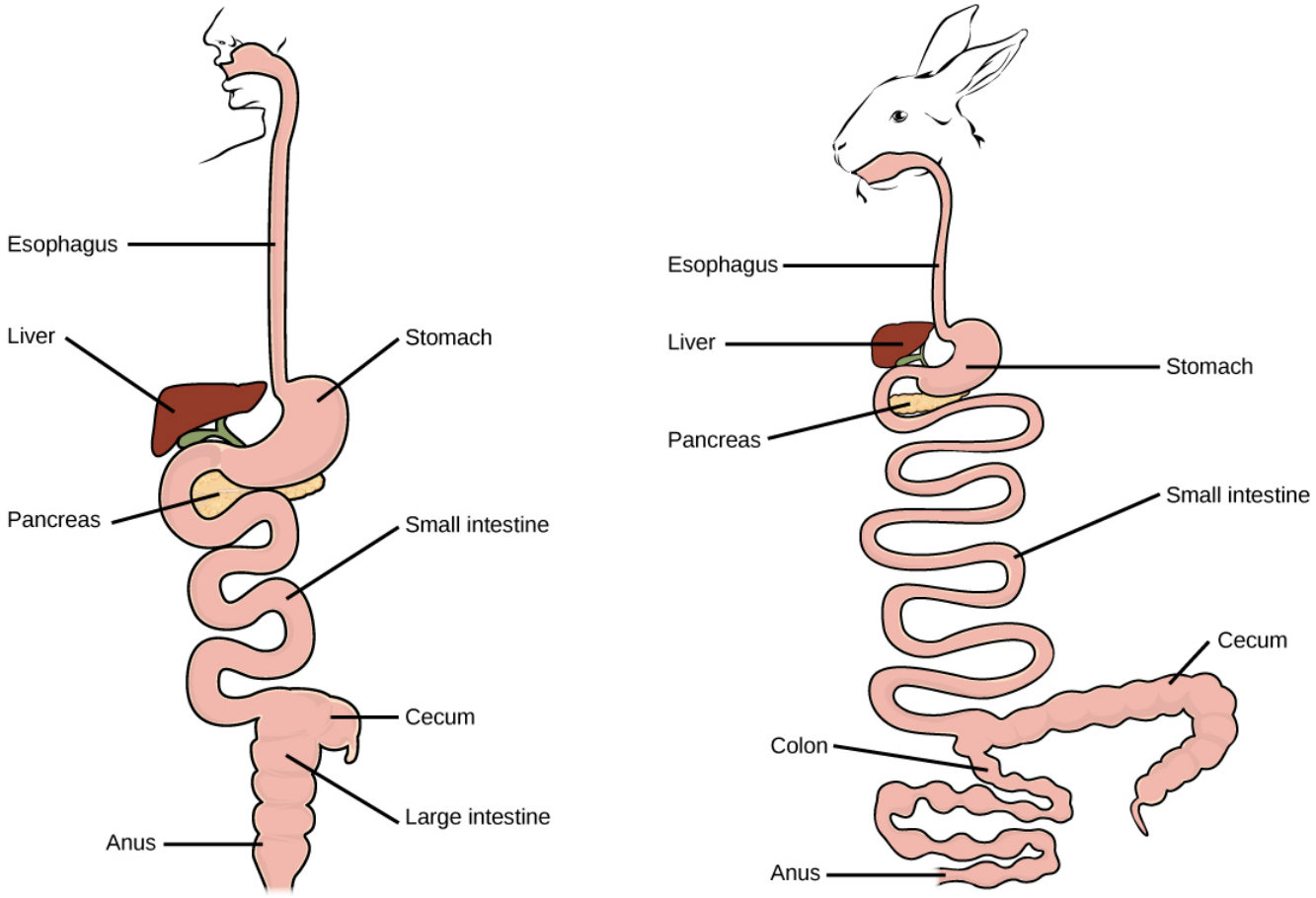


Figure **46.8.5**: (a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients. Rabbits digest their food twice: the first time food passes through the digestive system, it collects in the cecum, and then it passes as soft feces called cecotrophes. The rabbit re-ingests these cecotrophes to further digest them.

Avian

Birds face special challenges when it comes to obtaining nutrition from food. They do not have teeth and so their digestive system, shown in Figure **46.8.6**, must be able to process un-masticated food. Birds have evolved a variety of beak types that reflect the vast variety in their diet, ranging from seeds and insects to fruits and nuts. Because most birds fly, their metabolic rates are high in order to efficiently process food and keep their body weight low. The stomach of birds has two chambers: the proventriculus, where gastric juices are produced to digest the food before it enters the stomach, and the gizzard, where the food is stored, soaked, and mechanically ground. The undigested material forms food pellets that are sometimes regurgitated. Most of the chemical digestion and absorption happens in the intestine and the waste is excreted through the cloaca.

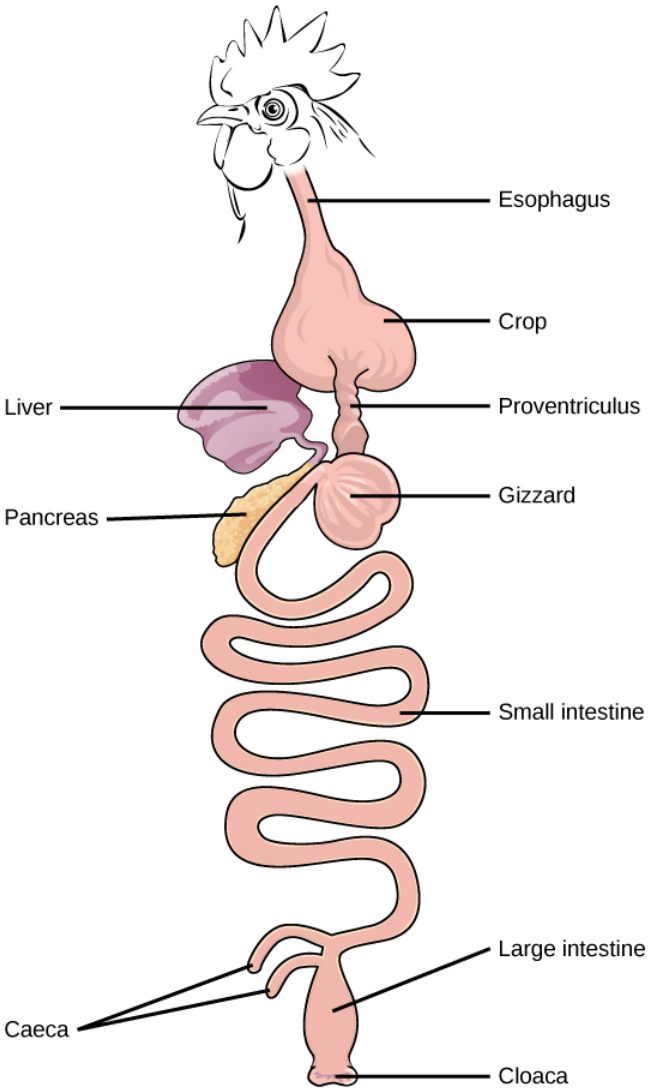


Figure **46.8.6**: The avian esophagus has a pouch, called a crop, which stores food. Food passes from the crop to the first of two stomachs, called the proventriculus, which contains digestive juices that break down food. From the proventriculus, the food enters the second stomach, called the gizzard, which grinds food. Some birds swallow stones or grit, which are stored in the gizzard, to aid the grinding process. Birds do not have separate openings to excrete urine and feces. Instead, uric acid from the kidneys is secreted into the large intestine and combined with waste from the digestive process. This waste is excreted through an opening called the cloaca.

Evolution Connection: Avian Adaptations

Birds have a highly efficient, simplified digestive system. Recent fossil evidence has shown that the evolutionary divergence of birds from other land animals was characterized by streamlining and simplifying the digestive system. Unlike many other animals, birds do not have teeth to chew their food. In place of lips, they have sharp pointy beaks. The horny beak, lack of jaws, and the smaller tongue of the birds can be traced back to their dinosaur ancestors. The emergence of these changes seems to coincide with the inclusion of seeds in the bird diet. Seed-eating birds have beaks that are shaped for grabbing seeds and the two-compartment stomach allows for delegation of tasks. Since birds need to remain light in order to fly, their metabolic rates are very high, which means they digest their food very quickly and need to eat often. Contrast this with the ruminants, where the digestion of plant matter takes a very long time.

Ruminants

Ruminants are mainly herbivores like cows, sheep, and goats, whose entire diet consists of eating large amounts of roughage or fiber. They have evolved digestive systems that help them digest vast amounts of cellulose. An interesting feature of the ruminants' mouth is that they do not have upper incisor teeth. They use their lower teeth, tongue and lips to tear and chew their food. From the mouth, the food travels to the esophagus and on to the stomach.

To help digest the large amount of plant material, the stomach of the ruminants is a multi-chambered organ, as illustrated in Figure 46.8.7. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that break down cellulose and ferment ingested food. The abomasum is the "true" stomach and is the equivalent of the monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary to digest plant material in ruminants. The fermentation process produces large amounts of gas in the stomach chamber, which must be eliminated. As in other animals, the small intestine plays an important role in nutrient absorption, and the large intestine helps in the elimination of waste.

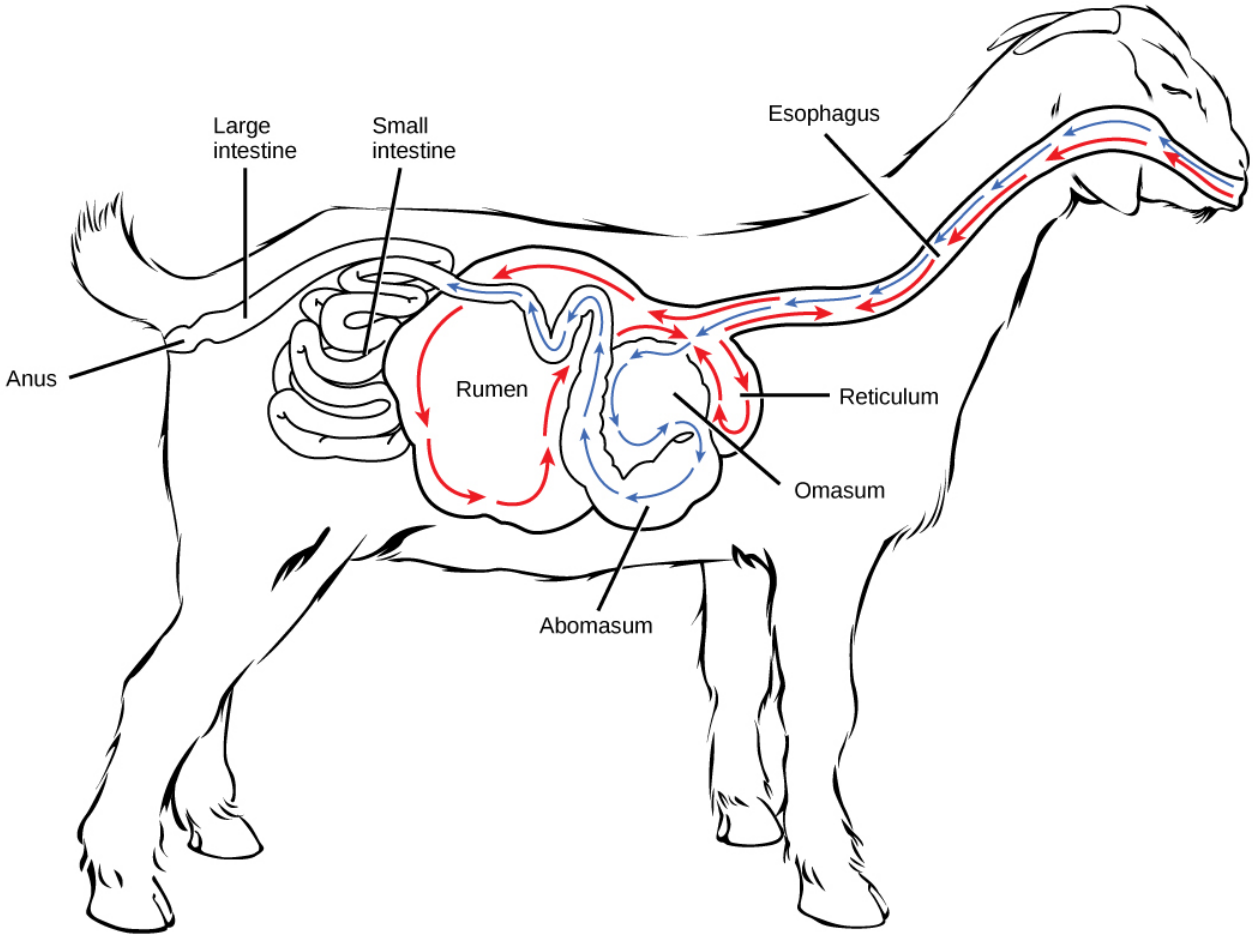


Figure 46.8.7: Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the omasum, which removes water. The cud then passes onto the fourth stomach, the abomasum, where it is digested by enzymes produced by the ruminant.

Pseudo-ruminants

Some animals, such as camels and alpacas, are pseudo-ruminants. They eat a lot of plant material and roughage. Digesting plant material is not easy because plant cell walls contain the polymeric sugar molecule cellulose. The digestive enzymes of these animals cannot break down cellulose, but microorganisms present in the digestive system can. Therefore, the digestive system must be able to handle large amounts of roughage and break down the cellulose. Pseudo-ruminants have a three-chamber stomach in the digestive system. However, their cecum—a pouched organ at the beginning of the large intestine containing many microorganisms that are necessary for the digestion of plant materials—is large and is the site where the roughage is fermented and digested. These animals do not have a rumen but have an omasum, abomasum, and reticulum.

Parts of the Digestive System

The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms.

Oral Cavity

The oral cavity, or mouth, is the point of entry of food into the digestive system, illustrated in Figure 46.8.8. The food consumed is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

The extensive chemical process of digestion begins in the mouth. As food is being chewed, saliva, produced by the salivary glands, mixes with the food. Saliva is a watery substance produced in the mouths of many animals. There are three major glands that secrete saliva—the parotid, the submandibular, and the sublingual. Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains immunoglobulins and lysozymes, which have antibacterial action to reduce tooth decay by inhibiting growth of some bacteria. Saliva also contains an enzyme called salivary amylase that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme called lipase is produced by the cells in the tongue. Lipases are a class of enzymes that can break down triglycerides. The lingual lipase begins the breakdown of fat components in the food. The chewing and wetting action provided by the teeth and saliva prepare the food into a mass called the bolus for swallowing. The tongue helps in swallowing—moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the trachea, which leads to the lungs, and the esophagus, which leads to the stomach. The trachea has an opening called the glottis, which is covered by a cartilaginous flap called the epiglottis. When swallowing, the epiglottis closes the glottis and food passes into the esophagus and not the trachea. This arrangement allows food to be kept out of the trachea.

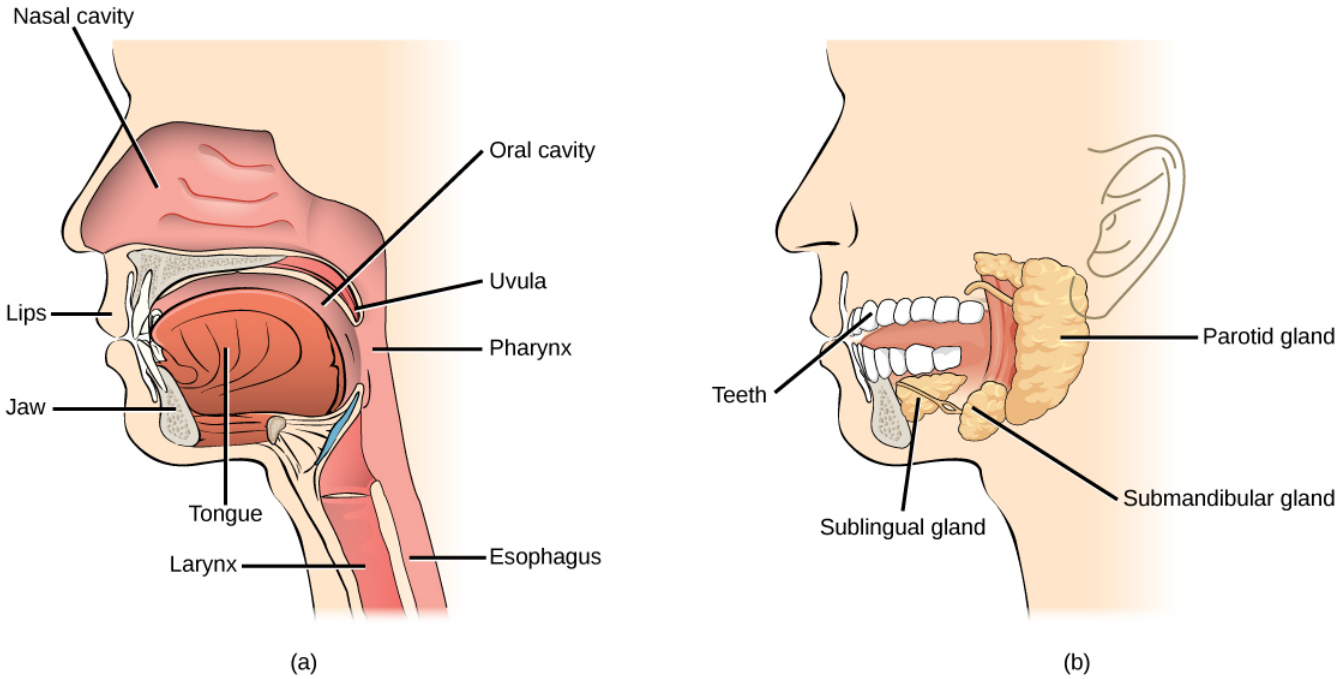


Figure 46.8.8: Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by the National Cancer Institute)

Esophagus

The esophagus is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave like movements called peristalsis that push the food toward the stomach, as illustrated in Figure 46.8.9. The peristalsis wave is unidirectional—it moves food from the mouth to the stomach, and reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.

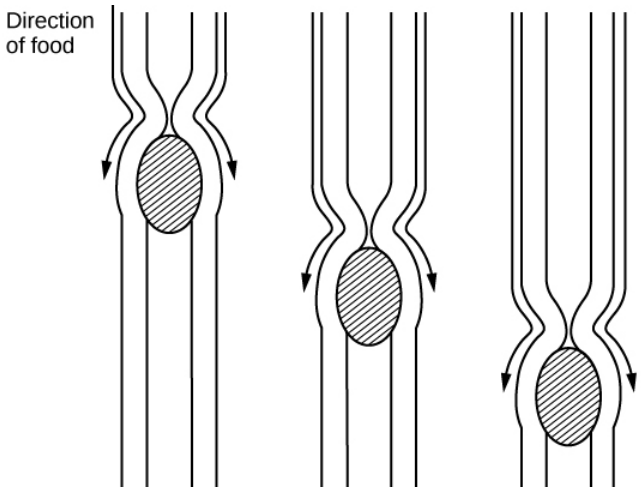


Figure 46.8.9: The esophagus transfers food from the mouth to the stomach through peristaltic movements.

A ring-like muscle called a sphincter forms valves in the digestive system. The gastro-esophageal sphincter is located at the stomach end of the esophagus. In response to swallowing and the pressure exerted by the bolus of food, this sphincter opens, and the bolus enters the stomach. When there is no swallowing action, this sphincter is shut and prevents the contents of the stomach from traveling up the esophagus. Many animals have a true sphincter; however, in humans, there is no true sphincter, but the esophagus remains closed when there is no swallowing action. Acid reflux or "heartburn" occurs when the acidic digestive juices escape into the esophagus.

Stomach

A large part of digestion occurs in the stomach, shown in Figure 46.8.10. The stomach is a saclike organ that secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

Art Connection

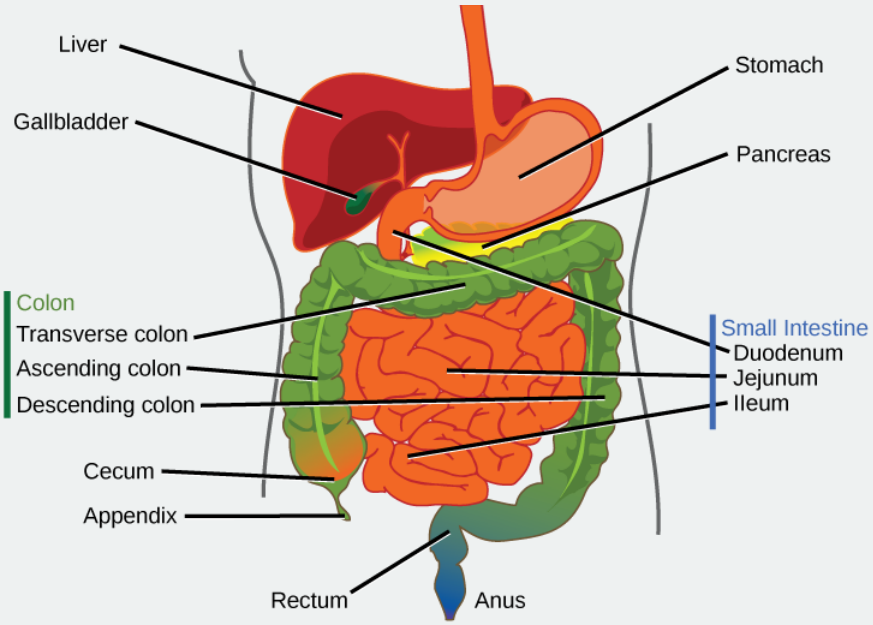


Figure 46.8.10: The human stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)

Which of the following statements about the digestive system is false?

A. Chyme is a mixture of food and digestive juices that is produced in the stomach.
B. Food enters the large intestine before the small intestine.
C. In the small intestine, chyme mixes with bile, which emulsifies fats.
D. The stomach is separated from the small intestine by the pyloric sphincter.

The stomach is also the major site for protein digestion in animals other than ruminants. Protein digestion is mediated by an enzyme called pepsin in the stomach chamber. Pepsin is secreted by the chief cells in the stomach in an inactive form called pepsinogen. Pepsin breaks peptide bonds and cleaves proteins into smaller polypeptides; it also helps activate more pepsinogen, starting a positive feedback mechanism that generates more pepsin. Another cell type—parietal cells—secrete hydrogen and chloride ions, which combine in the lumen to form hydrochloric acid, the primary acidic component of the stomach juices. Hydrochloric acid helps to convert the inactive pepsinogen to pepsin. The highly acidic environment also kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the hydrolysis of protein in the food. Chemical digestion is facilitated by the churning action of the stomach. Contraction and relaxation of smooth muscles mixes the stomach contents about every 20 minutes. The partially digested food and gastric juice mixture is called chyme. Chyme passes from the stomach to the small intestine. Further protein digestion takes place in the small intestine. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by the pyloric sphincter.

When digesting protein and some fats, the stomach lining must be protected from getting digested by pepsin. There are two points to consider when describing how the stomach lining is protected. First, as previously mentioned, the enzyme pepsin is synthesized in the inactive form. This protects the chief cells, because pepsinogen does not have the same enzyme functionality of pepsin. Second, the stomach has a thick mucus lining that protects the underlying tissue from the action of the digestive juices. When this mucus lining is ruptured, ulcers can form in the stomach. Ulcers are open wounds in or on an organ caused by bacteria (*Helicobacter pylori*) when the mucus lining is ruptured and fails to reform.

Small Intestine

Chyme moves from the stomach to the small intestine. The small intestine is the organ where the digestion of protein, fats, and carbohydrates is completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the villi. The apical surface of each villus has many microscopic projections called microvilli. These structures, illustrated in Figure **46.8.11**, are lined with epithelial cells on the luminal side and allow for the nutrients to be absorbed from the digested food and absorbed into the blood stream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients. Absorbed nutrients in the blood are carried into the hepatic portal vein, which leads to the liver. There, the liver regulates the distribution of nutrients to the rest of the body and removes toxic substances, including drugs, alcohol, and some pathogens.

Art Connection

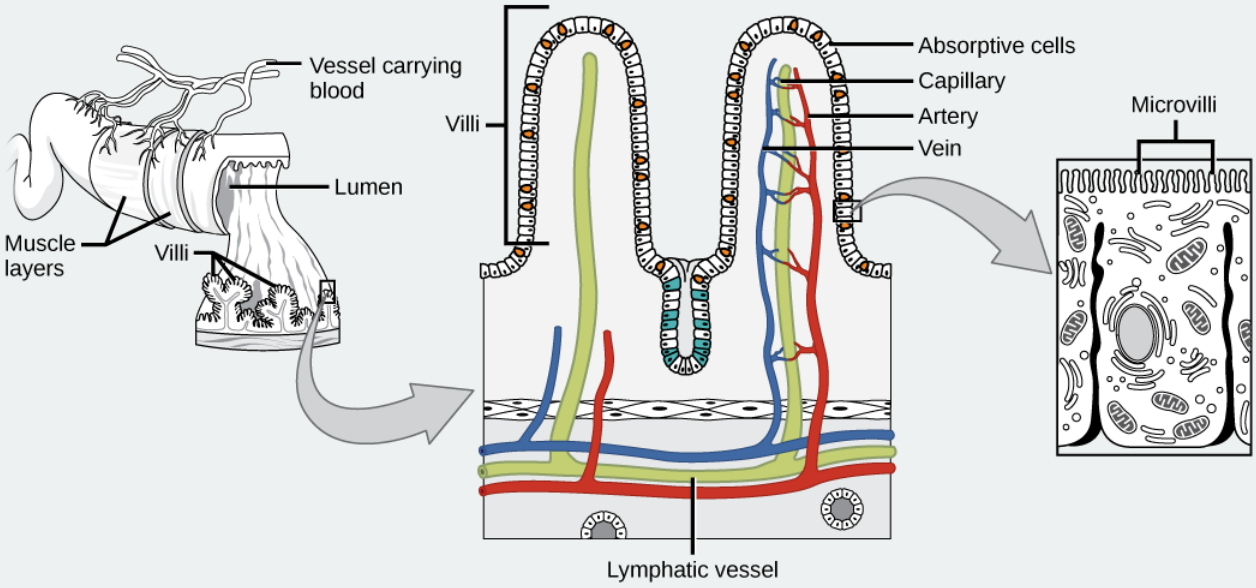


Figure 46.8.11: Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nutrients.

Which of the following statements about the small intestine is false?

A. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
B. The inside of the small intestine has many folds, called villi.
C. Microvilli are lined with blood vessels as well as lymphatic vessels.
D. The inside of the small intestine is called the lumen.

The human small intestine is over 6m long and is divided into three parts: the duodenum, the jejunum, and the ileum. The "C-shaped," fixed part of the small intestine is called the duodenum and is shown in Figure 46.8.11. The duodenum is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum. In the duodenum, chyme is mixed with pancreatic juices in an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Pancreatic juices also contain several digestive enzymes. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. Bile is produced in the liver and stored and concentrated in the gallbladder. Bile contains bile salts which emulsify lipids while the pancreas produces enzymes that catabolize starches, disaccharides, proteins, and fats. These digestive juices break down the food particles in the chyme into glucose, triglycerides, and amino acids. Some chemical digestion of food takes place in the duodenum. Absorption of fatty acids also takes place in the duodenum.

The second part of the small intestine is called the jejunum, shown in Figure 46.8.11. Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. The bulk of chemical digestion and nutrient absorption occurs in the jejunum.

The ileum, also illustrated in Figure 46.8.11 is the last part of the small intestine and here the bile salts and vitamins are absorbed into blood stream. The undigested food is sent to the colon from the ileum via peristaltic movements of the muscle. The ileum ends and the large intestine begins at the ileocecal valve. The vermiform, "worm-like," appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

The large intestine, illustrated in Figure 46.8.12, reabsorbs the water from the undigested food material and processes the waste material. The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or "intestinal flora" that aid in the digestive processes. The colon can be divided into four regions, the ascending colon, the transverse colon, the descending colon and the sigmoid colon. The main functions of the colon are

to extract the water and mineral salts from undigested food, and to store waste material. Carnivorous mammals have a shorter large intestine compared to herbivorous mammals due to their diet.

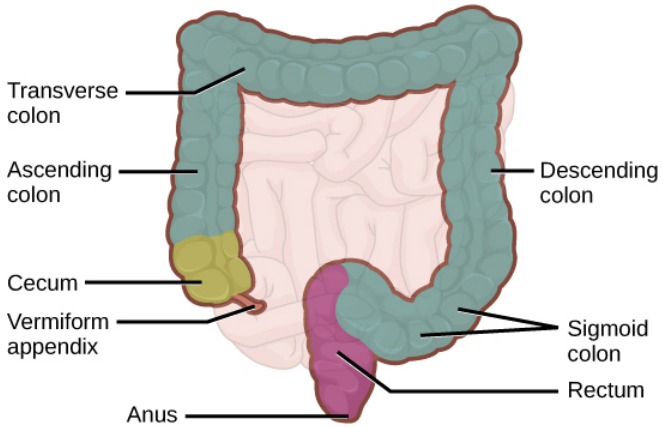


Figure 46.8.12: The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

Rectum and Anus

The rectum is the terminal end of the large intestine, as shown in Figure 46.8.12. The primary role of the rectum is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The anus is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

The organs discussed above are the organs of the digestive tract through which food passes. Accessory organs are organs that add secretions (enzymes) that catabolize food into nutrients. Accessory organs include salivary glands, the liver, the pancreas, and the gallbladder. The liver, pancreas, and gallbladder are regulated by hormones in response to the food consumed.

The liver is the largest internal organ in humans and it plays a very important role in digestion of fats and detoxifying blood. The liver produces bile, a digestive juice that is required for the breakdown of fatty components of the food in the duodenum. The liver also processes the vitamins and fats and synthesizes many plasma proteins.

The pancreas is another important gland that secretes digestive juices. The chyme produced from the stomach is highly acidic in nature; the pancreatic juices contain high levels of bicarbonate, an alkali that neutralizes the acidic chyme. Additionally, the pancreatic juices contain a large variety of enzymes that are required for the digestion of protein and carbohydrates.

The gallbladder is a small organ that aids the liver by storing bile and concentrating bile salts. When chyme containing fatty acids enters the duodenum, the bile is secreted from the gallbladder into the duodenum.

Summary

Different animals have evolved different types of digestive systems specialized to meet their dietary needs. Humans and many other animals have monogastric digestive systems with a single-chambered stomach. Birds have evolved a digestive system that includes a gizzard where the food is crushed into smaller pieces. This compensates for their inability to masticate. Ruminants that consume large amounts of plant material have a multi-chambered stomach that digests roughage. Pseudo-ruminants have similar digestive processes as ruminants but do not have the four-compartment stomach. Processing food involves ingestion (eating), digestion (mechanical and enzymatic breakdown of large molecules), absorption (cellular uptake of nutrients), and elimination (removal of undigested waste as feces).

Many organs work together to digest food and absorb nutrients. The mouth is the point of ingestion and the location where both mechanical and chemical breakdown of food begins. Saliva contains an enzyme called amylase that breaks down carbohydrates. The food bolus travels through the esophagus by peristaltic movements to the stomach. The stomach has an extremely acidic environment. An enzyme called pepsin digests protein in the stomach. Further digestion and absorption take place in the small intestine. The large intestine reabsorbs water from the undigested food and stores waste until elimination.

Art Connections

Figure 46.8.10: Which of the following statements about the digestive system is false?

A. Chyme is a mixture of food and digestive juices that is produced in the stomach.
B. Food enters the large intestine before the small intestine.
C. In the small intestine, chyme mixes with bile, which emulsifies fats.
D. The stomach is separated from the small intestine by the pyloric sphincter.

Answer

B

Figure 46.8.11: Which of the following statements about the small intestine is false?

A. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
B. The inside of the small intestine has many folds, called villi.
C. Microvilli are lined with blood vessels as well as lymphatic vessels.
D. The inside of the small intestine is called the lumen.

Answer

C

Glossary

alimentary canal
tubular digestive system with a mouth and anus

anus
exit point for waste material

bile
digestive juice produced by the liver; important for digestion of lipids

bolus
mass of food resulting from chewing action and wetting by saliva

carnivore
animal that consumes animal flesh

chyme
mixture of partially digested food and stomach juices

duodenum
first part of the small intestine where a large part of digestion of carbohydrates and fats occurs

esophagus
tubular organ that connects the mouth to the stomach

gallbladder
organ that stores and concentrates bile

gastrovascular cavity

digestive system consisting of a single opening

gizzard
muscular organ that grinds food

herbivore
animal that consumes strictly plant diet

ileum
last part of the small intestine; connects the small intestine to the large intestine; important for absorption of B-12

jejunum
second part of the small intestine

large intestine
digestive system organ that reabsorbs water from undigested material and processes waste matter

lipase
enzyme that chemically breaks down lipids

liver
organ that produces bile for digestion and processes vitamins and lipids

monogastric
digestive system that consists of a single-chambered stomach

omnivore
animal that consumes both plants and animals

pancreas
gland that secretes digestive juices

pepsin
enzyme found in the stomach whose main role is protein digestion

pepsinogen
inactive form of pepsin

peristalsis
wave-like movements of muscle tissue

proventriculus
glandular part of a bird’s stomach

rectum
area of the body where feces is stored until elimination

roughage
component of food that is low in energy and high in fiber

ruminant
animal with a stomach divided into four compartments

salivary amylase

enzyme found in saliva, which converts carbohydrates to maltose

small intestine
organ where digestion of protein, fats, and carbohydrates is completed

sphincter
band of muscle that controls movement of materials throughout the digestive tract

stomach
saclike organ containing acidic digestive juices

villi
folds on the inner surface of the small intestine whose role is to increase absorption area

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46.8.1: Nutrition and Energy Production

Skills to Develop

- Explain why an animal's diet should be balanced and meet the needs of the body
- Define the primary components of food
- Describe the essential nutrients required for cellular function that cannot be synthesized by the animal body
- Explain how energy is produced through diet and digestion
- Describe how excess carbohydrates and energy are stored in the body

Given the diversity of animal life on our planet, it is not surprising that the animal diet would also vary substantially. The animal diet is the source of materials needed for building DNA and other complex molecules needed for growth, maintenance, and reproduction; collectively these processes are called biosynthesis. The diet is also the source of materials for ATP production in the cells. The diet must be balanced to provide the minerals and vitamins that are required for cellular function.

Food Requirements

What are the fundamental requirements of the animal diet? The animal diet should be well balanced and provide nutrients required for bodily function and the minerals and vitamins required for maintaining structure and regulation necessary for good health and reproductive capability. These requirements for a human are illustrated graphically in Figure 46.8.1.1.

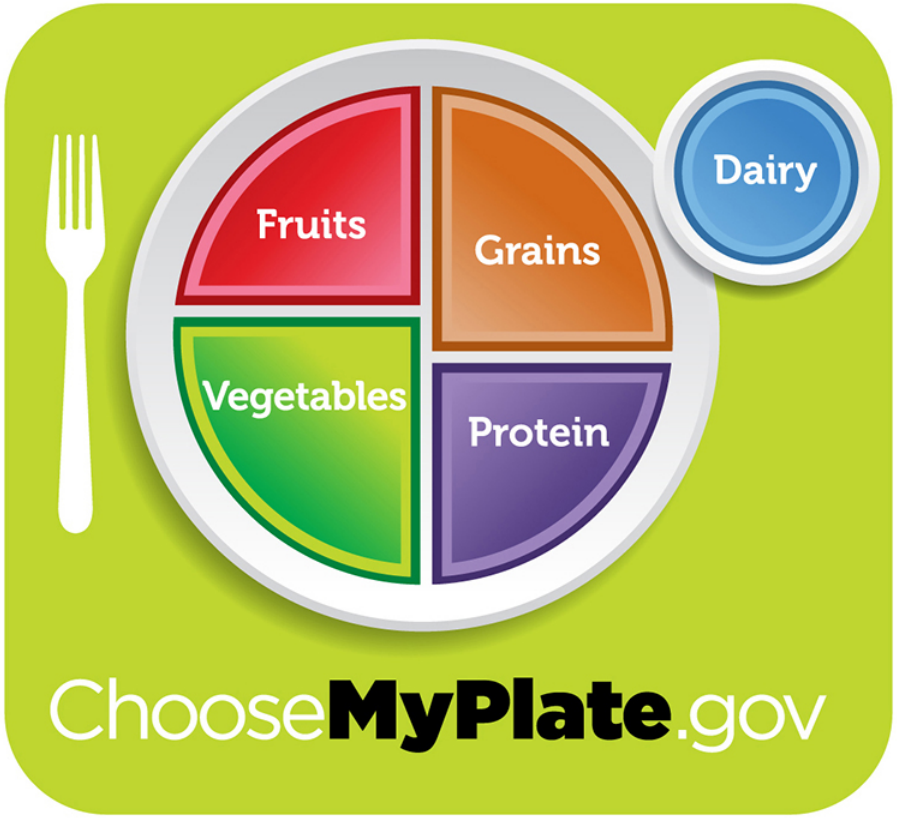


Figure 46.8.1.1: For humans, a balanced diet includes fruits, vegetables, grains, and protein. (credit: USDA)

Everyday Connection: Let's Move! Campaign

Obesity is a growing epidemic and the rate of obesity among children is rapidly rising in the United States. To combat childhood obesity and ensure that children get a healthy start in life, first lady Michelle Obama has launched the Let's Move! campaign. The goal of this campaign is to educate parents and caregivers on providing healthy nutrition and encouraging

active lifestyles to future generations. This program aims to involve the entire community, including parents, teachers, and healthcare providers to ensure that children have access to healthy foods—more fruits, vegetables, and whole grains—and consume fewer calories from processed foods. Another goal is to ensure that children get physical activity. With the increase in television viewing and stationary pursuits such as video games, sedentary lifestyles have become the norm. Learn more at www.letsmove.gov.

Organic Precursors

The organic molecules required for building cellular material and tissues must come from food. Carbohydrates or sugars are the primary source of organic carbons in the animal body. During digestion, digestible carbohydrates are ultimately broken down into glucose and used to provide energy through metabolic pathways. Complex carbohydrates, including polysaccharides, can be broken down into glucose through biochemical modification; however, humans do not produce the enzyme cellulase and lack the ability to derive glucose from the polysaccharide cellulose. In humans, these molecules provide the fiber required for moving waste through the large intestine and a healthy colon. The intestinal flora in the human gut are able to extract some nutrition from these plant fibers. The excess sugars in the body are converted into glycogen and stored in the liver and muscles for later use. Glycogen stores are used to fuel prolonged exertions, such as long-distance running, and to provide energy during food shortage. Excess glycogen can be converted to fats, which are stored in the lower layer of the skin of mammals for insulation and energy storage. Excess digestible carbohydrates are stored by mammals in order to survive famine and aid in mobility.

Another important requirement is that of nitrogen. Protein catabolism provides a source of organic nitrogen. Amino acids are the building blocks of proteins and protein breakdown provides amino acids that are used for cellular function. The carbon and nitrogen derived from these become the building block for nucleotides, nucleic acids, proteins, cells, and tissues. Excess nitrogen must be excreted as it is toxic. Fats add flavor to food and promote a sense of satiety or fullness. Fatty foods are also significant sources of energy because one gram of fat contains nine calories. Fats are required in the diet to aid the absorption of fat-soluble vitamins and the production of fat-soluble hormones.

Essential Nutrients

While the animal body can synthesize many of the molecules required for function from the organic precursors, there are some nutrients that need to be consumed from food. These nutrients are termed essential nutrients, meaning they must be eaten, and the body cannot produce them.

The omega-3 alpha-linolenic acid and the omega-6 linoleic acid are essential fatty acids needed to make some membrane phospholipids. Vitamins are another class of essential organic molecules that are required in small quantities for many enzymes to function and, for this reason, are considered to be co-enzymes. Absence or low levels of vitamins can have a dramatic effect on health, as outlined in the tables below. Both fat-soluble and water-soluble vitamins must be obtained from food. Minerals, listed in the table below, are inorganic essential nutrients that must be obtained from food. Among their many functions, minerals help in structure and regulation and are considered co-factors. Certain amino acids also must be procured from food and cannot be synthesized by the body. These amino acids are the “essential” amino acids. The human body can synthesize only 11 of the 20 required amino acids; the rest must be obtained from food. The essential amino acids are listed in the table below.

Table 46.8.1.1: Water-soluble Essential Vitamins

Vitamin	Function	Deficiencies Can Lead To	Sources
Vitamin B_1 (Thiamine)	Needed by the body to process lipids, proteins, and carbohydrates Coenzyme removes CO_2 from organic compounds	Muscle weakness, Beriberi: reduced heart function, CNS problems	Milk, meat, dried beans, whole grains
Vitamin B_2 (Riboflavin)	Takes an active role in metabolism, aiding in the conversion of food to energy (FAD and FMN)	Cracks or sores on the outer surface of the lips (cheliosis); inflammation and redness of the tongue; moist, scaly skin inflammation (seborrheic dermatitis)	Meat, eggs, enriched grains, vegetables
Vitamin B_3 (Niacin)	Used by the body to release energy from carbohydrates and to process alcohol; required for the synthesis of sex hormones; component of coenzyme NAD^+ and $NADP^+$	Pellagra, which can result in dermatitis, diarrhea, dementia, and death	Meat, eggs, grains, nuts, potatoes
Vitamin B_5 (Pantothenic acid)	Assists in producing energy from foods (lipids, in particular); component of coenzyme A	Fatigue, poor coordination, retarded growth, numbness, tingling of hands and feet	Meat, whole grains, milk, fruits, vegetables
Vitamin B_6 (Pyridoxine)	The principal vitamin for processing amino acids and lipids; also helps convert nutrients into energy	Irritability, depression, confusion, mouth sores or ulcers, anemia, muscular twitching	Meat, dairy products, whole grains, orange juice
Vitamin B_7 (Biotin)	Used in energy and amino acid metabolism, fat synthesis, and fat breakdown; helps the body use blood sugar	Hair loss, dermatitis, depression, numbness and tingling in the extremities; neuromuscular disorders	Meat, eggs, legumes and other vegetables
Vitamin B_9 (Folic acid)	Assists the normal development of cells, especially during fetal development; helps metabolize nucleic and amino acids	Deficiency during pregnancy is associated with birth defects, such as neural tube defects and anemia	Leafy green vegetables, whole wheat, fruits, nuts, legumes
Vitamin B_{12} (Cobalamin)	Maintains healthy nervous system and assists with blood cell formation; coenzyme in nucleic acid metabolism	Anemia, neurological disorders, numbness, loss of balance	Meat, eggs, animal products
Vitamin C (Ascorbic acid)	Helps maintain connective tissue: bone, cartilage, and dentin; boosts the immune system	Scurvy, which results in bleeding, hair and tooth loss; joint pain and swelling; delayed wound healing	Citrus fruits, broccoli, tomatoes, red sweet bell peppers

Table 46.8.1.2: Fat-soluble Essential Vitamins

Vitamin	Function	Deficiencies Can Lead To	Sources
Vitamin A (Retinol)	Critical to the development of bones, teeth, and skin; helps maintain eyesight, enhances the immune system, fetal development, gene expression	Night-blindness, skin disorders, impaired immunity	Dark green leafy vegetables, yellow-orange vegetables fruits, milk, butter
Vitamin D	Critical for calcium absorption for bone development and strength; maintains a stable nervous system; maintains a normal and strong heartbeat; helps in blood clotting	Rickets, osteomalacia, immunity	Cod liver oil, milk, egg yolk
Vitamin E (Tocopherol)	Lessens oxidative damage of cells,and prevents lung damage from pollutants; vital to the immune system	Deficiency is rare; anemia, nervous system degeneration	Wheat germ oil, unrefined vegetable oils, nuts, seeds, grains
Vitamin K (Phylloquinone)	Essential to blood clotting	Bleeding and easy bruising	Leafy green vegetables, tea



Figure 46.8.1.2: A healthy diet should include a variety of foods to ensure that needs for essential nutrients are met. (credit: Keith Weller, USDA ARS)

Table 46.8.1.3: Minerals and Their Function in the Human Body

Mineral	Function	Deficiencies Can Lead To	Sources
*Calcium	Needed for muscle and neuron function; heart health; builds bone and supports synthesis and function of blood cells; nerve function	Osteoporosis, rickets, muscle spasms, impaired growth	Milk, yogurt, fish, green leafy vegetables, legumes
*Chlorine	Needed for production of hydrochloric acid (HCl) in the stomach and nerve function; osmotic balance	Muscle cramps, mood disturbances, reduced appetite	Table salt
Copper (trace amounts)	Required component of many redox enzymes, including cytochrome c oxidase; cofactor for hemoglobin synthesis	Copper deficiency is rare	Liver, oysters, cocoa, chocolate, sesame, nuts
Iodine	Required for the synthesis of thyroid hormones	Goiter	Seafood, iodized salt, dairy products
Iron	Required for many proteins and enzymes, notably hemoglobin, to prevent anemia	Anemia, which causes poor concentration, fatigue, and poor immune function	Red meat, leafy green vegetables, fish (tuna, salmon), eggs, dried fruits, beans, whole grains
*Magnesium	Required co-factor for ATP formation; bone formation; normal membrane functions; muscle function	Mood disturbances, muscle spasms	Whole grains, leafy green vegetables
Manganese (trace amounts)	A cofactor in enzyme functions; trace amounts are required	Manganese deficiency is rare	Common in most foods
Molybdenum (trace amounts)	Acts as a cofactor for three essential enzymes in humans: sulfite oxidase, xanthine oxidase, and aldehyde oxidase	Molybdenum deficiency is rare	
*Phosphorus	A component of bones and teeth; helps regulate acid-base balance; nucleotide synthesis	Weakness, bone abnormalities, calcium loss	Milk, hard cheese, whole grains, meats
*Potassium	Vital for muscles, heart, and nerve function	Cardiac rhythm disturbance, muscle weakness	Legumes, potato skin, tomatoes, bananas
Selenium (trace amounts)	A cofactor essential to activity of antioxidant enzymes like glutathione peroxidase; trace amounts are required	Selenium deficiency is rare	Common in most foods
*Sodium	Systemic electrolyte required for many functions; acid-base balance; water balance; nerve function	Muscle cramps, fatigue, reduced appetite	Table salt
Zinc (trace amounts)	Required for several enzymes such as carboxypeptidase, liver	Anemia, poor wound healing, can lead to short stature	Common in most foods

Mineral	Function	Deficiencies Can Lead To	Sources
	alcohol dehydrogenase, and carbonic anhydrase		
*Greater than 200mg/day required			

Table 46.8.1.4: Essential Amino Acids

Amino acids that must be consumed	Amino acids anabolized by the body
isoleucine	alanine
leucine	selenocysteine
lysine	aspartate
methionine	cysteine
phenylalanine	glutamate
tryptophan	glycine
valine	proline
histidine*	serine
threonine	tyrosine
arginine*	asparagine
*The human body can synthesize histidine and arginine, but not in the quantities required, especially for growing children.	

Food Energy and ATP

Animals need food to obtain energy and maintain homeostasis. Homeostasis is the ability of a system to maintain a stable internal environment even in the face of external changes to the environment. For example, the normal body temperature of humans is 37°C (98.6°F). Humans maintain this temperature even when the external temperature is hot or cold. It takes energy to maintain this body temperature, and animals obtain this energy from food.

The primary source of energy for animals is carbohydrates, mainly glucose. Glucose is called the body's fuel. The digestible carbohydrates in an animal's diet are converted to glucose molecules through a series of catabolic chemical reactions.

Adenosine triphosphate, or ATP, is the primary energy currency in cells; ATP stores energy in phosphate ester bonds. ATP releases energy when the phosphodiester bonds are broken and ATP is converted to ADP and a phosphate group. ATP is produced by the oxidative reactions in the cytoplasm and mitochondrion of the cell, where carbohydrates, proteins, and fats undergo a series of metabolic reactions collectively called cellular respiration. For example, glycolysis is a series of reactions in which glucose is converted to pyruvic acid and some of its chemical potential energy is transferred to NADH and ATP.

ATP is required for all cellular functions. It is used to build the organic molecules that are required for cells and tissues; it provides energy for muscle contraction and for the transmission of electrical signals in the nervous system. When the amount of ATP is available in excess of the body's requirements, the liver uses the excess ATP and excess glucose to produce molecules called glycogen. Glycogen is a polymeric form of glucose and is stored in the liver and skeletal muscle cells. When blood sugar drops, the liver releases glucose from stores of glycogen. Skeletal muscle converts glycogen to glucose during intense exercise. The process of converting glucose and excess ATP to glycogen and the storage of excess energy is an evolutionarily important step in helping animals deal with mobility, food shortages, and famine.

Everyday Connection: Obesity

Obesity is a major health concern in the United States, and there is a growing focus on reducing obesity and the diseases it may lead to, such as type-2 diabetes, cancers of the colon and breast, and cardiovascular disease. How does the food consumed contribute to obesity?

Fatty foods are calorie-dense, meaning that they have more calories per unit mass than carbohydrates or proteins. One gram of carbohydrates has four calories, one gram of protein has four calories, and one gram of fat has nine calories. Animals tend to seek lipid-rich food for their higher energy content.

The signals of hunger (“time to eat”) and satiety (“time to stop eating”) are controlled in the hypothalamus region of the brain. Foods that are rich in fatty acids tend to promote satiety more than foods that are rich only in carbohydrates.

Excess carbohydrate and ATP are used by the liver to synthesize glycogen. The pyruvate produced during glycolysis is used to synthesize fatty acids. When there is more glucose in the body than required, the resulting excess pyruvate is converted into molecules that eventually result in the synthesis of fatty acids within the body. These fatty acids are stored in adipose cells—the fat cells in the mammalian body whose primary role is to store fat for later use.

It is important to note that some animals benefit from obesity. Polar bears and seals need body fat for insulation and to keep them from losing body heat during Arctic winters. When food is scarce, stored body fat provides energy for maintaining homeostasis. Fats prevent famine in mammals, allowing them to access energy when food is not available on a daily basis; fats are stored when a large kill is made or lots of food is available.

Summary

Animal diet should be balanced and meet the needs of the body. Carbohydrates, proteins, and fats are the primary components of food. Some essential nutrients are required for cellular function but cannot be produced by the animal body. These include vitamins, minerals, some fatty acids, and some amino acids. Food intake in more than necessary amounts is stored as glycogen in the liver and muscle cells, and in fat cells. Excess adipose storage can lead to obesity and serious health problems. ATP is the energy currency of the cell and is obtained from the metabolic pathways. Excess carbohydrates and energy are stored as glycogen in the body.

Glossary

essential nutrient
: nutrient that cannot be synthesized by the body; it must be obtained from food

mineral
: inorganic, elemental molecule that carries out important roles in the body

vitamin
: organic substance necessary in small amounts to sustain life

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CHAPTER OVERVIEW

47: The Respiratory System

47.1: Gas Exchange Across Respiratory Surfaces

47.2: Gills, Cutaneous Respirate, and Tracheal Systems

47.2.1: Amphibians

47.2.2: Systems of Gas Exchange

47.3: Lungs

47.3.1: Breathing

47.4: Structures, Mechanisms, and Control of Ventilation in Mammals

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47.1: Gas Exchange Across Respiratory Surfaces

Learning Objectives

By the end of this section, you will be able to do the following:

- Name and describe lung volumes and capacities
- Understand how gas pressure influences how gases move into and out of the body

The structure of the lung maximizes its surface area to increase gas diffusion. Because of the enormous number of alveoli (approximately 300 million in each human lung), the surface area of the lung is very large (75 m^2). Having such a large surface area increases the amount of gas that can diffuse into and out of the lungs.

Basic Principles of Gas Exchange

Gas exchange during respiration occurs primarily through diffusion. Diffusion is a process in which transport is driven by a concentration gradient. Gas molecules move from a region of high concentration to a region of low concentration. Blood that is low in oxygen concentration and high in carbon dioxide concentration undergoes gas exchange with air in the lungs. The air in the lungs has a higher concentration of oxygen than that of oxygen-depleted blood and a lower concentration of carbon dioxide. This concentration gradient allows for gas exchange during respiration.

Partial pressure is a measure of the concentration of the individual components in a mixture of gases. The total pressure exerted by the mixture is the sum of the partial pressures of the components in the mixture. The rate of diffusion of a gas is proportional to its partial pressure within the total gas mixture. This concept is discussed further in detail below.

Lung Volumes and Capacities

Different animals have different lung capacities based on their activities. Cheetahs have evolved a much higher lung capacity than humans; it helps provide oxygen to all the muscles in the body and allows them to run very fast. Elephants also have a high lung capacity. In this case, it is not because they run fast but because they have a large body and must be able to take up oxygen in accordance with their body size.

Human lung size is determined by genetics, sex, and height. At maximal capacity, an average lung can hold almost six liters of air, but lungs do not usually operate at maximal capacity. Air in the lungs is measured in terms of lung volumes and lung capacities (Figure 39.12 and Table 39.1). Volume measures the amount of air for one function (such as inhalation or exhalation). Capacity is any two or more volumes (for example, how much can be inhaled from the end of a maximal exhalation).

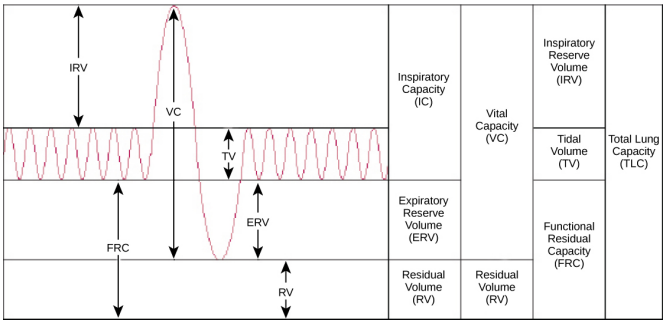


Figure 39.12 Human lung volumes and capacities are shown. The total lung capacity of the adult male is six liters. Tidal volume is the volume of air inhaled in a single, normal breath. Inspiratory capacity is the amount of air taken in during a deep breath, and residual volume is the amount of air left in the lungs after forceful respiration.
Lung Volumes and Capacities (Avg Adult Male)

Volume/Capacity	Definition	Volume (liters)	Equations
Tidal volume (TV)	Amount of air inhaled during a normal breath	0.5	-
Expiratory reserve volume (ERV)	Amount of air that can be exhaled after a normal exhalation	1.2	-
Inspiratory reserve volume (IRV)	Amount of air that can be further inhaled after a normal inhalation	3.1	-
Residual volume (RV)	Air left in the lungs after a forced exhalation	1.2	-
Vital capacity (VC)	Maximum amount of air that can be moved in or out of the lungs in a single respiratory cycle	4.8	ERV+TV+IRV
Inspiratory capacity (IC)	Volume of air that can be inhaled in addition to a normal exhalation	3.6	TV+IRV
Functional residual capacity (FRC)	Volume of air remaining after a normal exhalation	2.4	ERV+RV
Total lung capacity (TLC)	Total volume of air in the lungs after a maximal inspiration	6.0	RV+ERV+TV+IRV
Forced expiratory volume (FEV1)	How much air can be forced out of the lungs over a specific time period, usually one second	~4.1 to 5.5	-

Table 39.1

The volume in the lung can be divided into four units: tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume. Tidal volume (TV) measures the amount of air that is inspired and expired during a normal breath. On average, this volume is around one-half liter, which is a little less than the capacity of a 20-ounce drink bottle. The expiratory reserve volume (ERV) is the additional amount of air that can be exhaled after a normal exhalation. It is the reserve amount that can be exhaled beyond what is normal. Conversely, the inspiratory reserve volume (IRV) is the additional amount of air that can be inhaled after a normal inhalation. The residual volume (RV) is the amount of air that is left after expiratory reserve volume is exhaled. The lungs are never completely empty: There is always some air left in the lungs after a maximal exhalation. If this residual volume did not exist and the lungs emptied completely, the lung tissues would stick together and the energy necessary to reinflate the lung could be too great to overcome. Therefore, there is always some air remaining in the lungs. Residual volume is also important for preventing large fluctuations in respiratory gases (O_2 and CO_2). The residual volume is the only lung volume that cannot be measured directly because it is impossible to completely empty the lung of air. This volume can only be calculated rather than measured.

Capacities are measurements of two or more volumes. The vital capacity (VC) measures the maximum amount of air that can be inhaled or exhaled during a respiratory cycle. It is the sum of the expiratory reserve volume, tidal volume, and inspiratory reserve volume. The inspiratory capacity (IC) is the amount of air that can be inhaled after the end of a normal expiration. It is, therefore, the sum of the tidal volume and inspiratory reserve volume. The functional residual capacity (FRC) includes the expiratory reserve volume and the residual volume. The FRC measures the amount of additional air that can be exhaled after a normal exhalation.

Lastly, the total lung capacity (TLC) is a measurement of the total amount of air that the lung can hold. It is the sum of the residual volume, expiratory reserve volume, tidal volume, and inspiratory reserve volume.

Lung volumes are measured by a technique called spirometry. An important measurement taken during spirometry is the forced expiratory volume (FEV), which measures how much air can be forced out of the lung over a specific period, usually one second (FEV1). In addition, the forced vital capacity (FVC), which is the total amount of air that can be forcibly exhaled, is measured. The ratio of these values (FEV1/FVC ratio) is used to diagnose lung diseases including asthma, emphysema, and fibrosis. If the FEV1/FVC ratio is high, the lungs are not compliant (meaning they are stiff and unable to bend properly), and the patient most likely has lung fibrosis. Patients exhale most of the lung volume very quickly. Conversely, when the FEV1/FVC ratio is low, there is resistance in the lung that is characteristic of asthma. In this instance, it is hard for the patient to get the air out of their lungs, and it takes a long time to reach the maximal exhalation volume. In either case, breathing is difficult and complications arise.

Career Connection

Career Connection

Respiratory Therapist Respiratory therapists or respiratory practitioners evaluate and treat patients with lung and cardiovascular diseases. They work as part of a medical team to develop treatment plans for patients. Respiratory therapists may treat premature babies with underdeveloped lungs, patients with chronic conditions such as asthma, or older patients suffering from lung disease such as emphysema and chronic obstructive pulmonary disease (COPD). They may operate advanced equipment such as compressed gas delivery systems, ventilators, blood gas analyzers, and resuscitators. Specialized programs to become a respiratory therapist generally lead to a bachelor's degree with a respiratory therapist specialty. Because of a growing aging population, career opportunities as a respiratory therapist are expected to remain strong.

Gas Pressure and Respiration

The respiratory process can be better understood by examining the properties of gases. Gases move freely, but gas particles are constantly hitting the walls of their vessel, thereby producing gas pressure.

Air is a mixture of gases, primarily nitrogen (N_2; 78.6 percent), oxygen (O_2; 20.9 percent), water vapor (H_2O; 0.5 percent), and carbon dioxide (CO_2; 0.04 percent). Each gas component of that mixture exerts a pressure. The pressure for an individual gas in the mixture is the partial pressure of that gas. Approximately 21 percent of atmospheric gas is oxygen. Carbon dioxide, however, is found in relatively small amounts, 0.04 percent. The partial pressure for oxygen is much greater than that of carbon dioxide. The partial pressure of any gas can be calculated by:

$$\mathbf{P = (P_{atm}) \times (\text{percent content in mixture}).}$$

P_{atm}, the atmospheric pressure, is the sum of all of the partial pressures of the atmospheric gases added together,

$$\mathbf{P_{atm} = P_{N_2} + P_{O_2} + P_{H_2O} + P_{CO_2} = 760\ mm\ Hg}$$

× (percent content in mixture).

The pressure of the atmosphere at sea level is 760 mm Hg. Therefore, the partial pressure of oxygen is:

$$\mathbf{P_{O_2} = (760\ mm\ Hg)\ (0.21) = 160\ mm\ Hg}$$

and for carbon dioxide:

$$\mathbf{P_{CO_2} = (760\ mm\ Hg)\ (0.0004) = 0.3\ mm\ Hg.}$$

At high altitudes, P_{atm} decreases but concentration does not change; the partial pressure decrease is due to the reduction in P_{atm}.

When the air mixture reaches the lung, it has been humidified. The pressure of the water vapor in the lung does not change the pressure of the air, but it must be included in the partial pressure equation. For this calculation, the water pressure (47 mm Hg) is subtracted from the atmospheric pressure:

$$\mathbf{760\ mm\ Hg - 47\ mm\ Hg = 713\ mm\ Hg}$$

and the partial pressure of oxygen is:

$$(760 \text{ mm Hg} - 47 \text{ mm Hg}) \times 0.21 = 150 \text{ mm Hg}.$$

These pressures determine the gas exchange, or the flow of gas, in the system. Oxygen and carbon dioxide will flow according to their pressure gradient from high to low. Therefore, understanding the partial pressure of each gas will aid in understanding how gases move in the respiratory system.

Gas Exchange across the Alveoli

In the body, oxygen is used by cells of the body's tissues and carbon dioxide is produced as a waste product. The ratio of carbon dioxide production to oxygen consumption is the respiratory quotient (RQ). RQ varies between 0.7 and 1.0. If just glucose were used to fuel the body, the RQ would equal one. One mole of carbon dioxide would be produced for every mole of oxygen consumed. Glucose, however, is not the only fuel for the body. Protein and fat are also used as fuels for the body. Because of this, less carbon dioxide is produced than oxygen is consumed and the RQ is, on average, about 0.7 for fat and about 0.8 for protein.

The RQ is used to calculate the partial pressure of oxygen in the alveolar spaces within the lung, the alveolar $\mathbf{P_{O_2}}$. Above, the partial pressure of oxygen in the lungs was calculated to be 150 mm Hg. However, lungs never fully deflate with an exhalation; therefore, the inspired air mixes with this residual air and lowers the partial pressure of oxygen within the alveoli. This means that there is a lower concentration of oxygen in the lungs than is found in the air outside the body. Knowing the RQ, the partial pressure of oxygen in the alveoli can be calculated:

$$\text{alveolar } P_{CO_2} = \text{inspired } P_{O_2} - \left(\frac{\text{alveolar } P_{O_2}}{RQ}\right)$$

With an RQ of 0.8 and a $\mathbf{P_{CO_2}}$ in the alveoli of 40 mm Hg, the alveolar $\mathbf{P_{O_2}}$ is equal to:

$$\text{alveolar } P_{O_2} = 150 \text{ mm Hg} - \left(\frac{40 \text{ mm Hg}}{0.8}\right) = 100 \text{ mm Hg}.$$

Notice that this pressure is less than the external air. Therefore, the oxygen will flow from the inspired air in the lung ($\mathbf{P_{O_2}}$ = 150 mm Hg) into the bloodstream ($\mathbf{P_{O_2}}$ = 100 mm Hg) (Figure 39.13).

In the lungs, oxygen diffuses out of the alveoli and into the capillaries surrounding the alveoli. Oxygen (about 98 percent) binds reversibly to the respiratory pigment hemoglobin found in red blood cells (RBCs). RBCs carry oxygen to the tissues where oxygen dissociates from the hemoglobin and diffuses into the cells of the tissues. More specifically, alveolar $\mathbf{P_{O_2}}$ is higher in the alveoli ($\mathbf{P_{ALVO_2}}$ = 100 mm Hg) than blood $\mathbf{P_{O_2}}$ (40 mm Hg) in the capillaries. Because this pressure gradient exists, oxygen diffuses down its pressure gradient, moving out of the alveoli and entering the blood of the capillaries where O_2 binds to hemoglobin. At the same time, alveolar $\mathbf{P_{CO_2}}$ is lower $\mathbf{P_{ALVO_2}}$ = 40 mm Hg than blood $\mathbf{P_{CO_2}}$ = (45 mm Hg). CO_2 diffuses down its pressure gradient, moving out of the capillaries and entering the alveoli.

Oxygen and carbon dioxide move independently of each other; they diffuse down their own pressure gradients. As blood leaves the lungs through the pulmonary veins, the venous $\mathbf{P_{O_2}}$= 100 mm Hg, whereas the venous $\mathbf{P_{CO_2}}$ = 40 mm Hg. As blood enters the systemic capillaries, the blood will lose oxygen and gain carbon dioxide because of the pressure difference of the tissues and blood. In systemic capillaries, $\mathbf{P_{O_2}}$= 100 mm Hg, but in the tissue cells, $\mathbf{P_{O_2}}$= 40 mm Hg. This pressure gradient drives the diffusion of oxygen out of the capillaries and into the tissue cells. At the same time, blood $\mathbf{P_{CO_2}}$= 40 mm Hg and systemic tissue $\mathbf{P_{CO_2}}$= 45 mm Hg. The pressure gradient drives CO_2 out of tissue cells and into the capillaries. The blood returning to the lungs through the pulmonary arteries has a venous $\mathbf{P_{O_2}}$= 40 mm Hg and a $\mathbf{P_{CO_2}}$= 45 mm Hg. The blood enters the lung capillaries where the process of exchanging gases between the capillaries and alveoli begins again (Figure 39.13).

Visual Connection

Visual Connection

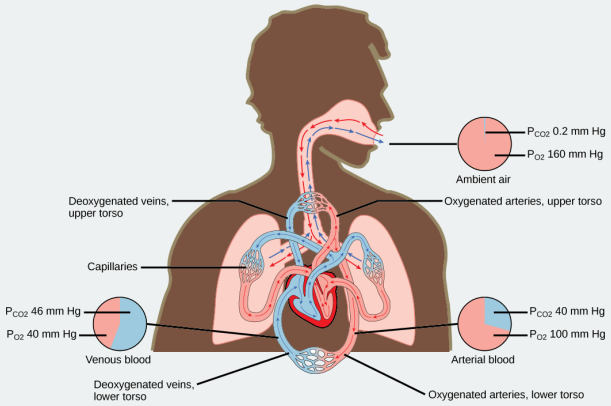


Figure 39.13 The partial pressures of oxygen and carbon dioxide change as blood moves through the body.

Which of the following statements is false?

1. In the tissues, $\mathbf{P_{O_2}}$ drops as blood passes from the arteries to the veins, while $\mathbf{P_{CO_2}}$ increases.
2. Blood travels from the lungs to the heart to body tissues, then back to the heart, then the lungs.
3. Blood travels from the lungs to the heart to body tissues, then back to the lungs, then the heart.
4. $\mathbf{P_{O_2}}$ is higher in air than in the lungs.

In short, the change in partial pressure from the alveoli to the capillaries drives the oxygen into the tissues and the carbon dioxide into the blood from the tissues. The blood is then transported to the lungs where differences in pressure in the alveoli result in the movement of carbon dioxide out of the blood into the lungs, and oxygen into the blood.

Link to Learning

Link to Learning

Watch this video to learn how to carry out spirometry.

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47.2: Gills, Cutaneous Respirate, and Tracheal Systems

Skills to Develop

- Describe the difference between jawless and jawed fishes
- Discuss the distinguishing features of sharks and rays compared to other modern fishes

Modern fishes include an estimated 31,000 species. Fishes were the earliest vertebrates, with jawless species being the earliest and jawed species evolving later. They are active feeders, rather than sessile, suspension feeders. Jawless fishes—the hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, distinguishing them from the invertebrate chordates.

Jawless Fishes

Jawless fishes are craniates that represent an ancient vertebrate lineage that arose over one half-billion years ago. In the past, the hagfishes and lampreys were classified together as agnathans. Today, hagfishes and lampreys are recognized as separate clades, primarily because lampreys are true vertebrates, whereas hagfishes are not. A defining feature is the lack of paired lateral appendages (fins). Some of the earliest jawless fishes were the ostracoderms (which translates to “shell-skin”). Ostracoderms were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

Myxini: Hagfishes

The clade Myxini includes at least 20 species of hagfishes. Hagfishes are eel-like scavengers that live on the ocean floor and feed on dead invertebrates, other fishes, and marine mammals (Figure **47.2.1**). Hagfishes are entirely marine and are found in oceans around the world, except for the polar regions. A unique feature of these animals is the slime glands beneath the skin that release mucus through surface pores. This mucus allows the hagfish to escape from the grip of predators. Hagfish can also twist their bodies in a knot to feed and sometimes eat carcasses from the inside out.

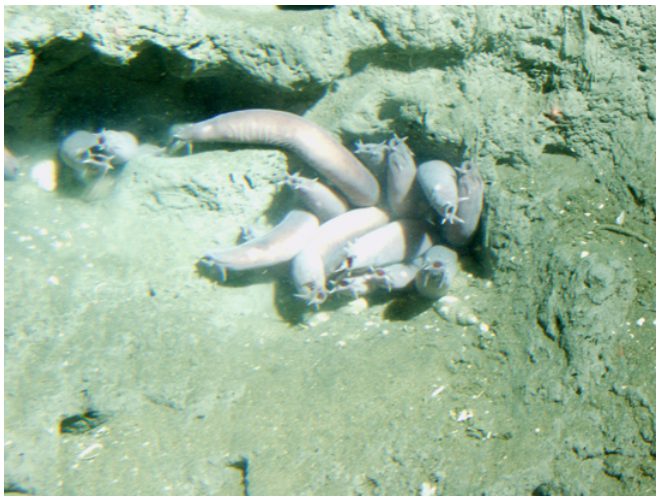


Figure **47.2.1**: Pacific hagfish are scavengers that live on the ocean floor. (credit: Linda Snook, NOAA/CBNMS)

The skeleton of a hagfish is composed of cartilage, which includes a cartilaginous notochord that runs the length of the body. This notochord provides support to the hagfish’s body. Hagfishes do not replace the notochord with a vertebral column during development, as do true vertebrates.

Petromyzontidae: Lampreys

The clade Petromyzontidae includes approximately 35–40 or more species of lampreys. Lampreys are similar to hagfishes in size and shape; however, lampreys possess some vertebral elements. Lampreys lack paired appendages and bone, as do the hagfishes. As adults, lampreys are characterized by a toothed, funnel-like sucking mouth. Many species have a parasitic stage of their life cycle during which they are ectoparasites of fishes (Figure **47.2.2**).



Figure **47.2.2**: These parasitic sea lampreys attach to their lake trout host by suction and use their rough tongues to rasp away flesh in order to feed on the trout's blood. (credit: USGS)

Lampreys live primarily in coastal and fresh waters, and have a worldwide distribution, except for in the tropics and polar regions. Some species are marine, but all species spawn in fresh water. Eggs are fertilized externally, and the larvae distinctly differ from the adult form, spending 3 to 15 years as suspension feeders. Once they attain sexual maturity, the adults reproduce and die within days.

Lampreys possess a notochord as adults; however, this notochord is surrounded by a cartilaginous structure called an arcualia, which may resemble an evolutionarily early form of the vertebral column.

Gnathostomes: Jawed Fishes

Gnathostomes or "jaw-mouths" are vertebrates that possess jaws. One of the most significant developments in early vertebrate evolution was the development of the jaw, which is a hinged structure attached to the cranium that allows an animal to grasp and tear its food. The evolution of jaws allowed early gnathostomes to exploit food resources that were unavailable to jawless fishes.

Early gnathostomes also possessed two sets of paired fins, allowing the fishes to maneuver accurately. Pectoral fins are typically located on the anterior body, and pelvic fins on the posterior. Evolution of the jaw and paired fins permitted gnathostomes to expand from the sedentary suspension feeding of jawless fishes to become mobile predators. The ability of gnathostomes to exploit new nutrient sources likely is one reason that they replaced most jawless fishes during the Devonian period. Two early groups of gnathostomes were the acanthodians and placoderms (Figure **47.2.3**), which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes.



Figure **47.2.3**: *Dunkleosteous* was an enormous placoderm from the Devonian period, 380–360 million years ago. It measured up to 10 meters in length and weighed up to 3.6 tons. (credit: Nobu Tamura)

Chondrichthyes: Cartilaginous Fishes

The clade Chondrichthyes is diverse, consisting of sharks (Figure **47.2.4**), rays, and skates, together with sawfishes and a few dozen species of fishes called *chimaeras*, or "ghost" sharks." Chondrichthyes are jawed fishes that possess paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the early or middle Devonian. They are thought to be descended from the placoderms, which had skeletons made of bone; thus, the cartilaginous skeleton of Chondrichthyes is a later development. Parts of shark skeleton are strengthened by granules of calcium carbonate, but this is not the same as bone.

Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for a part or all of their lives. Most sharks are carnivores that feed on live prey, either swallowing it whole or using their jaws and teeth to tear it into smaller pieces. Shark teeth likely evolved from the jagged scales that cover their skin, called placoid scales. Some species of sharks and rays are suspension feeders that feed on plankton.

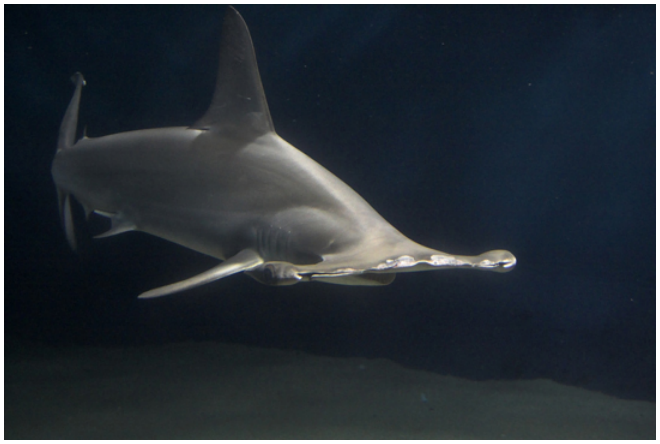


Figure **47.2.4**: Hammerhead sharks tend to school during the day and hunt prey at night. (credit: Masashi Sugawara)

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and electroreception, with the latter perhaps the most sensitive of any animal. Organs called ampullae of Lorenzini allow sharks to detect the electromagnetic fields that are produced by all living things, including their prey. Electroreception has only been observed in aquatic or amphibious animals. Sharks, together with most fishes and aquatic and larval amphibians, also have a sense organ called the lateral line, which is used to detect movement and vibration in the surrounding water, and is often considered homologous to "hearing" in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of a fish's body.

Sharks reproduce sexually, and eggs are fertilized internally. Most species are ovoviviparous: The fertilized egg is retained in the oviduct of the mother's body and the embryo is nourished by the egg yolk. The eggs hatch in the uterus, and young are born alive and fully functional. Some species of sharks are oviparous: They lay eggs that hatch outside of the mother's body. Embryos are protected by a shark egg case or "mermaid's purse" (Figure **47.2.5**) that has the consistency of leather. The shark egg case has tentacles that snag in seaweed and give the newborn shark cover. A few species of sharks are viviparous: The young develop within the mother's body and she gives live birth.

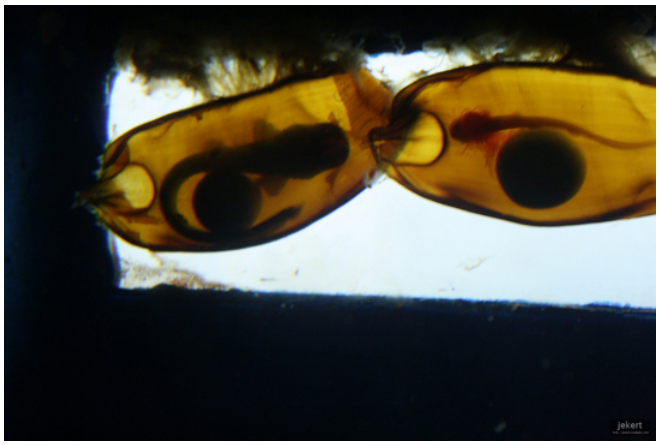


Figure **47.2.5**: Shark embryos are clearly visible through these transparent egg cases. The round structure is the yolk that nourishes the growing embryo. (credit: Jek Bacarisas)

Rays and skates comprise more than 500 species and are closely related to sharks. They can be distinguished from sharks by their flattened bodies, pectoral fins that are enlarged and fused to the head, and gill slits on their ventral surface (Figure **47.2.6**). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.



Figure **47.2.6**: This stingray blends into the sandy bottom of the ocean floor. (credit: "Sailn1"/Flickr)

Osteichthyes: Bony Fishes

Members of the clade Osteichthyes, also called bony fishes, are characterized by a bony skeleton. The vast majority of present-day fishes belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fishes have an ossified skeleton with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. This characteristic has only reversed in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered by overlapping scales, and glands in the skin secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fishes have a lateral line system that detects vibrations in water.

All bony fishes use gills to breathe. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Many bony fishes also have a swim bladder, a gas-filled organ that helps to control the buoyancy of the fish. Bony fishes are further divided into two extant clades: Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes).

Actinopterygii, the ray-finned fishes, include many familiar fishes—tuna, bass, trout, and salmon (Figure 47.2.7), among others. Ray-finned fishes are named for their fins that are webs of skin supported by bony spines called rays. In contrast, the fins of Sarcopterygii are fleshy and lobed, supported by bone (Figure 47.2.7). Living members of this clade include the less-familiar lungfishes and coelacanths.

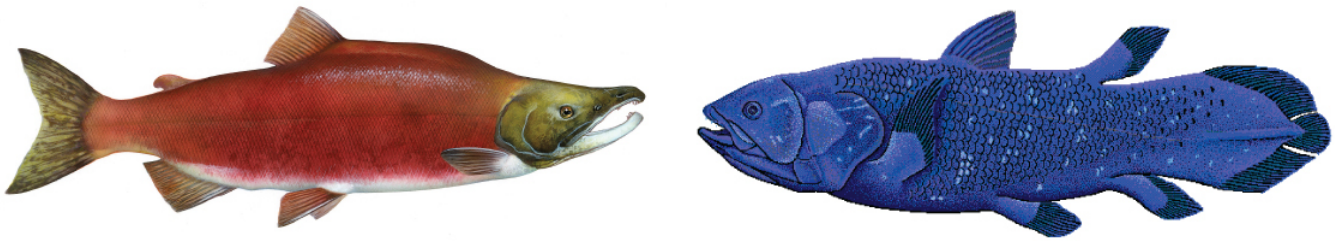


Figure 47.2.7: The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish, was thought to have gone extinct in the Late Cretaceous period, 100 million years ago, until one was discovered in 1938 near the Comoros Islands between Africa and Madagascar. (credit a: modification of work by Timothy Knepp, USFWS; credit b: modification of work by Robbie Cada)

Summary

The earliest vertebrates that diverged from the invertebrate chordates were the jawless fishes. Fishes with jaws (gnathostomes) evolved later. Jaws allowed early gnathostomes to exploit new food sources. Agnathans include the hagfishes and lampreys. Hagfishes are eel-like scavengers that feed on dead invertebrates and other fishes. Lampreys are characterized by a toothed, funnel-like sucking mouth, and most species are parasitic on other fishes. Gnathostomes include the cartilaginous fishes and the bony fishes, as well as all other tetrapods. Cartilaginous fishes include sharks, rays, skates, and ghost sharks. Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for part or all of their lives. The vast majority of present-day fishes belong to the clade Osteichthyes, which consists of approximately 30,000 species. Bony fishes can be divided into two clades: Actinopterygii (ray-finned fishes, virtually all extant species) and Sarcopterygii (lobe-finned fishes, comprising fewer than 10 extant species but which are the ancestors of tetrapods).

Glossary

Actinopterygii
ray-finned fishes

ampulla of Lorenzini
sensory organ that allows sharks to detect electromagnetic fields produced by living things

Chondrichthyes
jawed fish with paired fins and a skeleton made of cartilage

gnathostome
jawed fish

hagfish
eel-like jawless fish that live on the ocean floor and are scavengers

lamprey
jawless fish characterized by a toothed, funnel-like, sucking mouth

lateral line
sense organ that runs the length of a fish's body; used to detect vibration in the water

Myxini

hagfishes

Osteichthyes
bony fish

ostracoderm
one of the earliest jawless fish covered in bone

Petromyzontidae
clade of lampreys

Sarcopterygii
lobe-finned fish

swim bladder
in fishes, a gas filled organ that helps to control the buoyancy of the fish

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47.2.1: Amphibians

Skills to Develop

- Describe the important difference between the life cycle of amphibians and the life cycles of other vertebrates
- Distinguish between the characteristics of Urodela, Anura, and Apoda
- Describe the evolutionary history of amphibians

Amphibians are vertebrate tetrapods. Amphibia includes frogs, salamanders, and caecilians. The term amphibian loosely translates from the Greek as “dual life,” which is a reference to the metamorphosis that many frogs and salamanders undergo and their mixture of aquatic and terrestrial environments in their life cycle. Amphibians evolved during the Devonian period and were the earliest terrestrial tetrapods.

Link to Learning

Watch this series of Animal Planet videos on tetrapod evolution:

1: The evolution from fish to earliest tetrapod

2: Fish to Earliest Tetrapod

3: The discovery of coelacanth and *Acanthostega* fossils

4: The number of fingers on “legs”

Characteristics of Amphibians

As tetrapods, most amphibians are characterized by four well-developed limbs. Some species of salamanders and all caecilians are functionally limbless; their limbs are vestigial. An important characteristic of extant amphibians is a moist, permeable skin that is achieved via mucus glands that keep the skin moist; thus, exchange of oxygen and carbon dioxide with the environment can take place through it (cutaneous respiration). Additional characteristics of amphibians include pedicellate teeth—teeth in which the root and crown are calcified, separated by a zone of noncalcified tissue—and a papilla amphibiorum and papilla basilaris, structures of the inner ear that are sensitive to frequencies below and above 10,00 hertz, respectively. Amphibians also have an auricular operculum, which is an extra bone in the ear that transmits sounds to the inner ear. All extant adult amphibians are carnivorous, and some terrestrial amphibians have a sticky tongue that is used to capture prey.

Evolution of Amphibians

The fossil record provides evidence of the first tetrapods: now-extinct amphibian species dating to nearly 400 million years ago. Evolution of tetrapods from fishes represented a significant change in body plan from one suited to organisms that respired and swam in water, to organisms that breathed air and moved onto land; these changes occurred over a span of 50 million years during the Devonian period. One of the earliest known tetrapods is from the genus *Acanthostega*. *Acanthostega* was aquatic; fossils show that it had gills similar to fishes. However, it also had four limbs, with the skeletal structure of limbs found in present-day tetrapods, including amphibians. Therefore, it is thought that *Acanthostega* lived in shallow waters and was an intermediate form between lobe-finned fishes and early, fully terrestrial tetrapods. What preceded *Acanthostega*?

In 2006, researchers published news of their discovery of a fossil of a “tetrapod-like fish,” *Tiktaalik roseae*, which seems to be an intermediate form between fishes having fins and tetrapods having limbs (Figure **47.2.1.1**). *Tiktaalik* likely lived in a shallow water

environment about 375 million years ago.[1]

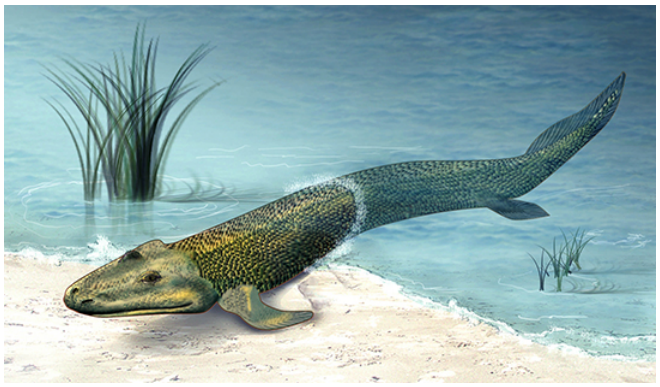


Figure **47.2.1.1**: The recent fossil discovery of *Tiktaalik roseae* suggests evidence for an animal intermediate to finned fish and legged tetrapods. (credit: Zina Deretsky, National Science Foundation)

The early tetrapods that moved onto land had access to new nutrient sources and relatively few predators. This led to the widespread distribution of tetrapods during the early Carboniferous period, a period sometimes called the "age of the amphibians."

Modern Amphibians

Amphibia comprises an estimated 6,770 extant species that inhabit tropical and temperate regions around the world. Amphibians can be divided into three clades: Urodela ("tailed-ones"), the salamanders; Anura ("tail-less ones"), the frogs; and Apoda ("legless ones"), the caecilians.

Urodela: Salamanders

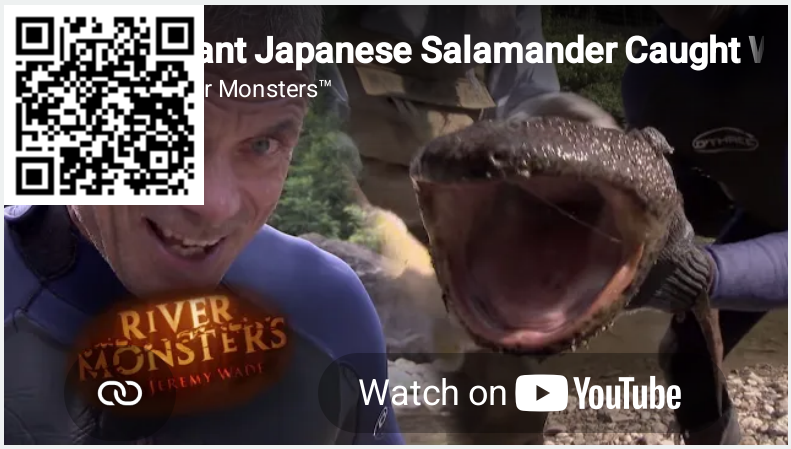
Salamanders are amphibians that belong to the order Urodela. Living salamanders (Figure **47.2.1.1**) include approximately 620 species, some of which are aquatic, other terrestrial, and some that live on land only as adults. Adult salamanders usually have a generalized tetrapod body plan with four limbs and a tail. They move by bending their bodies from side to side, called lateral undulation, in a fish-like manner while "walking" their arms and legs fore and aft. It is thought that their gait is similar to that used by early tetrapods. Respiration differs among different species. The majority of salamanders are lungless, and respiration occurs through the skin or through external gills. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs.

Unlike frogs, virtually all salamanders rely on internal fertilization of the eggs. The only male amphibians that possess copulatory structures are the caecilians, so fertilization among salamanders typically involves an elaborate and often prolonged courtship. Such a courtship allows the successful transfer of sperm from male to female via a spermatophore. Development in many of the most highly evolved salamanders, which are fully terrestrial, occurs during a prolonged egg stage, with the eggs guarded by the mother. During this time, the gilled larval stage is found only within the egg capsule, with the gills being resorbed, and metamorphosis being completed, before hatching. Hatchlings thus resemble tiny adults.



Figure **47.2.1.2**: Most salamanders have legs and a tail, but respiration varies among species. (credit: Valentina Storti)

Link to Learning



View River Monsters: Fish With Arms and Hands? to see a video about an unusually large salamander species.

Anura: Frogs

Frogs are amphibians that belong to the order Anura (Figure **47.2.1.3**). Anurans are among the most diverse groups of vertebrates, with approximately 5,965 species that occur on all of the continents except Antarctica. Anurans have a body plan that is more specialized for movement. Adult frogs use their hind limbs to jump on land. Frogs have a number of modifications that allow them to avoid predators, including skin that acts as camouflage. Many species of frogs and salamanders also release defensive chemicals from glands in the skin that are poisonous to predators.



Figure **47.2.1.3**: The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source.

Frog eggs are fertilized externally, and like other amphibians, frogs generally lay their eggs in moist environments. A moist environment is required as eggs lack a shell and thus dehydrate quickly in dry environments. Frogs demonstrate a great diversity of parental behaviors, with some species laying many eggs and exhibiting little parental care, to species that carry eggs and tadpoles on their hind legs or backs. The life cycle of frogs, as other amphibians, consists of two distinct stages: the larval stage followed by metamorphosis to an adult stage. The larval stage of a frog, the tadpole, is often a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, and lack limbs. At the end of the tadpole stage, frogs undergo metamorphosis into the adult form (Figure **47.2.1.4**). During this stage, the gills, tail, and lateral line system disappear, and four limbs develop. The jaws become larger and are suited for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop. These changes during metamorphosis allow the larvae to move onto land in the adult stage.



Figure 47.2.1.4: A juvenile frog metamorphoses into a frog. Here, the frog has started to develop limbs, but its tadpole tail is still evident.

Apoda: Caecilians

An estimated 185 species comprise caecilians, a group of amphibians that belong to the order Apoda. Although they are vertebrates, a complete lack of limbs leads to their resemblance to earthworms in appearance. They are adapted for a soil-burrowing or aquatic lifestyle, and they are nearly blind. These animals are found in the tropics of South America, Africa, and Southern Asia. They have vestigial limbs, evidence that they evolved from a legged ancestor.

Evolution Connection: The Paleozoic Era and the Evolution of Vertebrates

The climate and geography of Earth was vastly different during the Paleozoic Era, when vertebrates arose, as compared to today. The Paleozoic spanned from approximately 542 to 251 million years ago. The landmasses on Earth were very different from those of today. Laurentia and Gondwana were continents located near the equator that subsumed much of the current day landmasses in a different configuration (Figure 47.2.1.5). At this time, sea levels were very high, probably at a level that hasn't been reached since. As the Paleozoic progressed, glaciations created a cool global climate, but conditions warmed near the end of the first half of the Paleozoic. During the latter half of the Paleozoic, the landmasses began moving together, with the initial formation of a large northern block called Laurasia. This contained parts of what is now North America, along with Greenland, parts of Europe, and Siberia. Eventually, a single supercontinent, called Pangaea, was formed, starting in the latter third of the Paleozoic. Glaciations then began to affect Pangaea's climate, affecting the distribution of vertebrate life.

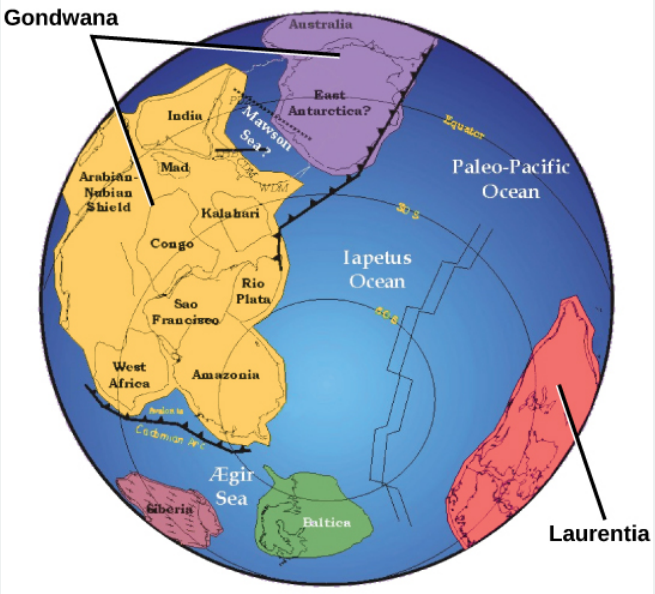
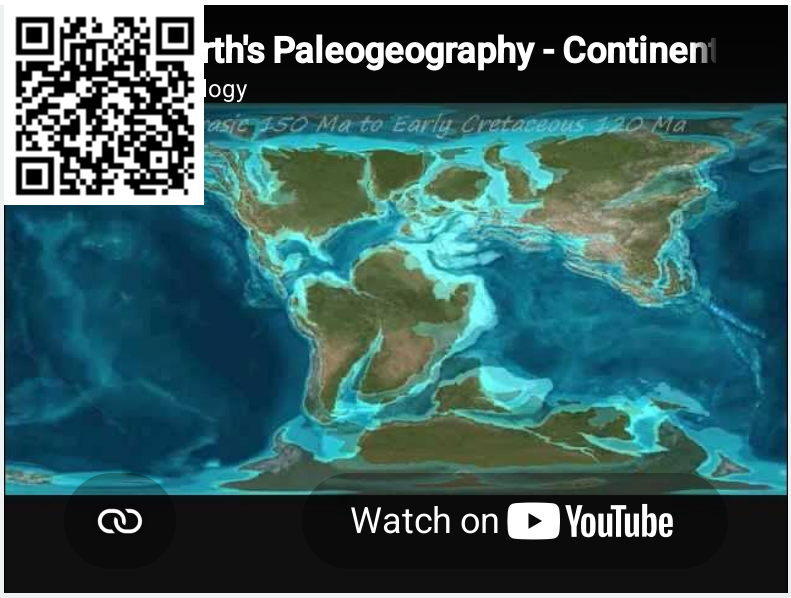


Figure **47.2.1.5**: During the Paleozoic Era, around 550 million years ago, the continent Gondwana formed. Both Gondwana and the continent Laurentia were located near the equator.

During the early Paleozoic, the amount of carbon dioxide in the atmosphere was much greater than it is today. This may have begun to change later, as land plants became more common. As the roots of land plants began to infiltrate rock and soil began to form, carbon dioxide was drawn out of the atmosphere and became trapped in the rock. This reduced the levels of carbon dioxide and increased the levels of oxygen in the atmosphere, so that by the end of the Paleozoic, atmospheric conditions were similar to those of today.

As plants became more common through the latter half of the Paleozoic, microclimates began to emerge and ecosystems began to change. As plants and ecosystems continued to grow and become more complex, vertebrates moved from the water to land. The presence of shoreline vegetation may have contributed to the movement of vertebrates onto land. One hypothesis suggests that the fins of aquatic vertebrates were used to maneuver through this vegetation, providing a precursor to the movement of fins on land and the development of limbs. The late Paleozoic was a time of diversification of vertebrates, as amniotes emerged and became two different lines that gave rise, on one hand, to mammals, and, on the other hand, to reptiles and birds. Many marine vertebrates became extinct near the end of the Devonian period, which ended about 360 million years ago, and both marine and terrestrial vertebrates were decimated by a mass extinction in the early Permian period about 250 million years ago.

Link to Learning



View Earth's Paleogeography: Continental Movements Through Time to see changes in Earth as life evolved.

Summary

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians are limbless. The most important characteristic of extant amphibians is a moist, permeable skin used for cutaneous respiration. The fossil record provides evidence of amphibian species, now extinct, that arose over 400 million years ago as the first tetrapods. Amphibia can be divided into three clades: salamanders (Urodela), frogs (Anura), and caecilians (Apoda). The life cycle of frogs, like the majority of amphibians, consists of two distinct stages: the larval stage and metamorphosis to an adult stage. Some species in all orders bypass a free-living larval stage.

Footnotes

1. 1 Daeschler, E. B., Shubin, N. H., and Jenkins, F. J. "A Devonian tetrapod-like fish and the evolution of the tetrapod body plan," *Nature* 440 (2006): 757–763, doi:10.1038/nature04639, http://www.nature.com/nature/journal/v440/n7085/abs/nature04639.html.

Glossary

Acanthostega
one of the earliest known tetrapods

Amphibia
frogs, salamanders, and caecilians

Anura
frogs

Apoda
caecilians

caecilian
legless amphibian that belongs to the clade Apoda

cutaneous respiration
gas exchange through the skin

frog

tail-less amphibian that belongs to the clade Anura

salamander

tailed amphibian that belongs to the clade Urodela

tadpole

larval stage of a frog

Urodela

salamanders

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47.2.2: Systems of Gas Exchange

Skills to Develop

- Describe the passage of air from the outside environment to the lungs
- Explain how the lungs are protected from particulate matter

The primary function of the respiratory system is to deliver oxygen to the cells of the body's tissues and remove carbon dioxide, a cell waste product. The main structures of the human respiratory system are the nasal cavity, the trachea, and lungs.

All aerobic organisms require oxygen to carry out their metabolic functions. Along the evolutionary tree, different organisms have devised different means of obtaining oxygen from the surrounding atmosphere. The environment in which the animal lives greatly determines how an animal respires. The complexity of the respiratory system is correlated with the size of the organism. As animal size increases, diffusion distances increase and the ratio of surface area to volume drops. In unicellular organisms, diffusion across the cell membrane is sufficient for supplying oxygen to the cell (Figure **47.2.2.1**). Diffusion is a slow, passive transport process. In order for diffusion to be a feasible means of providing oxygen to the cell, the rate of oxygen uptake must match the rate of diffusion across the membrane. In other words, if the cell were very large or thick, diffusion would not be able to provide oxygen quickly enough to the inside of the cell. Therefore, dependence on diffusion as a means of obtaining oxygen and removing carbon dioxide remains feasible only for small organisms or those with highly-flattened bodies, such as many flatworms (Platyhelminthes). Larger organisms had to evolve specialized respiratory tissues, such as gills, lungs, and respiratory passages accompanied by complex circulatory systems, to transport oxygen throughout their entire body.



Figure **47.2.2.1**: The cell of the unicellular algae *Ventricaria ventricosa* is one of the largest known, reaching one to five centimeters in diameter. Like all single-celled organisms, *V. ventricosa* exchanges gases across the cell membrane.

Direct Diffusion

For small multicellular organisms, diffusion across the outer membrane is sufficient to meet their oxygen needs. Gas exchange by direct diffusion across surface membranes is efficient for organisms less than 1 mm in diameter. In simple organisms, such as cnidarians and flatworms, every cell in the body is close to the external environment. Their cells are kept moist and gases diffuse quickly via direct diffusion. Flatworms are small, literally flat worms, which 'breathe' through diffusion across the outer membrane (Figure **47.2.2.2**). The flat shape of these organisms increases the surface area for diffusion, ensuring that each cell within the body is close to the outer membrane surface and has access to oxygen. If the flatworm had a cylindrical body, then the cells in the center would not be able to get oxygen.



Figure **47.2.2.2**: This flatworm's process of respiration works by diffusion across the outer membrane. (credit: Stephen Childs)

Skin and Gills

Earthworms and amphibians use their skin (integument) as a respiratory organ. A dense network of capillaries lies just below the skin and facilitates gas exchange between the external environment and the circulatory system. The respiratory surface must be kept moist in order for the gases to dissolve and diffuse across cell membranes.

Organisms that live in water need to obtain oxygen from the water. Oxygen dissolves in water but at a lower concentration than in the atmosphere. The atmosphere has roughly 21 percent oxygen. In water, the oxygen concentration is much smaller than that. Fish and many other aquatic organisms have evolved gills to take up the dissolved oxygen from water (Figure **47.2.2.3**). Gills are thin tissue filaments that are highly branched and folded. When water passes over the gills, the dissolved oxygen in water rapidly diffuses across the gills into the bloodstream. The circulatory system can then carry the oxygenated blood to the other parts of the body. In animals that contain coelomic fluid instead of blood, oxygen diffuses across the gill surfaces into the coelomic fluid. Gills are found in mollusks, annelids, and crustaceans.



Figure **47.2.2.3**: This common carp, like many other aquatic organisms, has gills that allow it to obtain oxygen from water. (credit: "Guitardude012"/Wikimedia Commons)

The folded surfaces of the gills provide a large surface area to ensure that the fish gets sufficient oxygen. Diffusion is a process in which material travels from regions of high concentration to low concentration until equilibrium is reached. In this case, blood with a low concentration of oxygen molecules circulates through the gills. The concentration of oxygen molecules in water is higher than the concentration of oxygen molecules in gills. As a result, oxygen molecules diffuse from water (high concentration) to blood (low concentration), as shown in Figure **47.2.2.4**. Similarly, carbon dioxide molecules in the blood diffuse from the blood (high concentration) to water (low concentration).

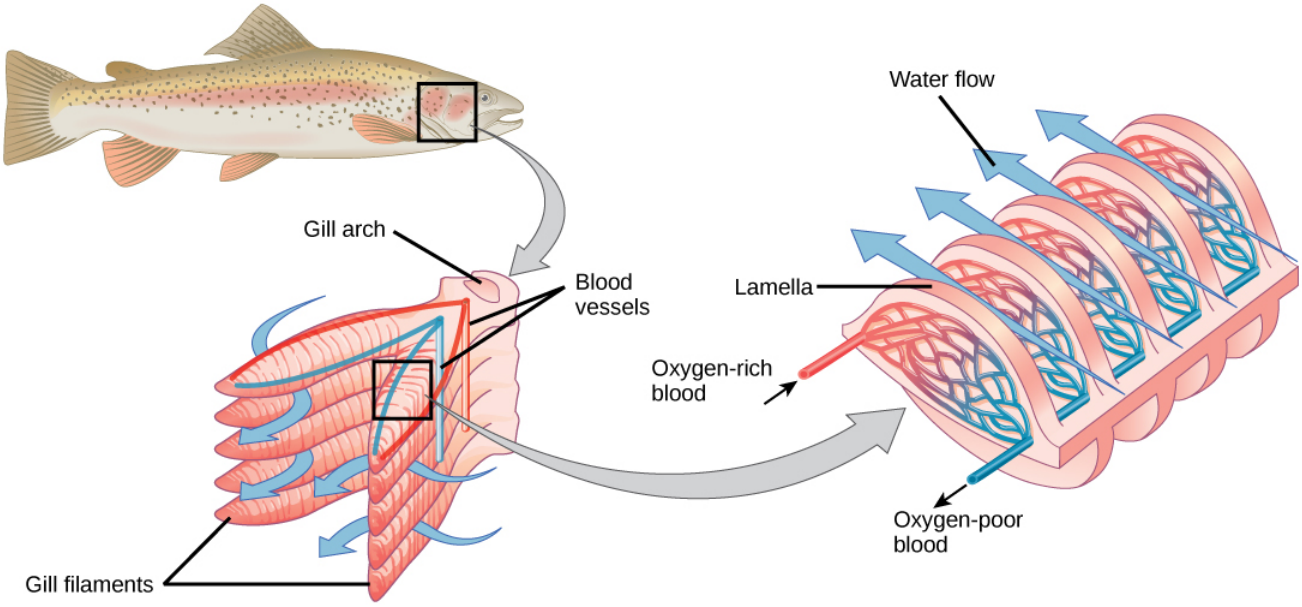


Figure **47.2.2.4**: As water flows over the gills, oxygen is transferred to blood via the veins. (credit "fish": modification of work by Duane Raver, NOAA)

Tracheal Systems

Insect respiration is independent of its circulatory system; therefore, the blood does not play a direct role in oxygen transport. Insects have a highly specialized type of respiratory system called the tracheal system, which consists of a network of small tubes that carries oxygen to the entire body. The tracheal system is the most direct and efficient respiratory system in active animals. The tubes in the tracheal system are made of a polymeric material called chitin.

Insect bodies have openings, called spiracles, along the thorax and abdomen. These openings connect to the tubular network, allowing oxygen to pass into the body (Figure **47.2.2.5**) and regulating the diffusion of CO_2 and water vapor. Air enters and leaves the tracheal system through the spiracles. Some insects can ventilate the tracheal system with body movements.

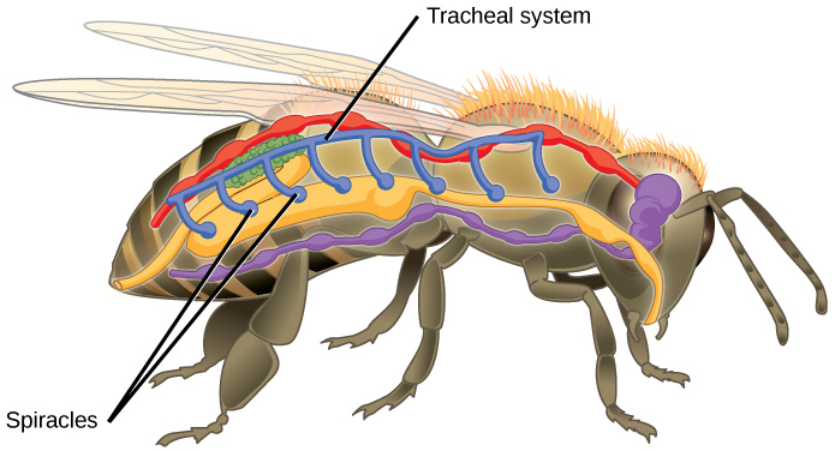


Figure **47.2.2.5**: Insects perform respiration via a tracheal system.

Mammalian Systems

In mammals, pulmonary ventilation occurs via inhalation (breathing). During inhalation, air enters the body through the nasal cavity located just inside the nose (Figure **47.2.2.6**). As air passes through the nasal cavity, the air is warmed to body temperature and humidified. The respiratory tract is coated with mucus to seal the tissues from direct contact with air. Mucus is high in water. As air crosses these surfaces of the mucous membranes, it picks up water. These processes help equilibrate the air to the body conditions, reducing any damage that cold, dry air can cause. Particulate matter that is floating in the air is removed in the nasal passages via mucus and cilia. The processes of warming, humidifying, and removing particles are important protective mechanisms

that prevent damage to the trachea and lungs. Thus, inhalation serves several purposes in addition to bringing oxygen into the respiratory system.

Art Connection

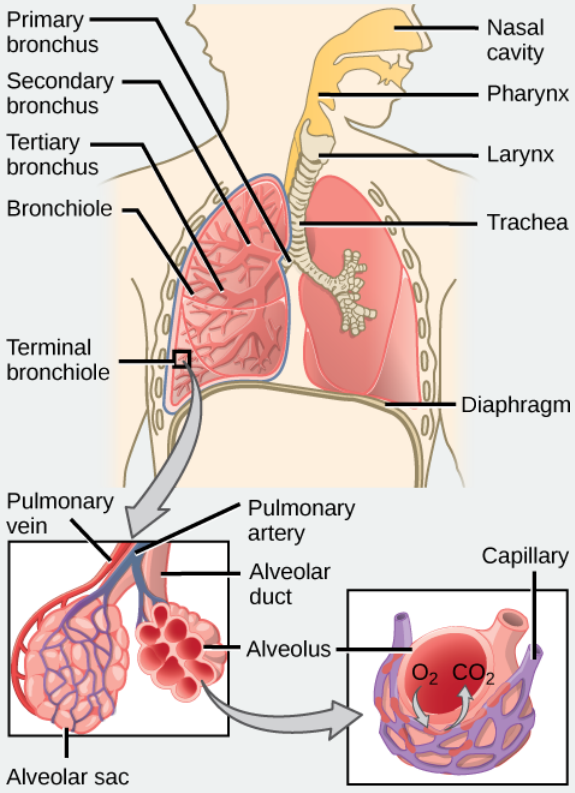


Figure **47.2.2.6**: Air enters the respiratory system through the nasal cavity and pharynx, and then passes through the trachea and into the bronchi, which bring air into the lungs. (credit: modification of work by NCI)

Which of the following statements about the mammalian respiratory system is false?

A. When we breathe in, air travels from the pharynx to the trachea.
B. The bronchioles branch into bronchi.
C. Alveolar ducts connect to alveolar sacs.
D. Gas exchange between the lung and blood takes place in the alveolus.

From the nasal cavity, air passes through the pharynx (throat) and the larynx (voice box), as it makes its way to the trachea (Figure **47.2.2.6**). The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder about 10 to 12 cm long and 2 cm in diameter that sits in front of the esophagus and extends from the larynx into the chest cavity where it divides into the two primary bronchi at the midthorax. It is made of incomplete rings of hyaline cartilage and smooth muscle (Figure **47.2.2.7**). The trachea is lined with mucus-producing goblet cells and ciliated epithelia. The cilia propel foreign particles trapped in the mucus toward the pharynx. The cartilage provides strength and support to the trachea to keep the passage open. The smooth muscle can contract, decreasing the trachea's diameter, which causes expired air to rush upwards from the lungs at a great force. The forced exhalation helps expel mucus when we cough. Smooth muscle can contract or relax, depending on stimuli from the external environment or the body's nervous system.

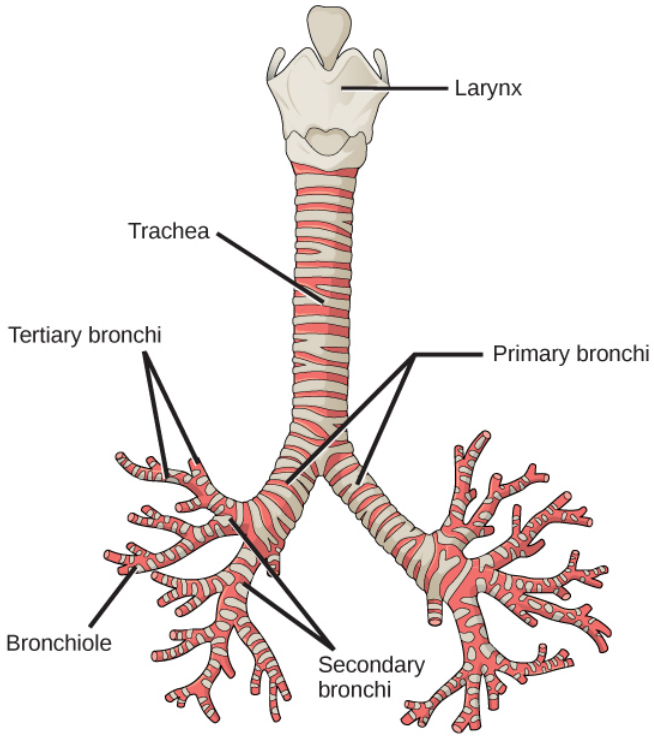


Figure 47.2.2.7: The trachea and bronchi are made of incomplete rings of cartilage. (credit: modification of work by Gray's Anatomy)

Lungs: Bronchi and Alveoli

The end of the trachea bifurcates (divides) to the right and left lungs. The lungs are not identical. The right lung is larger and contains three lobes, whereas the smaller left lung contains two lobes (Figure 47.2.2.8). The muscular diaphragm, which facilitates breathing, is inferior to (below) the lungs and marks the end of the thoracic cavity.

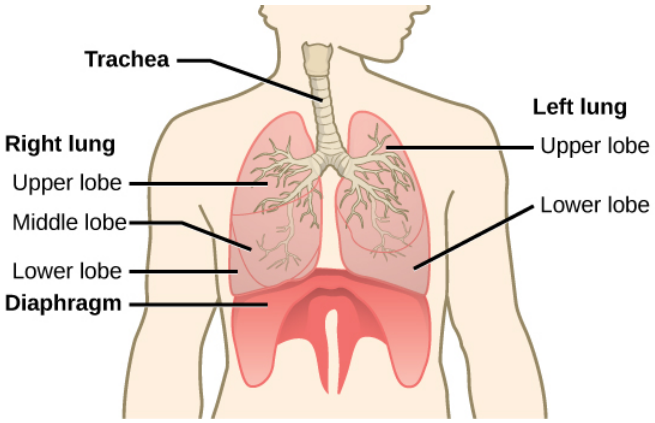


Figure 47.2.2.8: The trachea bifurcates into the right and left bronchi in the lungs. The right lung is made of three lobes and is larger. To accommodate the heart, the left lung is smaller and has only two lobes.

In the lungs, air is diverted into smaller and smaller passages, or bronchi. Air enters the lungs through the two primary (main) bronchi (singular: bronchus). Each bronchus divides into secondary bronchi, then into tertiary bronchi, which in turn divide, creating smaller and smaller diameter bronchioles as they split and spread through the lung. Like the trachea, the bronchi are made of cartilage and smooth muscle. At the bronchioles, the cartilage is replaced with elastic fibers. Bronchi are innervated by nerves of both the parasympathetic and sympathetic nervous systems that control muscle contraction (parasympathetic) or relaxation (sympathetic) in the bronchi and bronchioles, depending on the nervous system's cues. In humans, bronchioles with a diameter smaller than 0.5 mm are the respiratory bronchioles. They lack cartilage and therefore rely on inhaled air to support their shape. As the passageways decrease in diameter, the relative amount of smooth muscle increases.

The terminal bronchioles subdivide into microscopic branches called respiratory bronchioles. The respiratory bronchioles subdivide into several alveolar ducts. Numerous alveoli and alveolar sacs surround the alveolar ducts. The alveolar sacs resemble bunches of grapes tethered to the end of the bronchioles (Figure **47.2.2.9**). In the acinar region, the alveolar ducts are attached to the end of each bronchiole. At the end of each duct are approximately 100 alveolar sacs, each containing 20 to 30 alveoli that are 200 to 300 microns in diameter. Gas exchange occurs only in alveoli. Alveoli are made of thin-walled parenchymal cells, typically one-cell thick, that look like tiny bubbles within the sacs. Alveoli are in direct contact with capillaries (one-cell thick) of the circulatory system. Such intimate contact ensures that oxygen will diffuse from alveoli into the blood and be distributed to the cells of the body. In addition, the carbon dioxide that was produced by cells as a waste product will diffuse from the blood into alveoli to be exhaled. The anatomical arrangement of capillaries and alveoli emphasizes the structural and functional relationship of the respiratory and circulatory systems. Because there are so many alveoli (~300 million per lung) within each alveolar sac and so many sacs at the end of each alveolar duct, the lungs have a sponge-like consistency. This organization produces a very large surface area that is available for gas exchange. The surface area of alveoli in the lungs is approximately 75 m^2. This large surface area, combined with the thin-walled nature of the alveolar parenchymal cells, allows gases to easily diffuse across the cells.

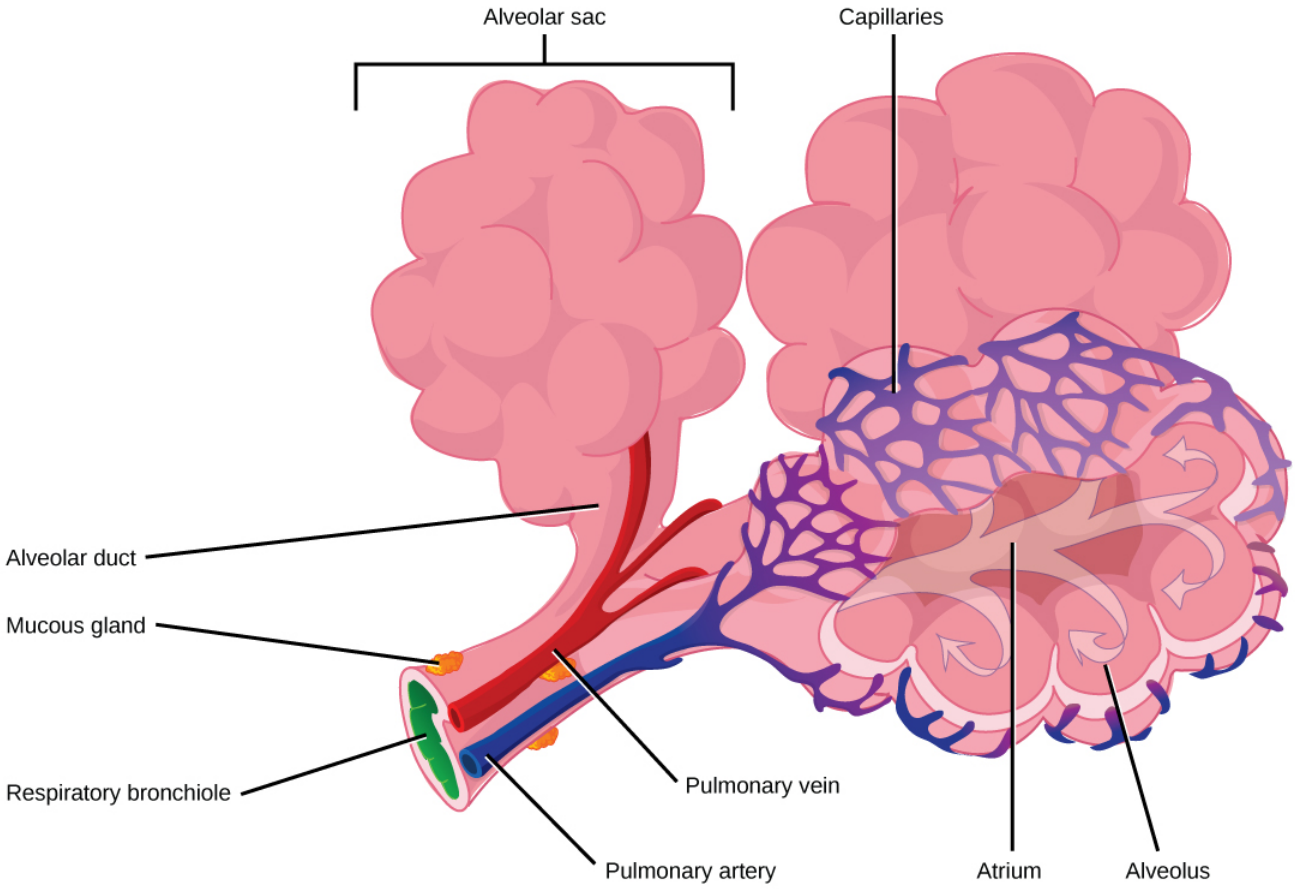
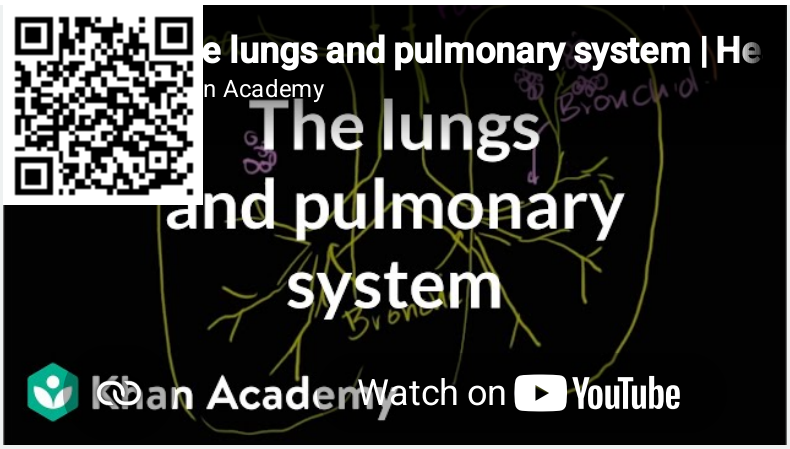


Figure **47.2.2.9**: Terminal bronchioles are connected by respiratory bronchioles to alveolar ducts and alveolar sacs. Each alveolar sac contains 20 to 30 spherical alveoli and has the appearance of a bunch of grapes. Air flows into the atrium of the alveolar sac, then circulates into alveoli where gas exchange occurs with the capillaries. Mucous glands secrete mucous into the airways, keeping them moist and flexible. (credit: modification of work by Mariana Ruiz Villareal)

Link to Learning



Watch the following video to review the respiratory system.

Protective Mechanisms

The air that organisms breathe contains particulate matter such as dust, dirt, viral particles, and bacteria that can damage the lungs or trigger allergic immune responses. The respiratory system contains several protective mechanisms to avoid problems or tissue damage. In the nasal cavity, hairs and mucus trap small particles, viruses, bacteria, dust, and dirt to prevent their entry.

If particulates do make it beyond the nose, or enter through the mouth, the bronchi and bronchioles of the lungs also contain several protective devices. The lungs produce mucus—a sticky substance made of mucin, a complex glycoprotein, as well as salts and water—that traps particulates. The bronchi and bronchioles contain cilia, small hair-like projections that line the walls of the bronchi and bronchioles (Figure 47.2.2.10). These cilia beat in unison and move mucus and particles out of the bronchi and bronchioles back up to the throat where it is swallowed and eliminated via the esophagus.

In humans, for example, tar and other substances in cigarette smoke destroy or paralyze the cilia, making the removal of particles more difficult. In addition, smoking causes the lungs to produce more mucus, which the damaged cilia are not able to move. This causes a persistent cough, as the lungs try to rid themselves of particulate matter, and makes smokers more susceptible to respiratory ailments.

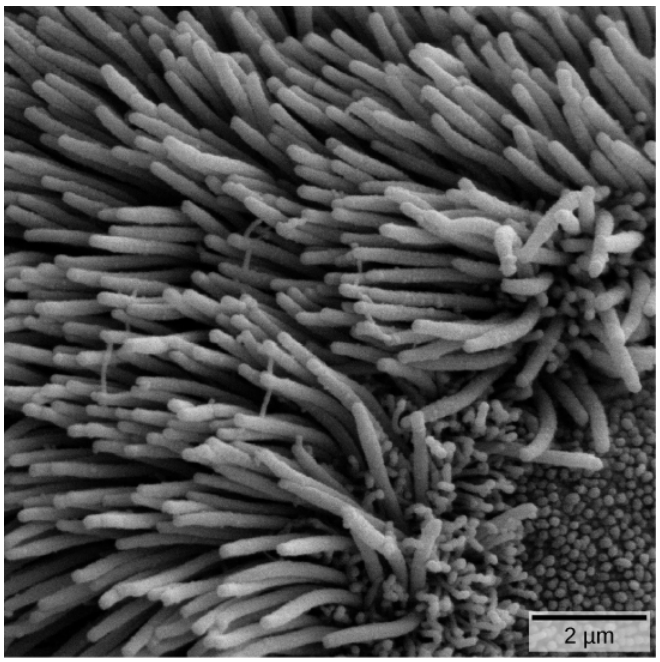


Figure 47.2.2.10: The bronchi and bronchioles contain cilia that help move mucus and other particles out of the lungs. (credit: Louisa Howard, modification of work by Dartmouth Electron Microscope Facility)

Summary

Animal respiratory systems are designed to facilitate gas exchange. In mammals, air is warmed and humidified in the nasal cavity. Air then travels down the pharynx, through the trachea, and into the lungs. In the lungs, air passes through the branching bronchi, reaching the respiratory bronchioles, which house the first site of gas exchange. The respiratory bronchioles open into the alveolar ducts, alveolar sacs, and alveoli. Because there are so many alveoli and alveolar sacs in the lung, the surface area for gas exchange is very large. Several protective mechanisms are in place to prevent damage or infection. These include the hair and mucus in the nasal cavity that trap dust, dirt, and other particulate matter before they can enter the system. In the lungs, particles are trapped in a mucus layer and transported via cilia up to the esophageal opening at the top of the trachea to be swallowed.

Art Connections

Figure **47.2.2.6**: Which of the following statements about the mammalian respiratory system is false?

A. When we breathe in, air travels from the pharynx to the trachea.
B. The bronchioles branch into bronchi.
C. Alveolar ducts connect to alveolar sacs.
D. Gas exchange between the lung and blood takes place in the alveolus.

Answer

B

Glossary

alveolar duct
duct that extends from the terminal bronchiole to the alveolar sac

alveolar sac
structure consisting of two or more alveoli that share a common opening

alveolus
(plural: alveoli) (also, air sac) terminal region of the lung where gas exchange occurs

bronchus
(plural: bronchi) smaller branch of cartilaginous tissue that stems off of the trachea; air is funneled through the bronchi to the region where gas exchange occurs in alveoli

bronchiole
airway that extends from the main tertiary bronchi to the alveolar sac

diaphragm
domed-shaped skeletal muscle located under lungs that separates the thoracic cavity from the abdominal cavity

larynx
voice box, a short passageway connecting the pharynx and the trachea

mucin
complex glycoprotein found in mucus

mucus
sticky protein-containing fluid secretion in the lung that traps particulate matter to be expelled from the body

nasal cavity
opening of the respiratory system to the outside environment

particulate matter

small particle such as dust, dirt, viral particles, and bacteria that are in the air

pharynx

throat; a tube that starts in the internal nares and runs partway down the neck, where it opens into the esophagus and the larynx

primary bronchus

(also, main bronchus) region of the airway within the lung that attaches to the trachea and bifurcates to each lung where it branches into secondary bronchi

respiratory bronchiole

terminal portion of the bronchiole tree that is attached to the terminal bronchioles and alveoli ducts, alveolar sacs, and alveoli

terminal bronchiole

region of bronchiole that attaches to the respiratory bronchioles

trachea

cartilaginous tube that transports air from the larynx to the primary bronchi

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47.3: Lungs

Skills to Develop

- Name and describe lung volumes and capacities
- Understand how gas pressure influences how gases move into and out of the body

The structure of the lung maximizes its surface area to increase gas diffusion. Because of the enormous number of alveoli (approximately 300 million in each human lung), the surface area of the lung is very large (75 m^2). Having such a large surface area increases the amount of gas that can diffuse into and out of the lungs.

Basic Principles of Gas Exchange

Gas exchange during respiration occurs primarily through diffusion. Diffusion is a process in which transport is driven by a concentration gradient. Gas molecules move from a region of high concentration to a region of low concentration. Blood that is low in oxygen concentration and high in carbon dioxide concentration undergoes gas exchange with air in the lungs. The air in the lungs has a higher concentration of oxygen than that of oxygen-depleted blood and a lower concentration of carbon dioxide. This concentration gradient allows for gas exchange during respiration.

Partial pressure is a measure of the concentration of the individual components in a mixture of gases. The total pressure exerted by the mixture is the sum of the partial pressures of the components in the mixture. The rate of diffusion of a gas is proportional to its partial pressure within the total gas mixture. This concept is discussed further in detail below.

Lung Volumes and Capacities

Different animals have different lung capacities based on their activities. Cheetahs have evolved a much higher lung capacity than humans; it helps provide oxygen to all the muscles in the body and allows them to run very fast. Elephants also have a high lung capacity. In this case, it is not because they run fast but because they have a large body and must be able to take up oxygen in accordance with their body size.

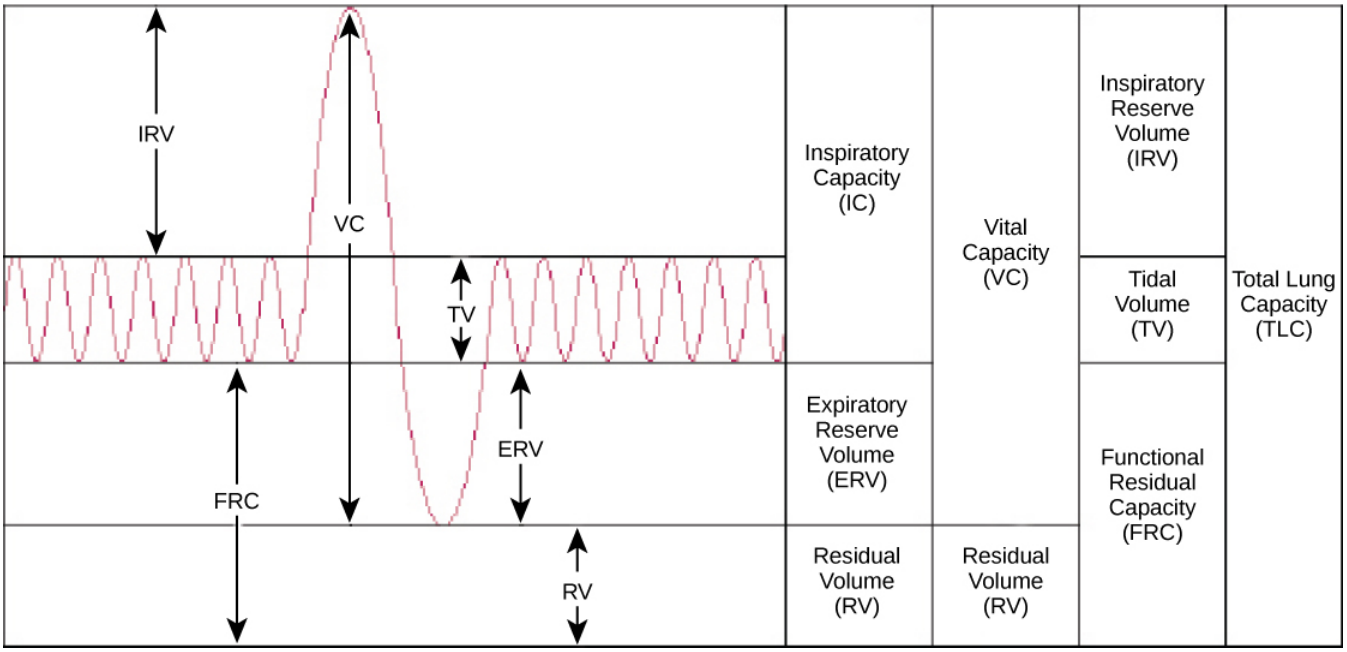


Figure **47.3.1**: Human lung volumes and capacities are shown. The total lung capacity of the adult male is six liters. Tidal volume is the volume of air inhaled in a single, normal breath. Inspiratory capacity is the amount of air taken in during a deep breath, and residual volume is the amount of air left in the lungs after forceful respiration.

Human lung size is determined by genetics, gender, and height. At maximal capacity, an average lung can hold almost six liters of air, but lungs do not usually operate at maximal capacity. Air in the lungs is measured in terms of lung volumes and lung capacities

(Figure 47.3.1 and Table 47.3.1). Volume measures the amount of air for one function (such as inhalation or exhalation). Capacity is any two or more volumes (for example, how much can be inhaled from the end of a maximal exhalation).

Table 47.3.1: Lung Volumes and Capacities (Avg Adult Male)

Volume/Capacity	Definition	Volume (liters)	Equations
Tidal volume (TV)	Amount of air inhaled during a normal breath	0.5	-
Expiratory reserve volume (ERV)	Amount of air that can be exhaled after a normal exhalation	1.2	-
Inspiratory reserve volume (IRV)	Amount of air that can be further inhaled after a normal inhalation	3.1	-
Residual volume (RV)	Air left in the lungs after a forced exhalation	1.2	-
Vital capacity (VC)	Maximum amount of air that can be moved in or out of the lungs in a single respiratory cycle	4.8	ERV+TV+IRV
Inspiratory capacity (IC)	Volume of air that can be inhaled in addition to a normal exhalation	3.6	TV+IRV
Functional residual capacity (FRC)	Volume of air remaining after a normal exhalation	2.4	ERV+RV
Total lung capacity (TLC)	Total volume of air in the lungs after a maximal inspiration	6.0	RV+ERV+TV+IRV
Forced expiratory volume (FEV1)	How much air can be forced out of the lungs over a specific time period, usually one second	~4.1 to 5.5	-

The volume in the lung can be divided into four units: tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume. Tidal volume (TV) measures the amount of air that is inspired and expired during a normal breath. On average, this volume is around one-half liter, which is a little less than the capacity of a 20-ounce drink bottle. The expiratory reserve volume (ERV) is the additional amount of air that can be exhaled after a normal exhalation. It is the reserve amount that can be exhaled beyond what is normal. Conversely, the inspiratory reserve volume (IRV) is the additional amount of air that can be inhaled after a normal inhalation. The residual volume (RV) is the amount of air that is left after expiratory reserve volume is exhaled. The lungs are never completely empty: There is always some air left in the lungs after a maximal exhalation. If this residual volume did not exist and the lungs emptied completely, the lung tissues would stick together and the energy necessary to re-inflate the lung could be too great to overcome. Therefore, there is always some air remaining in the lungs. Residual volume is also important for preventing large fluctuations in respiratory gases (O_2 and CO_2). The residual volume is the only lung volume that cannot be measured directly because it is impossible to completely empty the lung of air. This volume can only be calculated rather than measured.

Capacities are measurements of two or more volumes. The vital capacity (VC) measures the maximum amount of air that can be inhaled or exhaled during a respiratory cycle. It is the sum of the expiratory reserve volume, tidal volume, and inspiratory reserve volume. The inspiratory capacity (IC) is the amount of air that can be inhaled after the end of a normal expiration. It is, therefore, the sum of the tidal volume and inspiratory reserve volume. The functional residual capacity (FRC) includes the expiratory reserve

volume and the residual volume. The FRC measures the amount of additional air that can be exhaled after a normal exhalation. Lastly, the total lung capacity (TLC) is a measurement of the total amount of air that the lung can hold. It is the sum of the residual volume, expiratory reserve volume, tidal volume, and inspiratory reserve volume.

Lung volumes are measured by a technique called spirometry. An important measurement taken during spirometry is the forced expiratory volume (FEV), which measures how much air can be forced out of the lung over a specific period, usually one second (FEV1). In addition, the forced vital capacity (FVC), which is the total amount of air that can be forcibly exhaled, is measured. The ratio of these values (FEV1/FVC ratio) is used to diagnose lung diseases including asthma, emphysema, and fibrosis. If the FEV1/FVC ratio is high, the lungs are not compliant (meaning they are stiff and unable to bend properly), and the patient most likely has lung fibrosis. Patients exhale most of the lung volume very quickly. Conversely, when the FEV1/FVC ratio is low, there is resistance in the lung that is characteristic of asthma. In this instance, it is hard for the patient to get the air out of his or her lungs, and it takes a long time to reach the maximal exhalation volume. In either case, breathing is difficult and complications arise.

Career Connection: Respiratory Therapist

Respiratory therapists or respiratory practitioners evaluate and treat patients with lung and cardiovascular diseases. They work as part of a medical team to develop treatment plans for patients. Respiratory therapists may treat premature babies with underdeveloped lungs, patients with chronic conditions such as asthma, or older patients suffering from lung disease such as emphysema and chronic obstructive pulmonary disease (COPD). They may operate advanced equipment such as compressed gas delivery systems, ventilators, blood gas analyzers, and resuscitators. Specialized programs to become a respiratory therapist generally lead to a bachelor's degree with a respiratory therapist specialty. Because of a growing aging population, career opportunities as a respiratory therapist are expected to remain strong.

Gas Pressure and Respiration

The respiratory process can be better understood by examining the properties of gases. Gases move freely, but gas particles are constantly hitting the walls of their vessel, thereby producing gas pressure.

Air is a mixture of gases, primarily nitrogen (N_2; 78.6 percent), oxygen (O_2; 20.9 percent), water vapor (H_2O; 0.5 percent), and carbon dioxide (CO_2; 0.04 percent). Each gas component of that mixture exerts a pressure. The pressure for an individual gas in the mixture is the partial pressure of that gas. Approximately 21 percent of atmospheric gas is oxygen. Carbon dioxide, however, is found in relatively small amounts, 0.04 percent. The partial pressure for oxygen is much greater than that of carbon dioxide. The partial pressure of any gas can be calculated by:

$$\mathrm{P = (P_{atm}) * (\text{percent content in mixture})}$$

P_{atm}, the atmospheric pressure, is the sum of all of the partial pressures of the atmospheric gases added together,

$$\mathrm{P_{atm} = P_{N_2} + P_{O_2} + P_{H_2O} + P_{CO_2} = 760\ mm\ Hg}$$

× (percent content in mixture).

The pressure of the atmosphere at sea level is 760 mm Hg. Therefore, the partial pressure of oxygen is:

$$\mathrm{P_{O_2} = (760\ mm\ Hg)(0.21) = 160\ mm\ Hg}$$

and for carbon dioxide:

$$\mathrm{P_{CO_2} = (760\ mm\ Hg)(0.0004) = 0.3\ mm\ Hg}$$

At high altitudes, P_{atm} decreases but concentration does not change; the partial pressure decrease is due to the reduction in P_{atm}.

When the air mixture reaches the lung, it has been humidified. The pressure of the water vapor in the lung does not change the pressure of the air, but it must be included in the partial pressure equation. For this calculation, the water pressure (47 mm Hg) is subtracted from the atmospheric pressure:

$$\mathrm{760\ mm\ Hg - 47\ mm\ Hg = 713\ mm\ Hg}$$

and the partial pressure of oxygen is:

$$(760 \text{ mm Hg} - 47 \text{ mm Hg})(0.21) = 150 \text{ mm Hg}$$

These pressures determine the gas exchange, or the flow of gas, in the system. Oxygen and carbon dioxide will flow according to their pressure gradient from high to low. Therefore, understanding the partial pressure of each gas will aid in understanding how gases move in the respiratory system.

Gas Exchange across the Alveoli

In the body, oxygen is used by cells of the body's tissues and carbon dioxide is produced as a waste product. The ratio of carbon dioxide production to oxygen consumption is the respiratory quotient (RQ). RQ varies between 0.7 and 1.0. If just glucose were used to fuel the body, the RQ would equal one. One mole of carbon dioxide would be produced for every mole of oxygen consumed. Glucose, however, is not the only fuel for the body. Protein and fat are also used as fuels for the body. Because of this, less carbon dioxide is produced than oxygen is consumed and the RQ is, on average, about 0.7 for fat and about 0.8 for protein.

The RQ is used to calculate the partial pressure of oxygen in the alveolar spaces within the lung, the alveolar $\mathbf{P_{O_2}}$. Above, the partial pressure of oxygen in the lungs was calculated to be 150 mm Hg. However, lungs never fully deflate with an exhalation; therefore, the inspired air mixes with this residual air and lowers the partial pressure of oxygen within the alveoli. This means that there is a lower concentration of oxygen in the lungs than is found in the air outside the body. Knowing the RQ, the partial pressure of oxygen in the alveoli can be calculated:

$$\text{alveolar } P_{O_2} = \text{inspired } P_{O_2} - \frac{\text{alveolar } P_{O_2}}{\text{RQ}}$$

With an RQ of 0.8 and a $\mathbf{P_{CO_2}}$ in the alveoli of 40 mm Hg, the alveolar $\mathbf{P_{O_2}}$ is equal to:

$$\text{alveolar } P_{O_2} = 150 \text{ mm Hg} - \frac{40 \text{ mm Hg}}{0.8} = \text{mm Hg}$$

Notice that this pressure is less than the external air. Therefore, the oxygen will flow from the inspired air in the lung ($\mathbf{P_{O_2}}$ = 150 mm Hg) into the bloodstream ($\mathbf{P_{O_2}}$ = 100 mm Hg) (Figure **47.3.2**).

In the lungs, oxygen diffuses out of the alveoli and into the capillaries surrounding the alveoli. Oxygen (about 98 percent) binds reversibly to the respiratory pigment hemoglobin found in red blood cells (RBCs). RBCs carry oxygen to the tissues where oxygen dissociates from the hemoglobin and diffuses into the cells of the tissues. More specifically, alveolar $\mathbf{P_{O_2}}$ is higher in the alveoli $\mathbf{P_{ALVO_2}}$ = 100 mm Hg) than blood $\mathbf{P_{O_2}}$ (40 mm Hg) in the capillaries. Because this pressure gradient exists, oxygen diffuses down its pressure gradient, moving out of the alveoli and entering the blood of the capillaries where O_2 binds to hemoglobin. At the same time, alveolar $\mathbf{P_{CO_2}}$ is lower $\mathbf{P_{ALVO_2}}$ = 40 mm Hg than blood $\mathbf{P_{CO_2}}$ = (45 mm Hg). CO_2 diffuses down its pressure gradient, moving out of the capillaries and entering the alveoli.

Oxygen and carbon dioxide move independently of each other; they diffuse down their own pressure gradients. As blood leaves the lungs through the pulmonary veins, the venous $\mathbf{P_{O_2}}$= 100 mm Hg, whereas the venous $\mathbf{P_{CO_2}}$= 40 mm Hg. As blood enters the systemic capillaries, the blood will lose oxygen and gain carbon dioxide because of the pressure difference of the tissues and blood. In systemic capillaries, $\mathbf{P_{O_2}}$= 100 mm Hg, but in the tissue cells, $\mathbf{P_{O_2}}$= 40 mm Hg. This pressure gradient drives the diffusion of oxygen out of the capillaries and into the tissue cells. At the same time, blood $\mathbf{P_{CO_2}}$= 40 mm Hg and systemic tissue $\mathbf{P_{CO_2}}$= 45 mm Hg. The pressure gradient drives CO_2 out of tissue cells and into the capillaries. The blood returning to the lungs through the pulmonary arteries has a venous $\mathbf{P_{O_2}}$= 40 mm Hg and a $\mathbf{P_{CO_2}}$= 45 mm Hg. The blood enters the lung capillaries where the process of exchanging gases between the capillaries and alveoli begins again (Figure **47.3.2**).

Art Connection

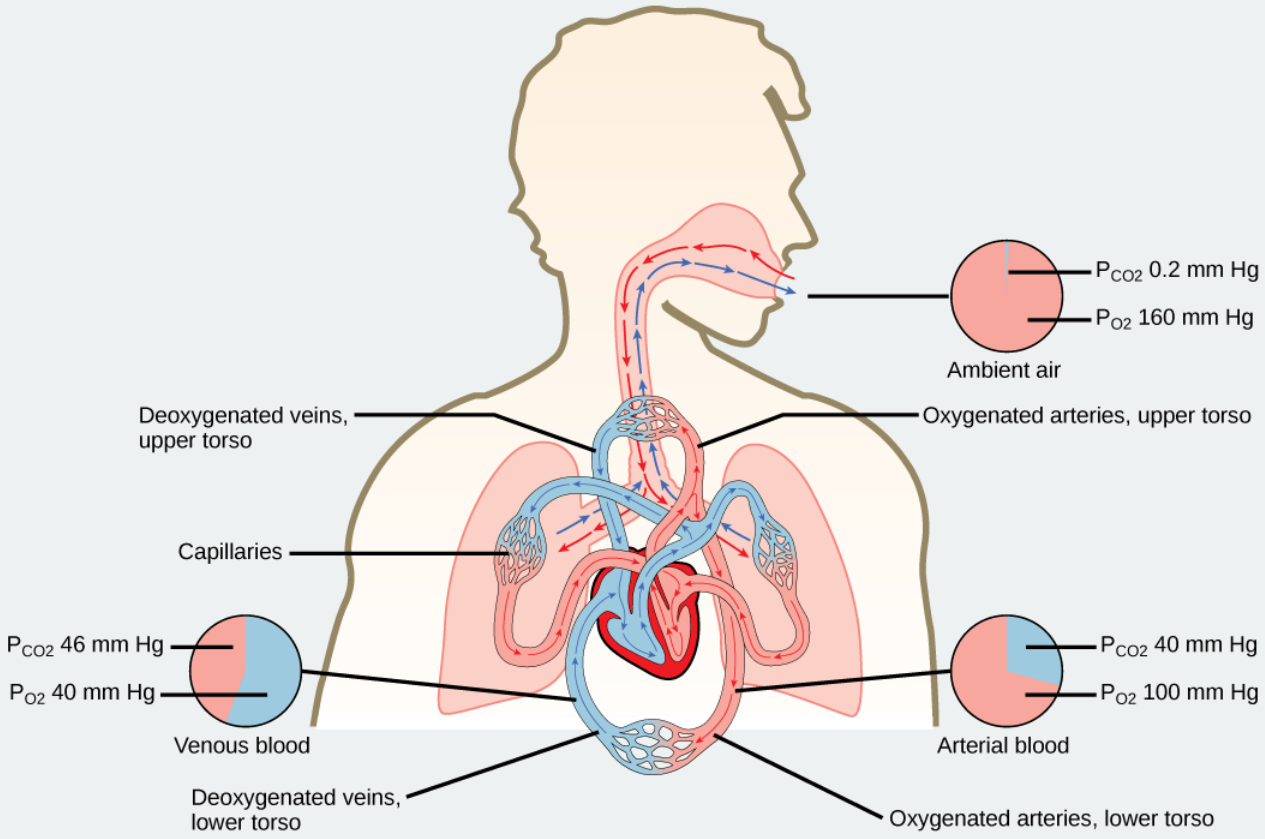


Figure **47.3.2**: The partial pressures of oxygen and carbon dioxide change as blood moves through the body.

Which of the following statements is false?

A. In the tissues, $\mathbf{P_{O_2}}$ drops as blood passes from the arteries to the veins, while $\mathbf{P_{CO_2}}$ increases.
B. Blood travels from the lungs to the heart to body tissues, then back to the heart, then the lungs.
C. Blood travels from the lungs to the heart to body tissues, then back to the lungs, then the heart.
D. $\mathbf{P_{O_2}}$ is higher in air than in the lungs.

In short, the change in partial pressure from the alveoli to the capillaries drives the oxygen into the tissues and the carbon dioxide into the blood from the tissues. The blood is then transported to the lungs where differences in pressure in the alveoli result in the movement of carbon dioxide out of the blood into the lungs, and oxygen into the blood.

Link to Learning



Watch this video to learn how to carry out spirometry.

Summary

The lungs can hold a large volume of air, but they are not usually filled to maximal capacity. Lung volume measurements include tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume. The sum of these equals the total lung capacity. Gas movement into or out of the lungs is dependent on the pressure of the gas. Air is a mixture of gases; therefore, the partial pressure of each gas can be calculated to determine how the gas will flow in the lung. The difference between the partial pressure of the gas in the air drives oxygen into the tissues and carbon dioxide out of the body.

Art Connections

Figure **47.3.2**: Which of the following statements is false?

A. In the tissues, $\mathbf{P_{O_2}}$ drops as blood passes from the arteries to the veins, while $\mathbf{P_{CO_2}}$ increases.
B. Blood travels from the lungs to the heart to body tissues, then back to the heart, then the lungs.
C. Blood travels from the lungs to the heart to body tissues, then back to the lungs, then the heart.
D. $\mathbf{P_{O_2}}$ is higher in air than in the lungs.

Answer

C

Glossary

alveolar $\mathbf{P_{O_2}}$
partial pressure of oxygen in the alveoli (usually around 100 mmHg)

expiratory reserve volume (ERV)
amount of additional air that can be exhaled after a normal exhalation

FEV1/FVC ratio
ratio of how much air can be forced out of the lung in one second to the total amount that is forced out of the lung; a measurement of lung function that can be used to detect disease states

forced expiratory volume (FEV)

(also, forced vital capacity) measure of how much air can be forced out of the lung from maximal inspiration over a specific amount of time

functional residual capacity (FRC)
expiratory reserve volume plus residual volume

inspiratory capacity (IC)
tidal volume plus inspiratory reserve volume

inspiratory reserve volume (IRV)
amount of additional air that can be inspired after a normal inhalation

lung capacity
measurement of two or more lung volumes (how much air can be inhaled from the end of an expiration to maximal capacity)

lung volume
measurement of air for one lung function (normal inhalation or exhalation)

partial pressure
amount of pressure exerted by one gas within a mixture of gases

residual volume (RV)
amount of air remaining in the lung after a maximal expiration

respiratory quotient (RQ)
ratio of carbon dioxide production to each oxygen molecule consumed

spirometry
method to measure lung volumes and to diagnose lung diseases

tidal volume (TV)
amount of air that is inspired and expired during normal breathing

total lung capacity (TLC)
sum of the residual volume, expiratory reserve volume, tidal volume, and inspiratory reserve volume

venous P_{CO_2}
partial pressure of carbon dioxide in the veins (40 mm Hg in the pulmonary veins)

venous P_{O_2}
partial pressure of oxygen in the veins (100 mm Hg in the pulmonary veins)

vital capacity (VC)
sum of the expiratory reserve volume, tidal volume, and inspiratory reserve volume

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47.3.1: Breathing

Skills to Develop

- Describe how the structures of the lungs and thoracic cavity control the mechanics of breathing
- Explain the importance of compliance and resistance in the lungs
- Discuss problems that may arise due to a V/Q mismatch

Mammalian lungs are located in the thoracic cavity where they are surrounded and protected by the rib cage, intercostal muscles, and bound by the chest wall. The bottom of the lungs is contained by the diaphragm, a skeletal muscle that facilitates breathing. Breathing requires the coordination of the lungs, the chest wall, and most importantly, the diaphragm.

Types of Breathing

Amphibians have evolved multiple ways of breathing. Young amphibians, like tadpoles, use gills to breathe, and they don't leave the water. Some amphibians retain gills for life. As the tadpole grows, the gills disappear and lungs grow. These lungs are primitive and not as evolved as mammalian lungs. Adult amphibians are lacking or have a reduced diaphragm, so breathing via lungs is forced. The other means of breathing for amphibians is diffusion across the skin. To aid this diffusion, amphibian skin must remain moist.

Birds face a unique challenge with respect to breathing: They fly. Flying consumes a great amount of energy; therefore, birds require a lot of oxygen to aid their metabolic processes. Birds have evolved a respiratory system that supplies them with the oxygen needed to enable flying. Similar to mammals, birds have lungs, which are organs specialized for gas exchange. Oxygenated air, taken in during inhalation, diffuses across the surface of the lungs into the bloodstream, and carbon dioxide diffuses from the blood into the lungs and expelled during exhalation. The details of breathing between birds and mammals differ substantially.

In addition to lungs, birds have air sacs inside their body. Air flows in one direction from the posterior air sacs to the lungs and out of the anterior air sacs. The flow of air is in the opposite direction from blood flow, and gas exchange takes place much more efficiently. This type of breathing enables birds to obtain the requisite oxygen, even at higher altitudes where the oxygen concentration is low. This directionality of airflow requires two cycles of air intake and exhalation to completely get the air out of the lungs.

Evolution Connection: Avian Respiration

Birds have evolved a respiratory system that enables them to fly. Flying is a high-energy process and requires a lot of oxygen. Furthermore, many birds fly in high altitudes where the concentration of oxygen in low. How did birds evolve a respiratory system that is so unique?

Decades of research by paleontologists have shown that birds evolved from therapods, meat-eating dinosaurs (Figure **47.3.1.1**). In fact, fossil evidence shows that meat-eating dinosaurs that lived more than 100 million years ago had a similar flow-through respiratory system with lungs and air sacs. *Archaeopteryx* and *Xiaotingia*, for example, were flying dinosaurs and are believed to be early precursors of birds.

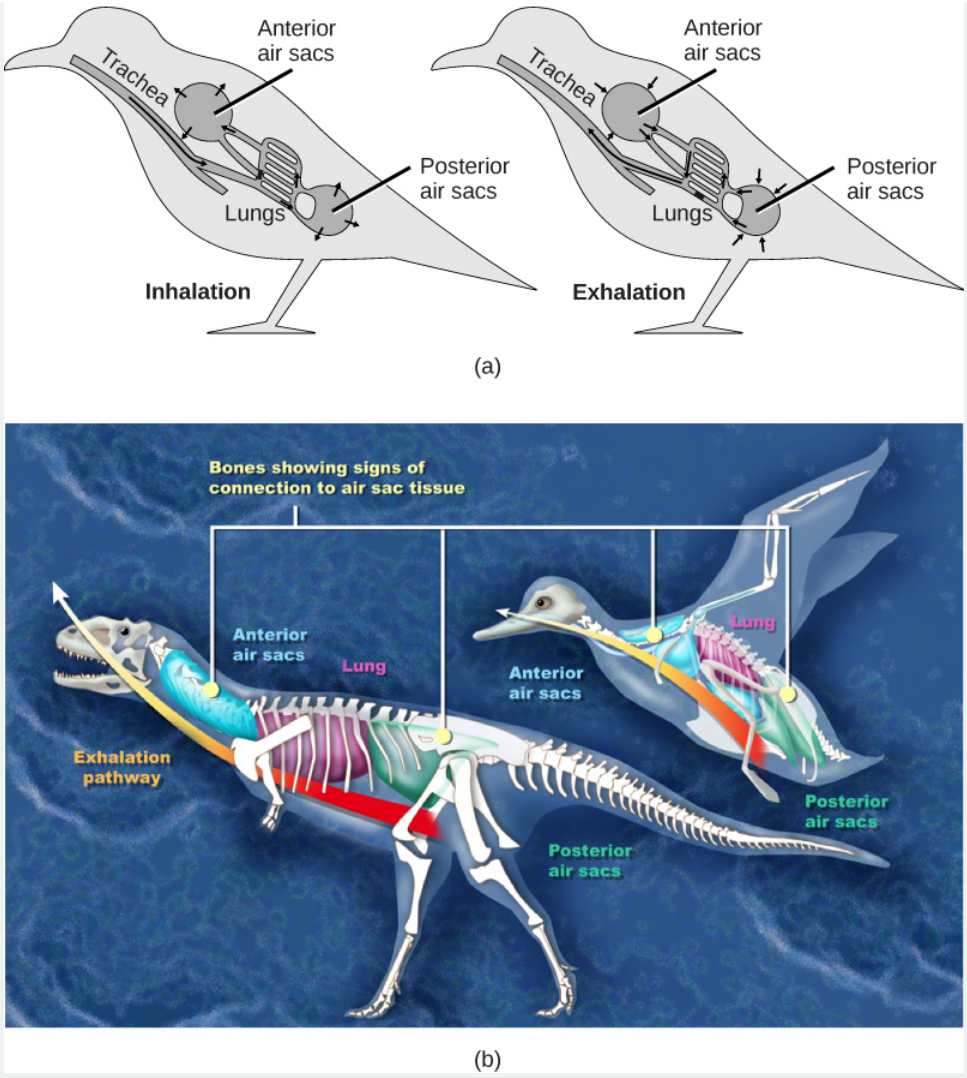


Figure **47.3.1.1**: (a) Birds have a flow-through respiratory system in which air flows unidirectionally from the posterior sacs into the lungs, then into the anterior air sacs. The air sacs connect to openings in hollow bones. (b) Dinosaurs, from which birds descended, have similar hollow bones and are believed to have had a similar respiratory system. (credit b: modification of work by Zina Deretsky, National Science Foundation)

Most of us consider that dinosaurs are extinct. However, modern birds are descendants of avian dinosaurs. The respiratory system of modern birds has been evolving for hundreds of millions of years.

All mammals have lungs that are the main organs for breathing. Lung capacity has evolved to support the animal's activities. During inhalation, the lungs expand with air, and oxygen diffuses across the lung's surface and enters the bloodstream. During exhalation, the lungs expel air and lung volume decreases. In the next few sections, the process of human breathing will be explained.

The Mechanics of Human Breathing

Boyle's Law is the gas law that states that in a closed space, pressure and volume are inversely related. As volume decreases, pressure increases and vice versa (Figure **47.3.1.2**). The relationship between gas pressure and volume helps to explain the mechanics of breathing.

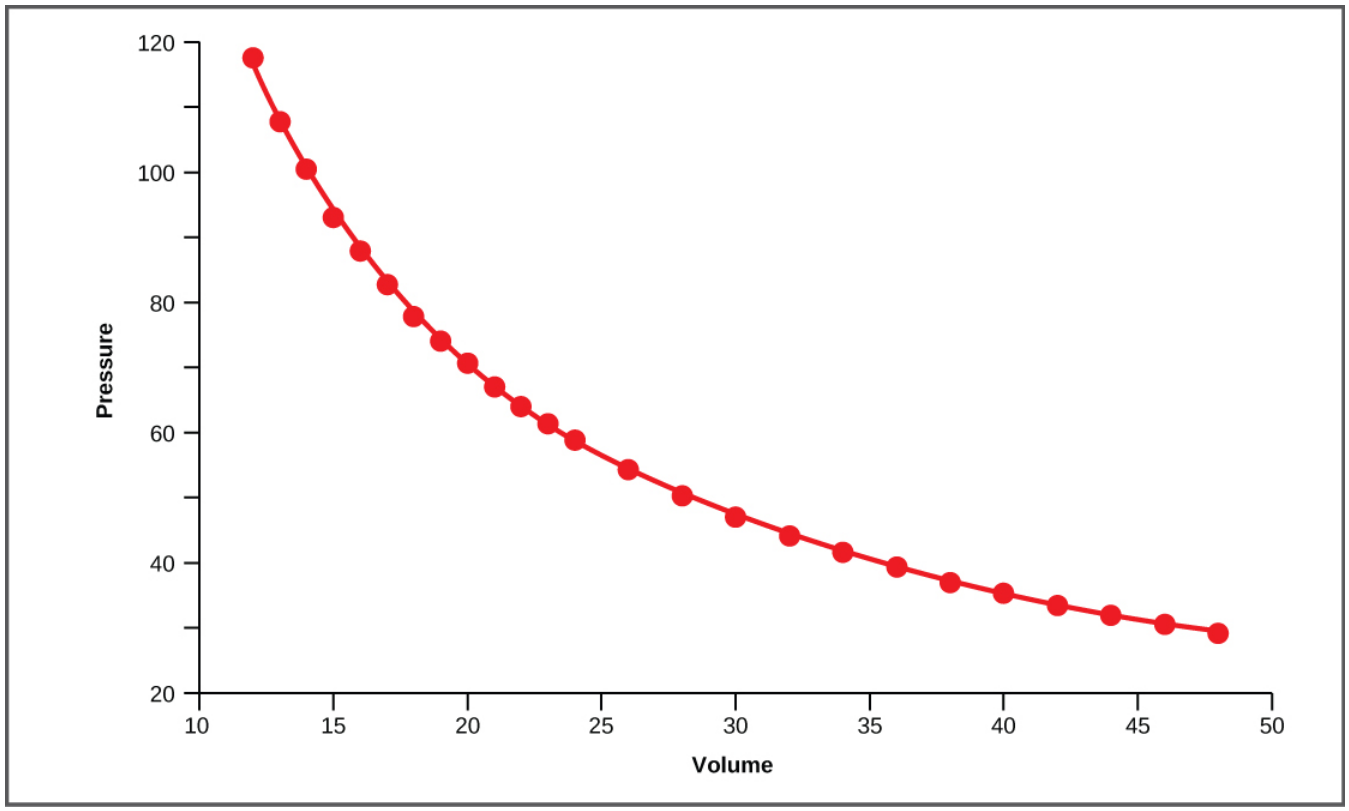


Figure **47.3.1.2**: This graph shows data from Boyle's original 1662 experiment, which shows that pressure and volume are inversely related. No units are given as Boyle used arbitrary units in his experiments.

There is always a slightly negative pressure within the thoracic cavity, which aids in keeping the airways of the lungs open. During inhalation, volume increases as a result of contraction of the diaphragm, and pressure decreases (according to Boyle's Law). This decrease of pressure in the thoracic cavity relative to the environment makes the cavity less than the atmosphere (Figure **47.3.1.3**a). Because of this drop in pressure, air rushes into the respiratory passages. To increase the volume of the lungs, the chest wall expands. This results from the contraction of the intercostal muscles, the muscles that are connected to the rib cage. Lung volume expands because the diaphragm contracts and the intercostals muscles contract, thus expanding the thoracic cavity. This increase in the volume of the thoracic cavity lowers pressure compared to the atmosphere, so air rushes into the lungs, thus increasing its volume. The resulting increase in volume is largely attributed to an increase in alveolar space, because the bronchioles and bronchi are stiff structures that do not change in size.

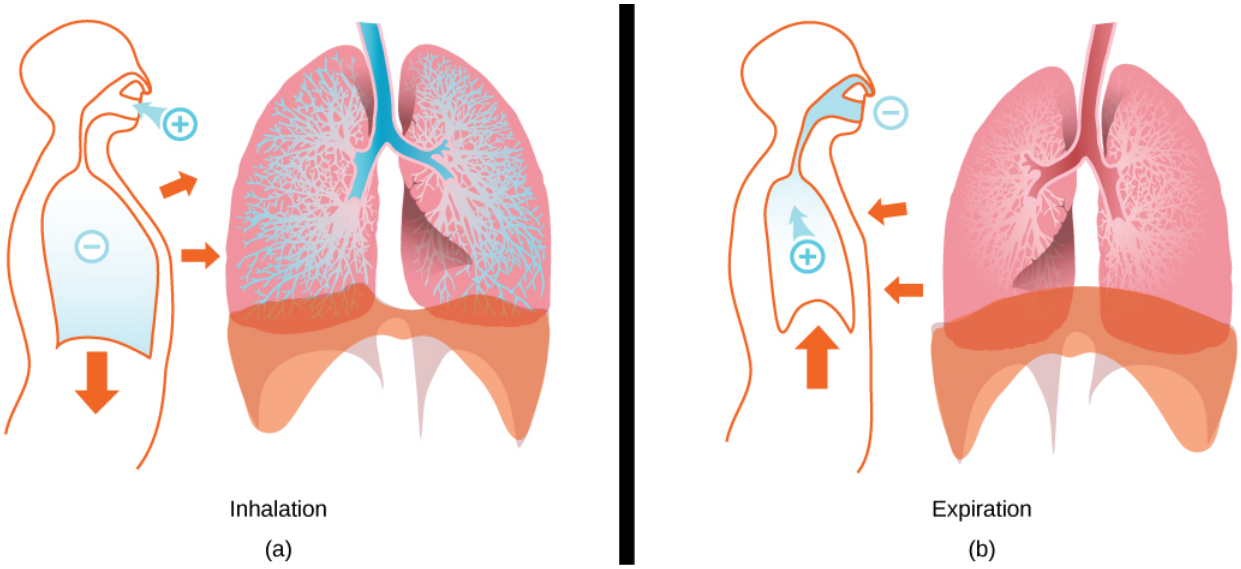


Figure **47.3.1.3**: The lungs, chest wall, and diaphragm are all involved in respiration, both (a) inhalation and (b) expiration. (credit: modification of work by Mariana Ruiz Villareal)

The chest wall expands out and away from the lungs. The lungs are elastic; therefore, when air fills the lungs, the elastic recoil within the tissues of the lung exerts pressure back toward the interior of the lungs. These outward and inward forces compete to inflate and deflate the lung with every breath. Upon exhalation, the lungs recoil to force the air out of the lungs, and the intercostal muscles relax, returning the chest wall back to its original position (Figure **47.3.1.3**b). The diaphragm also relaxes and moves higher into the thoracic cavity. This increases the pressure within the thoracic cavity relative to the environment, and air rushes out of the lungs. The movement of air out of the lungs is a passive event. No muscles are contracting to expel the air.

Each lung is surrounded by an invaginated sac. The layer of tissue that covers the lung and dips into spaces is called the visceral pleura. A second layer of parietal pleura lines the interior of the thorax (Figure **47.3.1.4**). The space between these layers, the intrapleural space, contains a small amount of fluid that protects the tissue and reduces the friction generated from rubbing the tissue layers together as the lungs contract and relax. Pleurisy results when these layers of tissue become inflamed; it is painful because the inflammation increases the pressure within the thoracic cavity and reduces the volume of the lung.

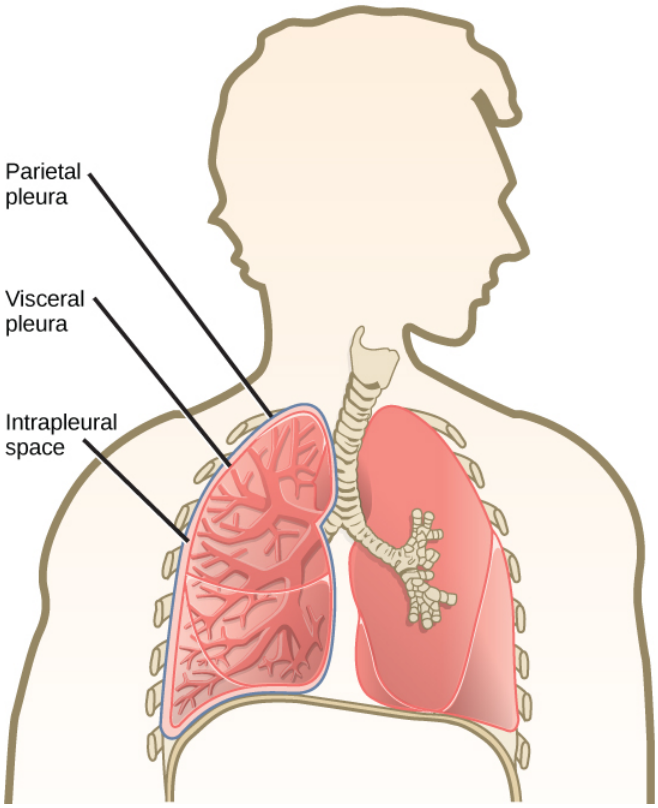


Figure 47.3.1.4: A tissue layer called pleura surrounds the lung and interior of the thoracic cavity. (credit: modification of work by NCI)

Link to Learning



View how Boyle's Law is related to breathing and watch this video on Boyle's Law.

The Work of Breathing

The number of breaths per minute is the respiratory rate. On average, under non-exertion conditions, the human respiratory rate is 12–15 breaths/minute. The respiratory rate contributes to the alveolar ventilation, or how much air moves into and out of the alveoli. Alveolar ventilation prevents carbon dioxide buildup in the alveoli. There are two ways to keep the alveolar ventilation

constant: increase the respiratory rate while decreasing the tidal volume of air per breath (shallow breathing), or decrease the respiratory rate while increasing the tidal volume per breath. In either case, the ventilation remains the same, but the work done and type of work needed are quite different. Both tidal volume and respiratory rate are closely regulated when oxygen demand increases.

There are two types of work conducted during respiration, flow-resistive and elastic work. Flow-resistive refers to the work of the alveoli and tissues in the lung, whereas elastic work refers to the work of the intercostal muscles, chest wall, and diaphragm. Increasing the respiration rate increases the flow-resistive work of the airways and decreases the elastic work of the muscles. Decreasing the respiratory rate reverses the type of work required.

Surfactant

The air-tissue/water interface of the alveoli has a high surface tension. This surface tension is similar to the surface tension of water at the liquid-air interface of a water droplet that results in the bonding of the water molecules together. Surfactant is a complex mixture of phospholipids and lipoproteins that works to reduce the surface tension that exists between the alveoli tissue and the air found within the alveoli. By lowering the surface tension of the alveolar fluid, it reduces the tendency of alveoli to collapse.

Surfactant works like a detergent to reduce the surface tension and allows for easier inflation of the airways. When a balloon is first inflated, it takes a large amount of effort to stretch the plastic and start to inflate the balloon. If a little bit of detergent was applied to the interior of the balloon, then the amount of effort or work needed to begin to inflate the balloon would decrease, and it would become much easier to start blowing up the balloon. This same principle applies to the airways. A small amount of surfactant to the airway tissues reduces the effort or work needed to inflate those airways. Babies born prematurely sometimes do not produce enough surfactant. As a result, they suffer from respiratory distress syndrome, because it requires more effort to inflate their lungs. Surfactant is also important for preventing collapse of small alveoli relative to large alveoli.

Lung Resistance and Compliance

Pulmonary diseases reduce the rate of gas exchange into and out of the lungs. Two main causes of decreased gas exchange are compliance (how elastic the lung is) and resistance (how much obstruction exists in the airways). A change in either can dramatically alter breathing and the ability to take in oxygen and release carbon dioxide.

Examples of restrictive diseases are respiratory distress syndrome and pulmonary fibrosis. In both diseases, the airways are less compliant and they are stiff or fibrotic. There is a decrease in compliance because the lung tissue cannot bend and move. In these types of restrictive diseases, the intrapleural pressure is more positive and the airways collapse upon exhalation, which traps air in the lungs. Forced or functional vital capacity (FVC), which is the amount of air that can be forcibly exhaled after taking the deepest breath possible, is much lower than in normal patients, and the time it takes to exhale most of the air is greatly prolonged (Figure **47.3.1.5**). A patient suffering from these diseases cannot exhale the normal amount of air.

Obstructive diseases and conditions include emphysema, asthma, and pulmonary edema. In emphysema, which mostly arises from smoking tobacco, the walls of the alveoli are destroyed, decreasing the surface area for gas exchange. The overall compliance of the lungs is increased, because as the alveolar walls are damaged, lung elastic recoil decreases due to a loss of elastic fibers, and more air is trapped in the lungs at the end of exhalation. Asthma is a disease in which inflammation is triggered by environmental factors. Inflammation obstructs the airways. The obstruction may be due to edema (fluid accumulation), smooth muscle spasms in the walls of the bronchioles, increased mucus secretion, damage to the epithelia of the airways, or a combination of these events. Those with asthma or edema experience increased occlusion from increased inflammation of the airways. This tends to block the airways, preventing the proper movement of gases (Figure **47.3.1.5**). Those with obstructive diseases have large volumes of air trapped after exhalation and breathe at a very high lung volume to compensate for the lack of airway recruitment.

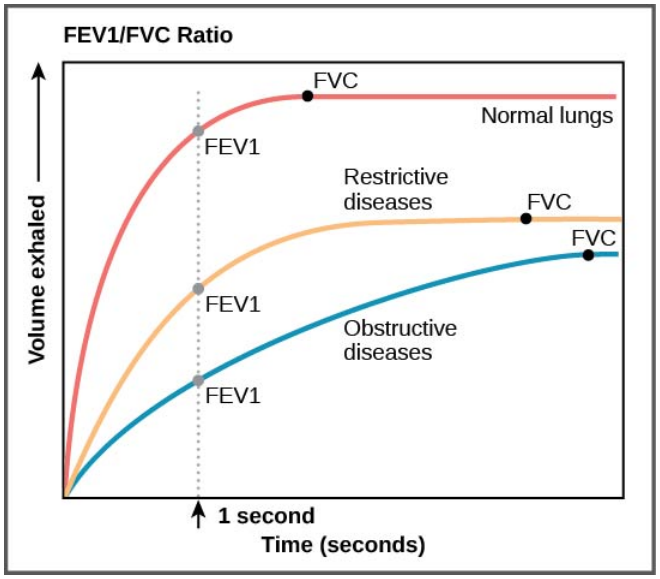


Figure 47.3.1.5: The ratio of FEV1 (the amount of air that can be forcibly exhaled in one second after taking a deep breath) to FVC (the total amount of air that can be forcibly exhaled) can be used to diagnose whether a person has restrictive or obstructive lung disease. In restrictive lung disease, FVC is reduced but airways are not obstructed, so the person is able to expel air reasonably fast. In obstructive lung disease, airway obstruction results in slow exhalation as well as reduced FVC. Thus, the FEV1/FVC ratio is lower in persons with obstructive lung disease (less than 69 percent) than in persons with restrictive disease (88 to 90 percent).

Dead Space: V/Q Mismatch

Pulmonary circulation pressure is very low compared to that of the systemic circulation. It is also independent of cardiac output. This is because of a phenomenon called recruitment, which is the process of opening airways that normally remain closed when cardiac output increases. As cardiac output increases, the number of capillaries and arteries that are perfused (filled with blood) increases. These capillaries and arteries are not always in use but are ready if needed. At times, however, there is a mismatch between the amount of air (ventilation, V) and the amount of blood (perfusion, Q) in the lungs. This is referred to as ventilation/perfusion (V/Q) mismatch.

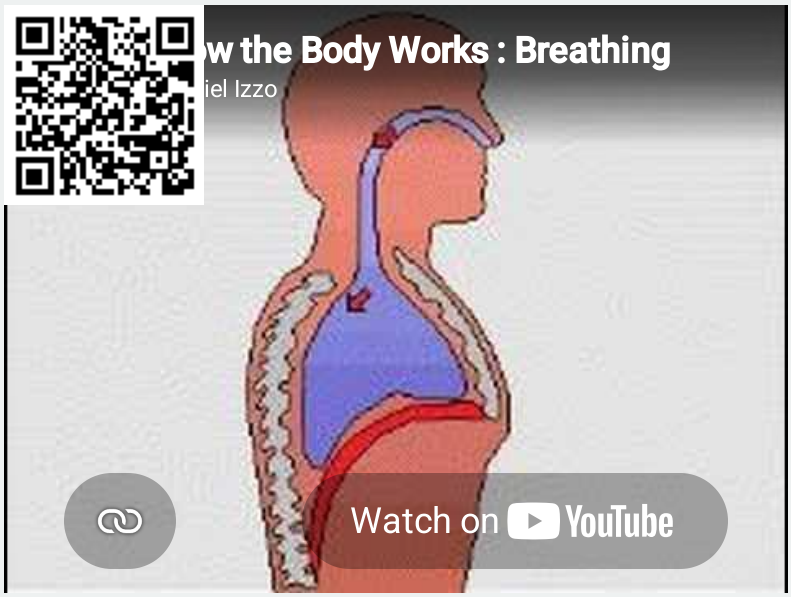
There are two types of V/Q mismatch. Both produce dead space, regions of broken down or blocked lung tissue. Dead spaces can severely impact breathing, because they reduce the surface area available for gas diffusion. As a result, the amount of oxygen in the blood decreases, whereas the carbon dioxide level increases. Dead space is created when no ventilation and/or perfusion takes place. Anatomical dead space or anatomical shunt, arises from an anatomical failure, while physiological dead space or physiological shunt, arises from a functional impairment of the lung or arteries.

An example of an anatomical shunt is the effect of gravity on the lungs. The lung is particularly susceptible to changes in the magnitude and direction of gravitational forces. When someone is standing or sitting upright, the pleural pressure gradient leads to increased ventilation further down in the lung. As a result, the intrapleural pressure is more negative at the base of the lung than at the top, and more air fills the bottom of the lung than the top. Likewise, it takes less energy to pump blood to the bottom of the lung than to the top when in a prone position. Perfusion of the lung is not uniform while standing or sitting. This is a result of hydrostatic forces combined with the effect of airway pressure. An anatomical shunt develops because the ventilation of the airways does not match the perfusion of the arteries surrounding those airways. As a result, the rate of gas exchange is reduced. Note that this does not occur when lying down, because in this position, gravity does not preferentially pull the bottom of the lung down.

A physiological shunt can develop if there is infection or edema in the lung that obstructs an area. This will decrease ventilation but not affect perfusion; therefore, the V/Q ratio changes and gas exchange is affected.

The lung can compensate for these mismatches in ventilation and perfusion. If ventilation is greater than perfusion, the arterioles dilate and the bronchioles constrict. This increases perfusion and reduces ventilation. Likewise, if ventilation is less than perfusion, the arterioles constrict and the bronchioles dilate to correct the imbalance.

Link to Learning



Visit this site to view the mechanics of breathing.

Summary

The structure of the lungs and thoracic cavity control the mechanics of breathing. Upon inspiration, the diaphragm contracts and lowers. The intercostal muscles contract and expand the chest wall outward. The intrapleural pressure drops, the lungs expand, and air is drawn into the airways. When exhaling, the intercostal muscles and diaphragm relax, returning the intrapleural pressure back to the resting state. The lungs recoil and airways close. The air passively exits the lung. There is high surface tension at the air-airway interface in the lung. Surfactant, a mixture of phospholipids and lipoproteins, acts like a detergent in the airways to reduce surface tension and allow for opening of the alveoli.

Breathing and gas exchange are both altered by changes in the compliance and resistance of the lung. If the compliance of the lung decreases, as occurs in restrictive diseases like fibrosis, the airways stiffen and collapse upon exhalation. Air becomes trapped in the lungs, making breathing more difficult. If resistance increases, as happens with asthma or emphysema, the airways become obstructed, trapping air in the lungs and causing breathing to become difficult. Alterations in the ventilation of the airways or perfusion of the arteries can affect gas exchange. These changes in ventilation and perfusion, called V/Q mismatch, can arise from anatomical or physiological changes.

Glossary

alveolar ventilation
: how much air is in the alveoli

anatomical dead space
: (also, anatomical shunt) region of the lung that lacks proper ventilation/perfusion due to an anatomical block

compliance
: measurement of the elasticity of the lung

dead space
: area in the lung that lacks proper ventilation or perfusion

elastic recoil
: property of the lung that drives the lung tissue inward

elastic work

work conducted by the intercostal muscles, chest wall, and diaphragm

flow-resistive

work of breathing performed by the alveoli and tissues in the lung

functional vital capacity (FVC)

amount of air that can be forcibly exhaled after taking the deepest breath possible

intercostal muscle

muscle connected to the rib cage that contracts upon inspiration

intrapleural space

space between the layers of pleura

obstructive disease

disease (such as emphysema and asthma) that arises from obstruction of the airways; compliance increases in these diseases

physiological dead space

(also, physiological shunt) region of the lung that lacks proper ventilation/perfusion due to a physiological change in the lung (like inflammation or edema)

pleura

tissue layer that surrounds the lungs and lines the interior of the thoracic cavity

pleurisy

painful inflammation of the pleural tissue layers

recruitment

process of opening airways that normally remain closed when the cardiac output increases

resistance

measurement of lung obstruction

respiratory distress syndrome

disease that arises from a deficient amount of surfactant

respiratory rate

number of breaths per minute

restrictive disease

disease that results from a restriction and decreased compliance of the alveoli; respiratory distress syndrome and pulmonary fibrosis are examples

surfactant

detergent-like liquid in the airways that lowers the surface tension of the alveoli to allow for expansion

ventilation/perfusion (V/Q) mismatch

region of the lung that lacks proper alveolar ventilation (V) and/or arterial perfusion (Q)

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47.4: Structures, Mechanisms, and Control of Ventilation in Mammals

In mammals, pulmonary ventilation occurs via inhalation (breathing). During inhalation, air enters the body through the **nasal cavity** located just inside the nose (Figure 1). As air passes through the nasal cavity, the air is warmed to body temperature and humidified. The respiratory tract is coated with mucus to seal the tissues from direct contact with air. Mucus is high in water. As air crosses these surfaces of the mucous membranes, it picks up water. These processes help equilibrate the air to the body conditions, reducing any damage that cold, dry air can cause. Particulate matter that is floating in the air is removed in the nasal passages via mucus and cilia. The processes of warming, humidifying, and removing particles are important protective mechanisms that prevent damage to the trachea and lungs. Thus, inhalation serves several purposes in addition to bringing oxygen into the respiratory system.

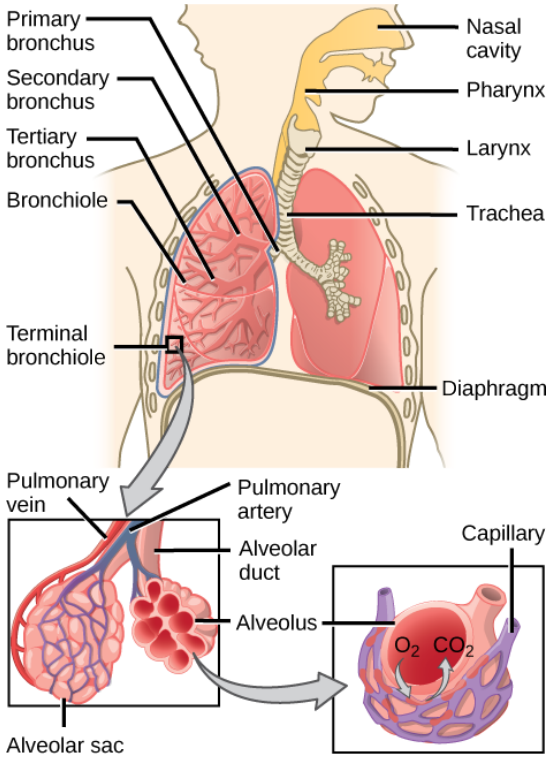


Figure 1. Air enters the respiratory system through the nasal cavity and pharynx, and then passes through the trachea and into the bronchi, which bring air into the lungs. (credit: modification of work by NCI)

? Practice Question

Which of the following statements about the mammalian respiratory system is false?

a. When we breathe in, air travels from the pharynx to the trachea.
b. The bronchioles branch into bronchi.
c. Alveolar ducts connect to alveolar sacs.
d. Gas exchange between the lung and blood takes place in the alveolus.

[reveal-answer q="997523"]Show Answer[/reveal-answer]
[hidden-answer a="997523"]Statement b is false.[/hidden-answer]

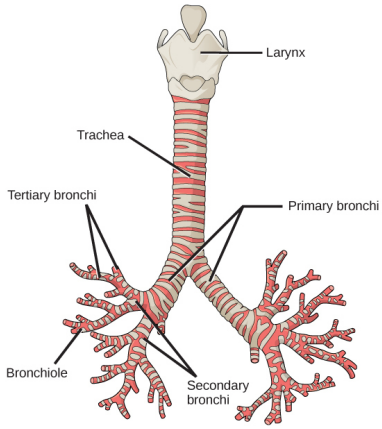


Figure 2. The trachea and bronchi are made of incomplete rings of cartilage. (credit: modification of work by Gray's Anatomy)

From the nasal cavity, air passes through the **pharynx** (throat) and the **larynx** (voice box), as it makes its way to the **trachea** (Figure 1). The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder about 10 to 12 cm long and 2 cm in diameter that sits in front of the esophagus and extends from the larynx into the chest cavity where it divides into the two primary bronchi at the midthorax. It is made of incomplete rings of hyaline cartilage and smooth muscle (Figure 2).

The trachea is lined with mucus-producing goblet cells and ciliated epithelia. The cilia propel foreign particles trapped in the mucus toward the pharynx. The cartilage provides strength and support to the trachea to keep the passage open. The smooth muscle can contract, decreasing the trachea's diameter, which causes expired air to rush upwards from the lungs at a great force. The forced exhalation helps expel mucus when we cough. Smooth muscle can contract or relax, depending on stimuli from the external environment or the body's nervous system.

Lungs: Bronchi and Alveoli

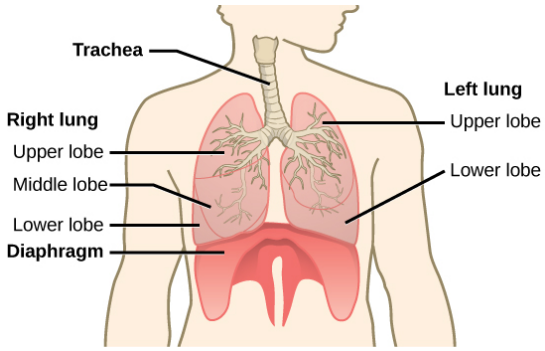


Figure 3. The trachea bifurcates into the right and left bronchi in the lungs. The right lung is made of three lobes and is larger. To accommodate the heart, the left lung is smaller and has only two lobes.

The end of the trachea bifurcates (divides) to the right and left lungs. The lungs are not identical. The right lung is larger and contains three lobes, whereas the smaller left lung contains two lobes (Figure 3). The muscular **diaphragm**, which facilitates breathing, is inferior (below) to the lungs and marks the end of the thoracic cavity.

In the lungs, air is diverted into smaller and smaller passages, or **bronchi**. Air enters the lungs through the two **primary (main) bronchi** (singular: bronchus). Each bronchus divides into secondary bronchi, then into tertiary bronchi, which in turn divide, creating smaller and smaller diameter **bronchioles** as they split and spread through the lung. Like the trachea, the bronchi are made of cartilage and smooth muscle. At the bronchioles, the cartilage is replaced with elastic fibers. Bronchi are innervated by nerves of both the parasympathetic and sympathetic nervous systems that control muscle contraction (parasympathetic) or relaxation (sympathetic) in the bronchi and bronchioles, depending on the nervous system's cues. In humans, bronchioles with a diameter smaller than 0.5 mm are the **respiratory bronchioles**. They lack cartilage and therefore rely on inhaled air to support their shape. As the passageways decrease in diameter, the relative amount of smooth muscle increases.

The **terminal bronchioles** subdivide into microscopic branches called respiratory bronchioles. The respiratory bronchioles subdivide into several alveolar ducts. Numerous alveoli and alveolar sacs surround the alveolar ducts. The alveolar sacs resemble bunches of grapes tethered to the end of the bronchioles (Figure 4).

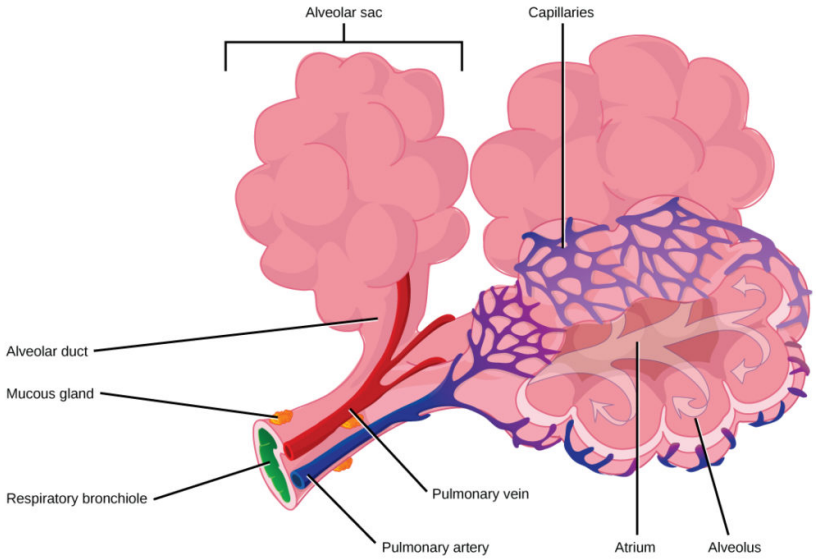


Figure 4. Terminal bronchioles are connected by respiratory bronchioles to alveolar ducts and alveolar sacs. Each alveolar sac contains 20 to 30 spherical alveoli and has the appearance of a bunch of grapes. Air flows into the atrium of the alveolar sac, then circulates into alveoli where gas exchange occurs with the capillaries. Mucous glands secrete mucous into the airways, keeping them moist and flexible. (credit: modification of work by Mariana Ruiz Villareal)

In the acinar region, the **alveolar ducts** are attached to the end of each bronchiole. At the end of each duct are approximately 100 **alveolar sacs**, each containing 20 to 30 **alveoli** that are 200 to 300 microns in diameter. Gas exchange occurs only in alveoli. Alveoli are made of thin-walled parenchymal cells, typically one-cell thick, that look like tiny bubbles within the sacs. Alveoli are in direct contact with capillaries (one-cell thick) of the circulatory system. Such intimate contact ensures that oxygen will diffuse from alveoli into the blood and be distributed to the cells of the body. In addition, the carbon dioxide that was produced by cells as a waste product will diffuse from the blood into alveoli to be exhaled. The anatomical arrangement of capillaries and alveoli emphasizes the structural and functional relationship of the respiratory and circulatory systems. Because there are so many alveoli (~300 million per lung) within each alveolar sac and so many sacs at the end of each alveolar duct, the lungs have a sponge-like consistency. This organization produces a very large surface area that is available for gas exchange. The surface area of alveoli in the lungs is approximately 75 m^2. This large surface area, combined with the thin-walled nature of the alveolar parenchymal cells, allows gases to easily diffuse across the cells.

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47.5: Transport of Gases in Body Fluid

Skills to Develop

- Describe how oxygen is bound to hemoglobin and transported to body tissues
- Explain how carbon dioxide is transported from body tissues to the lungs

Once the oxygen diffuses across the alveoli, it enters the bloodstream and is transported to the tissues where it is unloaded, and carbon dioxide diffuses out of the blood and into the alveoli to be expelled from the body. Although gas exchange is a continuous process, the oxygen and carbon dioxide are transported by different mechanisms.

Transport of Oxygen in the Blood

Although oxygen dissolves in blood, only a small amount of oxygen is transported this way. Only 1.5 percent of oxygen in the blood is dissolved directly into the blood itself. Most oxygen—98.5 percent—is bound to a protein called hemoglobin and carried to the tissues.

Hemoglobin

Hemoglobin, or Hb, is a protein molecule found in red blood cells (erythrocytes) made of four subunits: two alpha subunits and two beta subunits (Figure **47.5.1**). Each subunit surrounds a central heme group that contains iron and binds one oxygen molecule, allowing each hemoglobin molecule to bind four oxygen molecules. Molecules with more oxygen bound to the heme groups are brighter red. As a result, oxygenated arterial blood where the Hb is carrying four oxygen molecules is bright red, while venous blood that is deoxygenated is darker red.

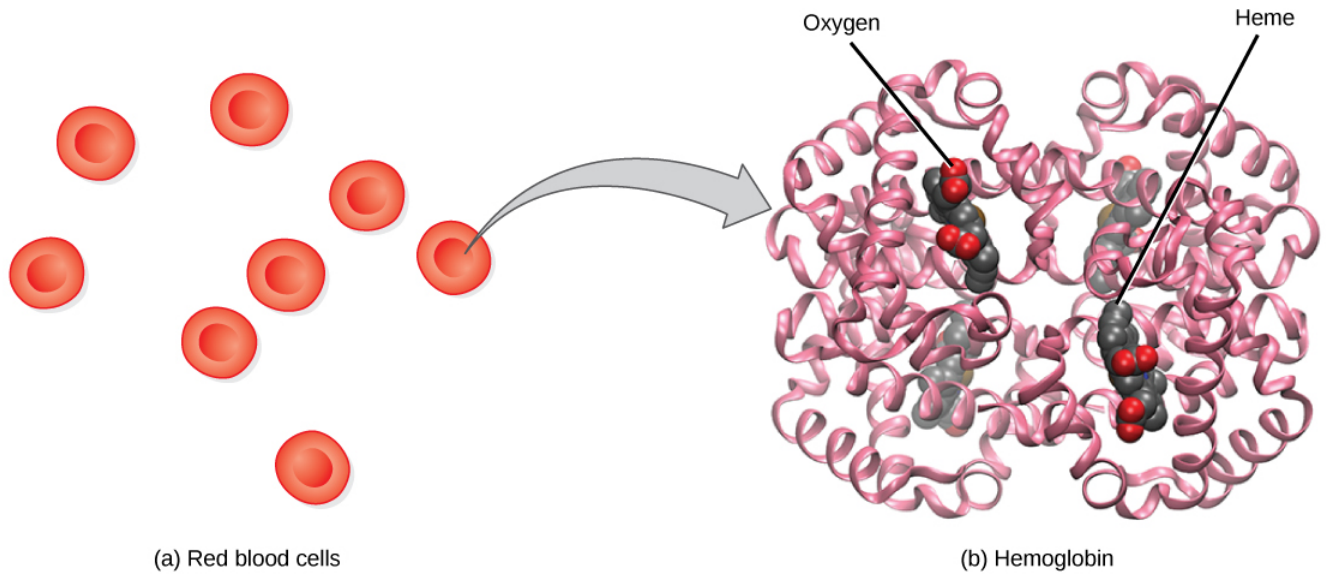


Figure **47.5.1**: The protein inside (a) red blood cells that carries oxygen to cells and carbon dioxide to the lungs is (b) hemoglobin. Hemoglobin is made up of four symmetrical subunits and four heme groups. Iron associated with the heme binds oxygen. It is the iron in hemoglobin that gives blood its red color.

It is easier to bind a second and third oxygen molecule to Hb than the first molecule. This is because the hemoglobin molecule changes its shape, or conformation, as oxygen binds. The fourth oxygen is then more difficult to bind. The binding of oxygen to hemoglobin can be plotted as a function of the partial pressure of oxygen in the blood (x-axis) versus the relative Hb-oxygen saturation (y-axis). The resulting graph—an oxygen dissociation curve—is sigmoidal, or S-shaped (Figure **47.5.2**). As the partial pressure of oxygen increases, the hemoglobin becomes increasingly saturated with oxygen.

Art Connection

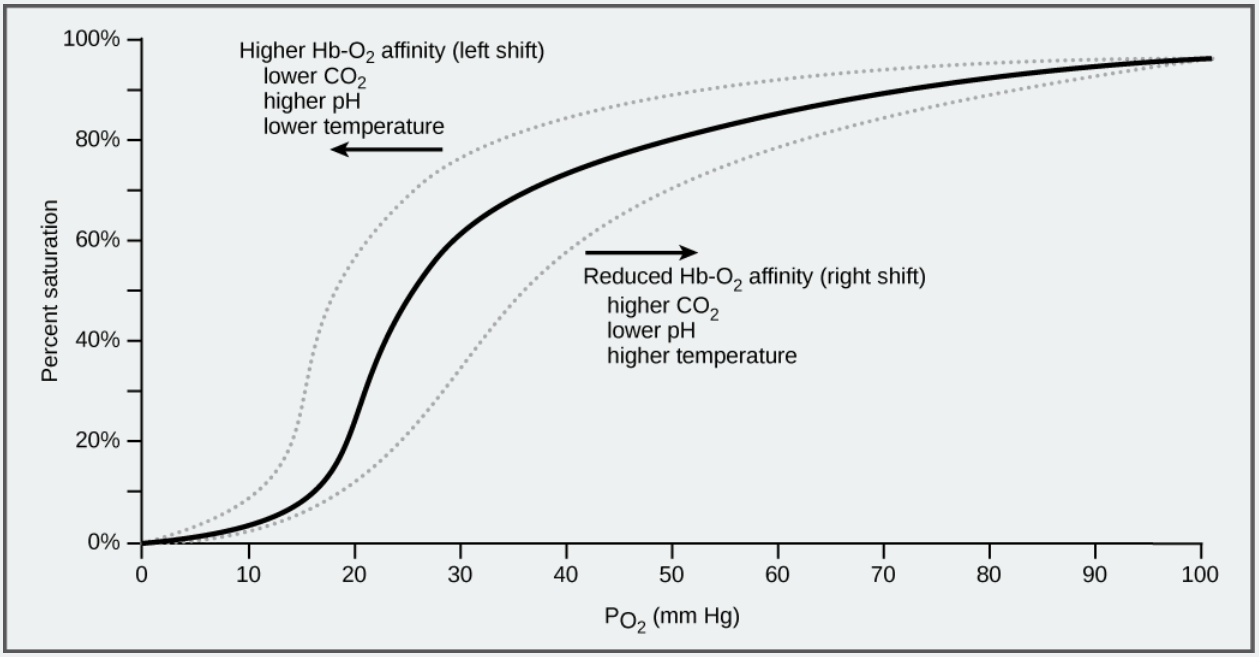


Figure 47.5.2: The oxygen dissociation curve demonstrates that, as the partial pressure of oxygen increases, more oxygen binds hemoglobin. However, the affinity of hemoglobin for oxygen may shift to the left or the right depending on environmental conditions.

The kidneys are responsible for removing excess H^+ ions from the blood. If the kidneys fail, what would happen to blood pH and to hemoglobin affinity for oxygen?

Factors That Affect Oxygen Binding

The oxygen-carrying capacity of hemoglobin determines how much oxygen is carried in the blood. In addition to $\mathbf{P_{O_2}}$, other environmental factors and diseases can affect oxygen carrying capacity and delivery.

Carbon dioxide levels, blood pH, and body temperature affect oxygen-carrying capacity (Figure 47.5.2). When carbon dioxide is in the blood, it reacts with water to form bicarbonate ($\mathbf{HCO_3^-}$) and hydrogen ions (H^+). As the level of carbon dioxide in the blood increases, more H^+ is produced and the pH decreases. This increase in carbon dioxide and subsequent decrease in pH reduce the affinity of hemoglobin for oxygen. The oxygen dissociates from the Hb molecule, shifting the oxygen dissociation curve to the right. Therefore, more oxygen is needed to reach the same hemoglobin saturation level as when the pH was higher. A similar shift in the curve also results from an increase in body temperature. Increased temperature, such as from increased activity of skeletal muscle, causes the affinity of hemoglobin for oxygen to be reduced.

Diseases like sickle cell anemia and thalassemia decrease the blood's ability to deliver oxygen to tissues and its oxygen-carrying capacity. In sickle cell anemia, the shape of the red blood cell is crescent-shaped, elongated, and stiffened, reducing its ability to deliver oxygen (Figure 47.5.3). In this form, red blood cells cannot pass through the capillaries. This is painful when it occurs. Thalassemia is a rare genetic disease caused by a defect in either the alpha or the beta subunit of Hb. Patients with thalassemia produce a high number of red blood cells, but these cells have lower-than-normal levels of hemoglobin. Therefore, the oxygen-carrying capacity is diminished.

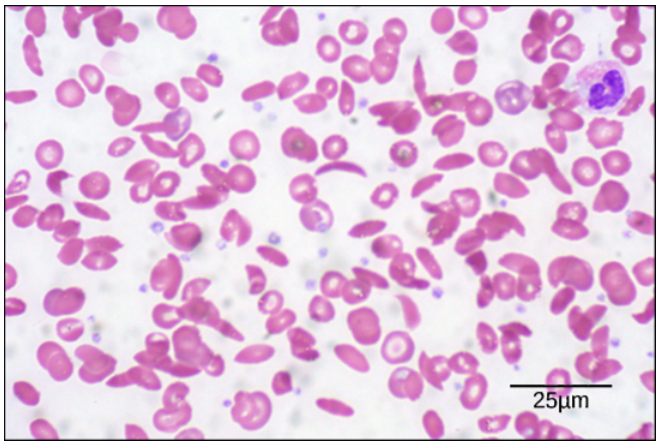


Figure **47.5.3**: Individuals with sickle cell anemia have crescent-shaped red blood cells. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Transport of Carbon Dioxide in the Blood

Carbon dioxide molecules are transported in the blood from body tissues to the lungs by one of three methods: dissolution directly into the blood, binding to hemoglobin, or carried as a bicarbonate ion. Several properties of carbon dioxide in the blood affect its transport. First, carbon dioxide is more soluble in blood than oxygen. About 5 to 7 percent of all carbon dioxide is dissolved in the plasma. Second, carbon dioxide can bind to plasma proteins or can enter red blood cells and bind to hemoglobin. This form transports about 10 percent of the carbon dioxide. When carbon dioxide binds to hemoglobin, a molecule called carbaminohemoglobin is formed. Binding of carbon dioxide to hemoglobin is reversible. Therefore, when it reaches the lungs, the carbon dioxide can freely dissociate from the hemoglobin and be expelled from the body.

Third, the majority of carbon dioxide molecules (85 percent) are carried as part of the bicarbonate buffer system. In this system, carbon dioxide diffuses into the red blood cells. Carbonic anhydrase (CA) within the red blood cells quickly converts the carbon dioxide into carbonic acid (H_2CO_3). Carbonic acid is an unstable intermediate molecule that immediately dissociates into bicarbonate ions ($\mathbf{HCO_3^-}$) and hydrogen (H^+) ions. Since carbon dioxide is quickly converted into bicarbonate ions, this reaction allows for the continued uptake of carbon dioxide into the blood down its concentration gradient. It also results in the production of H^+ ions. If too much H^+ is produced, it can alter blood pH. However, hemoglobin binds to the free H^+ ions and thus limits shifts in pH. The newly synthesized bicarbonate ion is transported out of the red blood cell into the liquid component of the blood in exchange for a chloride ion (Cl^-); this is called the chloride shift. When the blood reaches the lungs, the bicarbonate ion is transported back into the red blood cell in exchange for the chloride ion. The H^+ ion dissociates from the hemoglobin and binds to the bicarbonate ion. This produces the carbonic acid intermediate, which is converted back into carbon dioxide through the enzymatic action of CA. The carbon dioxide produced is expelled through the lungs during exhalation.

$$\mathbf{CO_2 + H_2O \leftrightharpoons \underset{\text{(carbonic acid)}}{H_2CO_3} \leftrightarrow \underset{\text{(bicarbonate)}}{HCO_3 + H^+}}$$

The benefit of the bicarbonate buffer system is that carbon dioxide is “soaked up” into the blood with little change to the pH of the system. This is important because it takes only a small change in the overall pH of the body for severe injury or death to result. The presence of this bicarbonate buffer system also allows for people to travel and live at high altitudes: When the partial pressure of oxygen and carbon dioxide change at high altitudes, the bicarbonate buffer system adjusts to regulate carbon dioxide while maintaining the correct pH in the body.

Carbon Monoxide Poisoning

While carbon dioxide can readily associate and dissociate from hemoglobin, other molecules such as carbon monoxide (CO) cannot. Carbon monoxide has a greater affinity for hemoglobin than oxygen. Therefore, when carbon monoxide is present, it binds to hemoglobin preferentially over oxygen. As a result, oxygen cannot bind to hemoglobin, so very little oxygen is transported through the body (Figure **47.5.4**). Carbon monoxide is a colorless, odorless gas and is therefore difficult to detect. It is produced by gas-powered vehicles and tools. Carbon monoxide can cause headaches, confusion, and nausea; long-term exposure can cause

brain damage or death. Administering 100 percent (pure) oxygen is the usual treatment for carbon monoxide poisoning. Administration of pure oxygen speeds up the separation of carbon monoxide from hemoglobin.

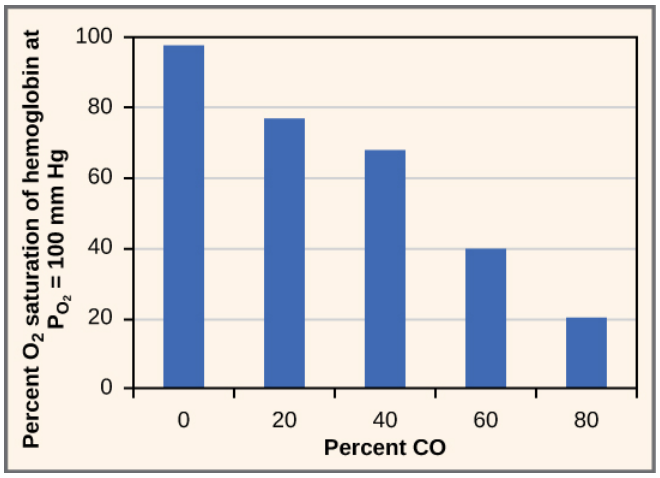


Figure **47.5.4**: As percent CO increases, the oxygen saturation of hemoglobin decreases.

Summary

Hemoglobin is a protein found in red blood cells that is comprised of two alpha and two beta subunits that surround an iron-containing heme group. Oxygen readily binds this heme group. The ability of oxygen to bind increases as more oxygen molecules are bound to heme. Disease states and altered conditions in the body can affect the binding ability of oxygen, and increase or decrease its ability to dissociate from hemoglobin.

Carbon dioxide can be transported through the blood via three methods. It is dissolved directly in the blood, bound to plasma proteins or hemoglobin, or converted into bicarbonate. The majority of carbon dioxide is transported as part of the bicarbonate system. Carbon dioxide diffuses into red blood cells. Inside, carbonic anhydrase converts carbon dioxide into carbonic acid (H_2CO_3), which is subsequently hydrolyzed into bicarbonate ($\mathbf{HCO_3^-}$) and H^+. The H^+ ion binds to hemoglobin in red blood cells, and bicarbonate is transported out of the red blood cells in exchange for a chloride ion. This is called the chloride shift. Bicarbonate leaves the red blood cells and enters the blood plasma. In the lungs, bicarbonate is transported back into the red blood cells in exchange for chloride. The H^+ dissociates from hemoglobin and combines with bicarbonate to form carbonic acid with the help of carbonic anhydrase, which further catalyzes the reaction to convert carbonic acid back into carbon dioxide and water. The carbon dioxide is then expelled from the lungs.

Art Connections

Figure **47.5.2**: The kidneys are responsible for removing excess H^+ ions from the blood. If the kidneys fail, what would happen to blood pH and to hemoglobin affinity for oxygen?

Answer

The blood pH will drop and hemoglobin affinity for oxygen will decrease.

Glossary

bicarbonate buffer system

system in the blood that absorbs carbon dioxide and regulates pH levels

bicarbonate ($\mathbf{HCO_3^-}$) ion

ion created when carbonic acid dissociates into H^+ and ($\mathbf{HCO_3^-}$)

carbaminohemoglobin

molecule that forms when carbon dioxide binds to hemoglobin

carbonic anhydrase (CA)
enzyme that catalyzes carbon dioxide and water into carbonic acid

chloride shift
chloride shift exchange of chloride for bicarbonate into or out of the red blood cell

heme group
centralized iron-containing group that is surrounded by the alpha and beta subunits of hemoglobin

hemoglobin
molecule in red blood cells that can bind oxygen, carbon dioxide, and carbon monoxide

oxygen-carrying capacity
amount of oxygen that can be transported in the blood

oxygen dissociation curve
curve depicting the affinity of oxygen for hemoglobin

sickle cell anemia
genetic disorder that affects the shape of red blood cells, and their ability to transport oxygen and move through capillaries

thalassemia
rare genetic disorder that results in mutation of the alpha or beta subunits of hemoglobin, creating smaller red blood cells with less hemoglobin

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CHAPTER OVERVIEW

48: The Circulatory System

48.1: Invertebrate Circulatory Systems

48.2: Components of Vertebrate Blood

48.3: Vertebrate Circulatory System

48.4: Cardiac Cycle, Electrical Conduction, ECG, and Cardiac Output

48.5: Blood Pressure and Blood Vessels

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48.1: Invertebrate Circulatory Systems

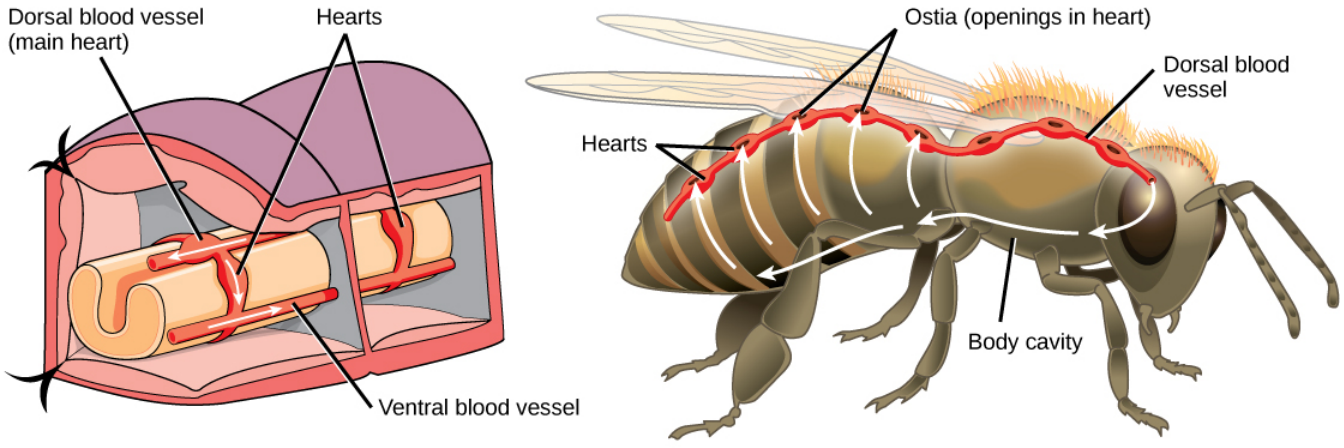
Skills to Develop

- Describe an open and closed circulatory system
- Describe interstitial fluid and hemolymph
- Compare and contrast the organization and evolution of the vertebrate circulatory system.

In all animals, except a few simple types, the circulatory system is used to transport nutrients and gases through the body. Simple diffusion allows some water, nutrient, waste, and gas exchange into primitive animals that are only a few cell layers thick; however, bulk flow is the only method by which the entire body of larger more complex organisms is accessed.

Circulatory System Architecture

The circulatory system is effectively a network of cylindrical vessels: the arteries, veins, and capillaries that emanate from a pump, the heart. In all vertebrate organisms, as well as some invertebrates, this is a closed-loop system, in which the blood is not free in a cavity. In a closed circulatory system, blood is contained inside blood vessels and circulates unidirectionally from the heart around the systemic circulatory route, then returns to the heart again, as illustrated in Figure 48.1.1a. As opposed to a closed system, arthropods—including insects, crustaceans, and most mollusks—have an open circulatory system, as illustrated in Figure 48.1.1b. In an open circulatory system, the blood is not enclosed in the blood vessels but is pumped into a cavity called a hemocoel and is called hemolymph because the blood mixes with the interstitial fluid. As the heart beats and the animal moves, the hemolymph circulates around the organs within the body cavity and then reenters the hearts through openings called ostia. This movement allows for gas and nutrient exchange. An open circulatory system does not use as much energy as a closed system to operate or to maintain; however, there is a trade-off with the amount of blood that can be moved to metabolically active organs and tissues that require high levels of oxygen. In fact, one reason that insects with wing spans of up to two feet wide (70 cm) are not around today is probably because they were outcompeted by the arrival of birds 150 million years ago. Birds, having a closed circulatory system, are thought to have moved more agilely, allowing them to get food faster and possibly to prey on the insects.



(a) Closed circulatory system (b) Open circulatory system

Figure 48.1.1: In (a) closed circulatory systems, the heart pumps blood through vessels that are separate from the interstitial fluid of the body. Most vertebrates and some invertebrates, like this annelid earthworm, have a closed circulatory system. In (b) open circulatory systems, a fluid called hemolymph is pumped through a blood vessel that empties into the body cavity. Hemolymph returns to the blood vessel through openings called ostia. Arthropods like this bee and most mollusks have open circulatory systems.

Circulatory System Variation in Animals

The circulatory system varies from simple systems in invertebrates to more complex systems in vertebrates. The simplest animals, such as the sponges (Porifera) and rotifers (Rotifera), do not need a circulatory system because diffusion allows adequate exchange of water, nutrients, and waste, as well as dissolved gases, as shown in Figure 48.1.2a. Organisms that are more complex but still only have two layers of cells in their body plan, such as jellies (Cnidaria) and comb jellies (Ctenophora) also use diffusion through

their epidermis and internally through the gastrovascular compartment. Both their internal and external tissues are bathed in an aqueous environment and exchange fluids by diffusion on both sides, as illustrated in Figure 48.1.2b. Exchange of fluids is assisted by the pulsing of the jellyfish body.

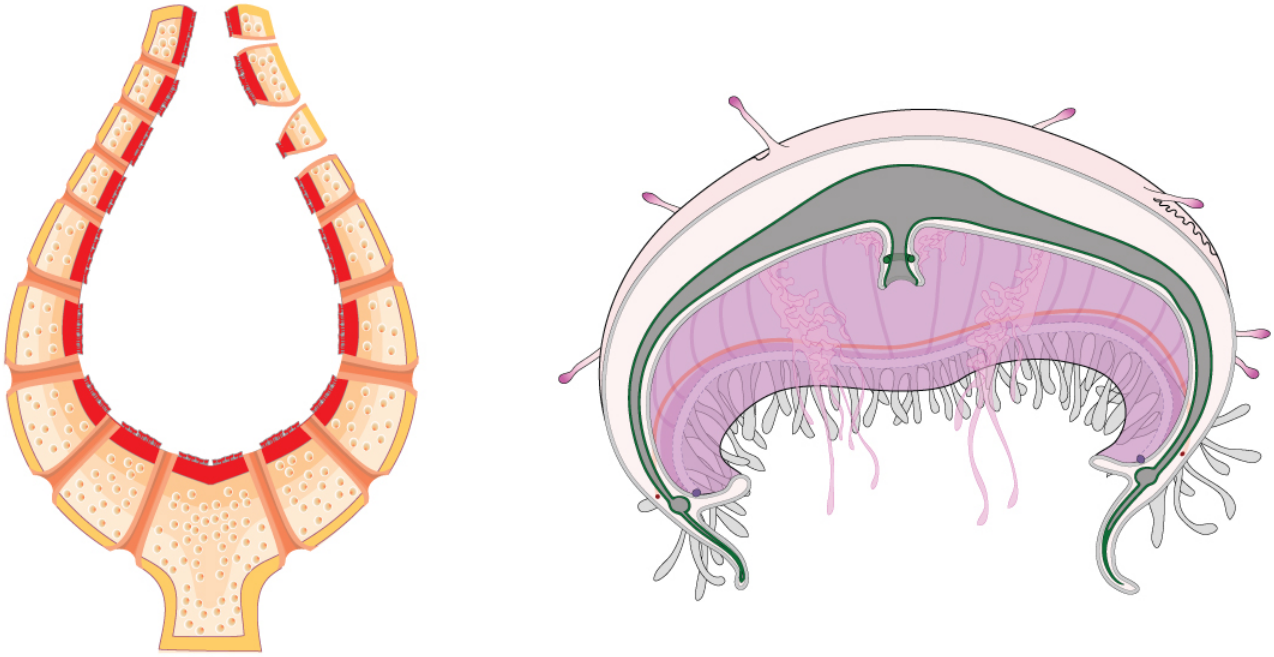
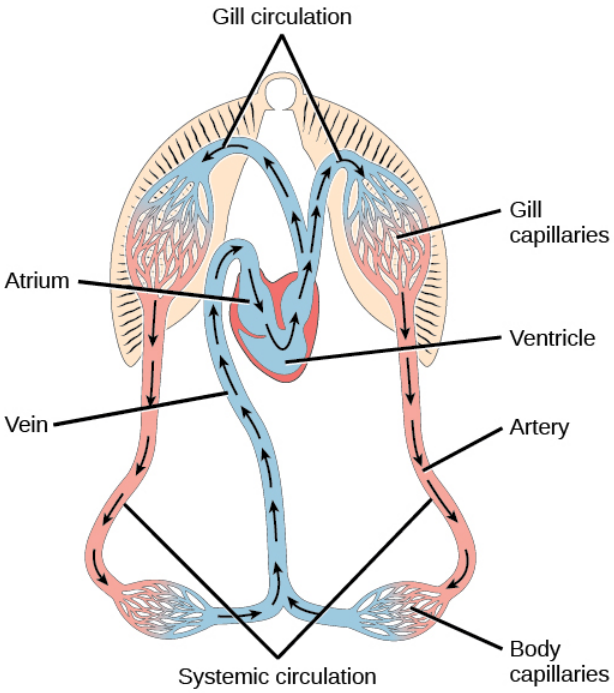
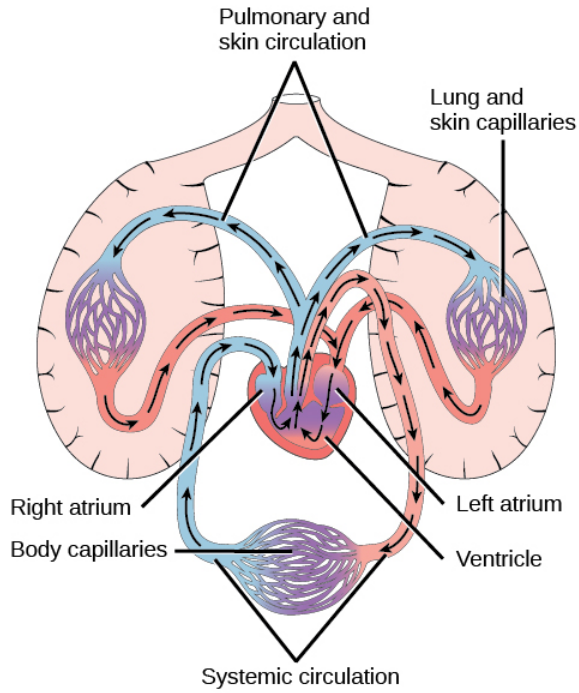


Figure 48.1.2: Simple animals consisting of a single cell layer such as the (a) sponge or only a few cell layers such as the (b) jellyfish do not have a circulatory system. Instead, gases, nutrients, and wastes are exchanged by diffusion.

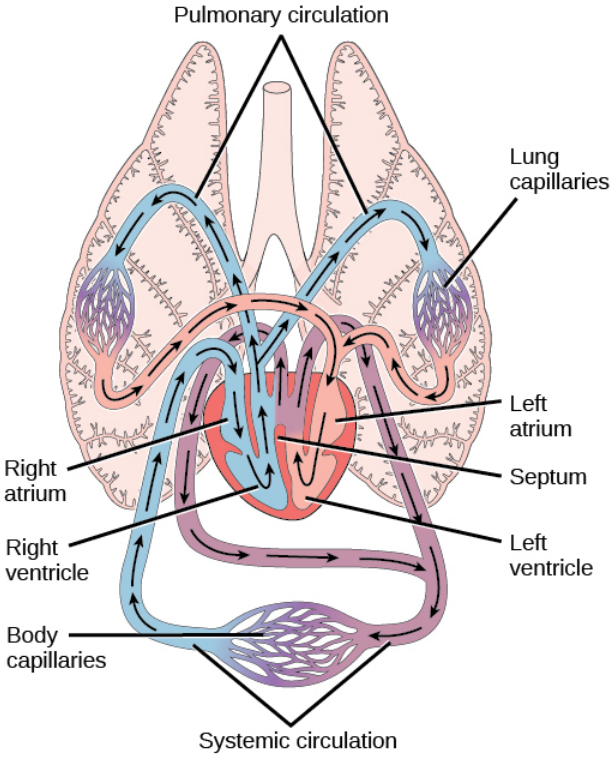
For more complex organisms, diffusion is not efficient for cycling gases, nutrients, and waste effectively through the body; therefore, more complex circulatory systems evolved. Most arthropods and many mollusks have open circulatory systems. In an open system, an elongated beating heart pushes the hemolymph through the body and muscle contractions help to move fluids. The larger more complex crustaceans, including lobsters, have developed arterial-like vessels to push blood through their bodies, and the most active mollusks, such as squids, have evolved a closed circulatory system and are able to move rapidly to catch prey. Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptation during evolution and associated differences in anatomy. Figure 48.1.3 illustrates the basic circulatory systems of some vertebrates: fish, amphibians, reptiles, and mammals.



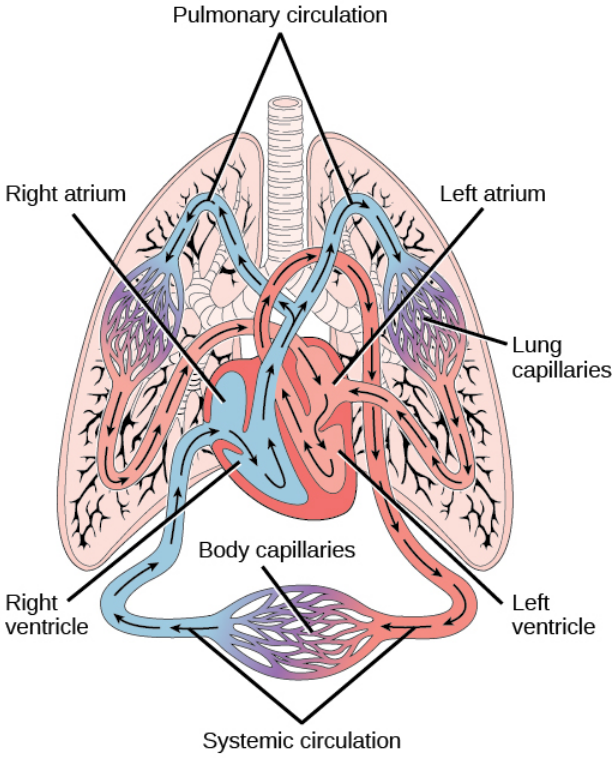
(a) Fish



(b) Amphibians



(c) Reptile



(d) Mammals

Figure 48.1.3: (a) Fish have the simplest circulatory systems of the vertebrates: blood flows unidirectionally from the two-chambered heart through the gills and then the rest of the body. (b) Amphibians have two circulatory routes: one for oxygenation of the blood through the lungs and skin, and the other to take oxygen to the rest of the body. The blood is pumped from a three-chambered heart with two atria and a single ventricle. (c) Reptiles also have two circulatory routes; however, blood is only oxygenated through the lungs. The heart is three chambered, but the ventricles are partially separated so some mixing of oxygenated and deoxygenated blood occurs except in crocodilians and birds. (d) Mammals and birds have the most efficient heart with four chambers that completely separate the oxygenated and deoxygenated blood; it pumps only oxygenated blood through the body and deoxygenated blood to the lungs.

As illustrated in Figure 48.1.3a Fish have a single circuit for blood flow and a two-chambered heart that has only a single atrium and a single ventricle. The atrium collects blood that has returned from the body and the ventricle pumps the blood to the gills where gas exchange occurs and the blood is re-oxygenated; this is called gill circulation. The blood then continues through the rest of the body before arriving back at the atrium; this is called systemic circulation. This unidirectional flow of blood produces a gradient of oxygenated to deoxygenated blood around the fish's systemic circuit. The result is a limit in the amount of oxygen that can reach some of the organs and tissues of the body, reducing the overall metabolic capacity of fish.

In amphibians, reptiles, birds, and mammals, blood flow is directed in two circuits: one through the lungs and back to the heart, which is called pulmonary circulation, and the other throughout the rest of the body and its organs including the brain (systemic circulation). In amphibians, gas exchange also occurs through the skin during pulmonary circulation and is referred to as pulmocutaneous circulation.

As shown in Figure 48.1.3b, amphibians have a three-chambered heart that has two atria and one ventricle rather than the two-chambered heart of fish. The two atria (superior heart chambers) receive blood from the two different circuits (the lungs and the systems), and then there is some mixing of the blood in the heart's ventricle (inferior heart chamber), which reduces the efficiency of oxygenation. The advantage to this arrangement is that high pressure in the vessels pushes blood to the lungs and body. The mixing is mitigated by a ridge within the ventricle that diverts oxygen-rich blood through the systemic circulatory system and deoxygenated blood to the pulmocutaneous circuit. For this reason, amphibians are often described as having double circulation.

Most reptiles also have a three-chambered heart similar to the amphibian heart that directs blood to the pulmonary and systemic circuits, as shown in Figure 48.1.3c. The ventricle is divided more effectively by a partial septum, which results in less mixing of oxygenated and deoxygenated blood. Some reptiles (alligators and crocodiles) are the most primitive animals to exhibit a four-chambered heart. Crocodilians have a unique circulatory mechanism where the heart shunts blood from the lungs toward the stomach and other organs during long periods of submergence, for instance, while the animal waits for prey or stays underwater waiting for prey to rot. One adaptation includes two main arteries that leave the same part of the heart: one takes blood to the lungs and the other provides an alternate route to the stomach and other parts of the body. Two other adaptations include a hole in the heart between the two ventricles, called the foramen of Panizza, which allows blood to move from one side of the heart to the other, and specialized connective tissue that slows the blood flow to the lungs. Together these adaptations have made crocodiles and alligators one of the most evolutionarily successful animal groups on earth.

In mammals and birds, the heart is also divided into four chambers: two atria and two ventricles, as illustrated in Figure 40.1.3d. The oxygenated blood is separated from the deoxygenated blood, which improves the efficiency of double circulation and is probably required for the warm-blooded lifestyle of mammals and birds. The four-chambered heart of birds and mammals evolved independently from a three-chambered heart. The independent evolution of the same or a similar biological trait is referred to as convergent evolution.

Summary

In most animals, the circulatory system is used to transport blood through the body. Some primitive animals use diffusion for the exchange of water, nutrients, and gases. However, complex organisms use the circulatory system to carry gases, nutrients, and waste through the body. Circulatory systems may be open (mixed with the interstitial fluid) or closed (separated from the interstitial fluid). Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptions during evolution and associated differences in anatomy. Fish have a two-chambered heart with unidirectional circulation. Amphibians have a three-chambered heart, which has some mixing of the blood, and they have double circulation. Most non-avian reptiles have a three-chambered heart, but have little mixing of the blood; they have double circulation. Mammals and birds have a four-chambered heart with no mixing of the blood and double circulation.

Glossary

atrium
(plural: atria) chamber of the heart that receives blood from the veins and sends blood to the ventricles

closed circulatory system
system in which the blood is separated from the bodily interstitial fluid and contained in blood vessels

double circulation
flow of blood in two circuits: the pulmonary circuit through the lungs and the systemic circuit through the organs and body

gill circulation
circulatory system that is specific to animals with gills for gas exchange; the blood flows through the gills for oxygenation

hemocoel
cavity into which blood is pumped in an open circulatory system

hemolymph
mixture of blood and interstitial fluid that is found in insects and other arthropods as well as most mollusks

interstitial fluid
fluid between cells

open circulatory system
system in which the blood is mixed with interstitial fluid and directly covers the organs

ostium
(plural: ostia) holes between blood vessels that allow the movement of hemolymph through the body of insects, arthropods, and mollusks with open circulatory systems

pulmocutaneous circulation
circulatory system in amphibians; the flow of blood to the lungs and the moist skin for gas exchange

pulmonary circulation
flow of blood away from the heart through the lungs where oxygenation occurs and then returns to the heart again

systemic circulation
flow of blood away from the heart to the brain, liver, kidneys, stomach, and other organs, the limbs, and the muscles of the body, and then the return of this blood to the heart

unidirectional circulation
flow of blood in a single circuit; occurs in fish where the blood flows through the gills, then past the organs and the rest of the body, before returning to the heart

ventricle
(heart) large inferior chamber of the heart that pumps blood into arteries

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48.2: Components of Vertebrate Blood

Skills to Develop

- List the basic components of the blood
- Compare red and white blood cells
- Describe blood plasma and serum

Hemoglobin is responsible for distributing oxygen, and to a lesser extent, carbon dioxide, throughout the circulatory systems of humans, vertebrates, and many invertebrates. The blood is more than the proteins, though. Blood is actually a term used to describe the liquid that moves through the vessels and includes plasma (the liquid portion, which contains water, proteins, salts, lipids, and glucose) and the cells (red and white cells) and cell fragments called platelets. Blood plasma is actually the dominant component of blood and contains the water, proteins, electrolytes, lipids, and glucose. The cells are responsible for carrying the gases (red cells) and immune the response (white). The platelets are responsible for blood clotting. Interstitial fluid that surrounds cells is separate from the blood, but in hemolymph, they are combined. In humans, cellular components make up approximately 45 percent of the blood and the liquid plasma 55 percent. Blood is 20 percent of a person's extracellular fluid and eight percent of weight.

The Role of Blood in the Body

Blood, like the human blood illustrated in Figure 48.2.1 is important for regulation of the body's systems and homeostasis. Blood helps maintain homeostasis by stabilizing pH, temperature, osmotic pressure, and by eliminating excess heat. Blood supports growth by distributing nutrients and hormones, and by removing waste. Blood plays a protective role by transporting clotting factors and platelets to prevent blood loss and transporting the disease-fighting agents or white blood cells to sites of infection.

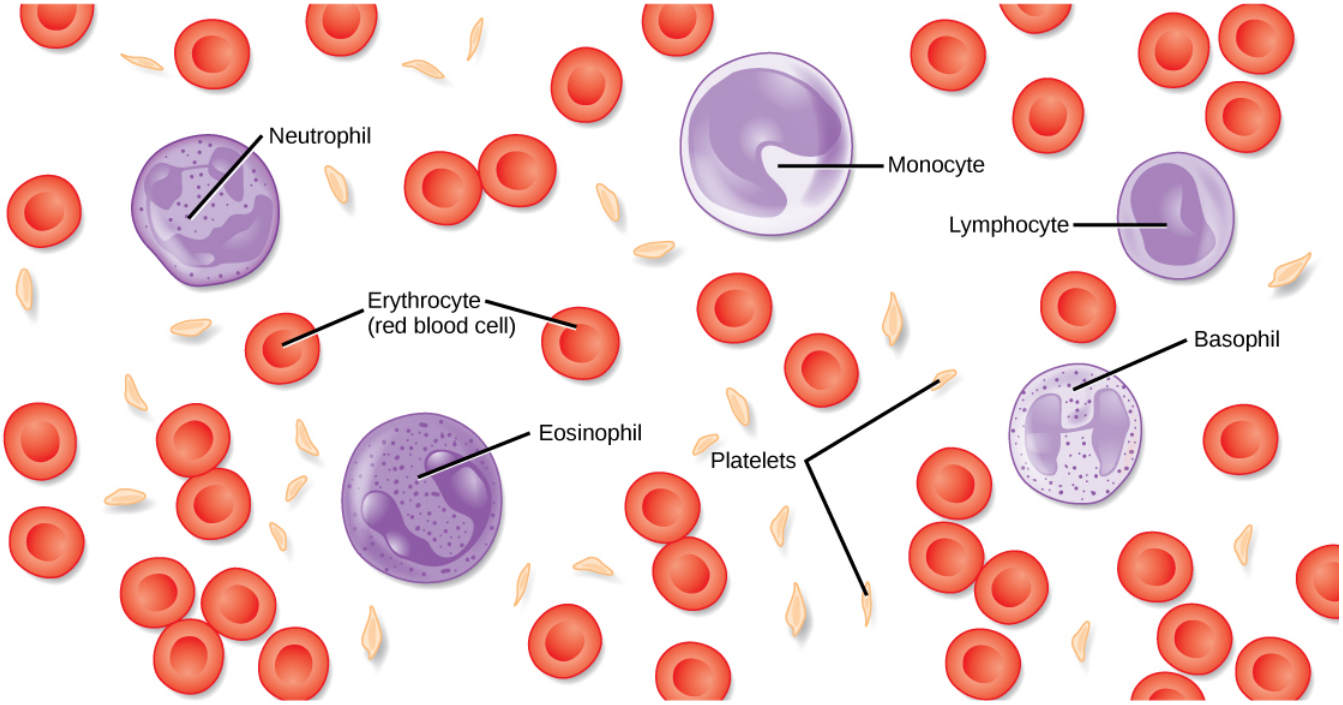


Figure 48.2.1: The cells and cellular components of human blood are shown. Red blood cells deliver oxygen to the cells and remove carbon dioxide. White blood cells—including neutrophils, monocytes, lymphocytes, eosinophils, and basophils—are involved in the immune response. Platelets form clots that prevent blood loss after injury.

Red Blood Cells

Red blood cells, or erythrocytes (erythro- = "red"; -cyte = "cell"), are specialized cells that circulate through the body delivering oxygen to cells; they are formed from stem cells in the bone marrow. In mammals, red blood cells are small biconcave cells that at maturity do not contain a nucleus or mitochondria and are only 7–8 µm in size. In birds and non-avian reptiles, a nucleus is still maintained in red blood cells.

The red coloring of blood comes from the iron-containing protein hemoglobin, illustrated in Figure 48.2.2a. The principal job of this protein is to carry oxygen, but it also transports carbon dioxide as well. Hemoglobin is packed into red blood cells at a rate of about 250 million molecules of hemoglobin per cell. Each hemoglobin molecule binds four oxygen molecules so that each red blood cell carries one billion molecules of oxygen. There are approximately 25 trillion red blood cells in the five liters of blood in the human body, which could carry up to 25 sextillion (25×10^{21}) molecules of oxygen in the body at any time. In mammals, the lack of organelles in erythrocytes leaves more room for the hemoglobin molecules, and the lack of mitochondria also prevents use of the oxygen for metabolic respiration. Only mammals have anucleated red blood cells, and some mammals (camels, for instance) even have nucleated red blood cells. The advantage of nucleated red blood cells is that these cells can undergo mitosis. Anucleated red blood cells metabolize anaerobically (without oxygen), making use of a primitive metabolic pathway to produce ATP and increase the efficiency of oxygen transport.

Not all organisms use hemoglobin as the method of oxygen transport. Invertebrates that utilize hemolymph rather than blood use different pigments to bind to the oxygen. These pigments use copper or iron to the oxygen. Invertebrates have a variety of other respiratory pigments. Hemocyanin, a blue-green, copper-containing protein, illustrated in Figure 48.2.2b is found in mollusks, crustaceans, and some of the arthropods. Chlorocruorin, a green-colored, iron-containing pigment is found in four families of polychaete tubeworms. Hemerythrin, a red, iron-containing protein is found in some polychaete worms and annelids and is illustrated in Figure 48.2.2c. Despite the name, hemerythrin does not contain a heme group and its oxygen-carrying capacity is poor compared to hemoglobin.

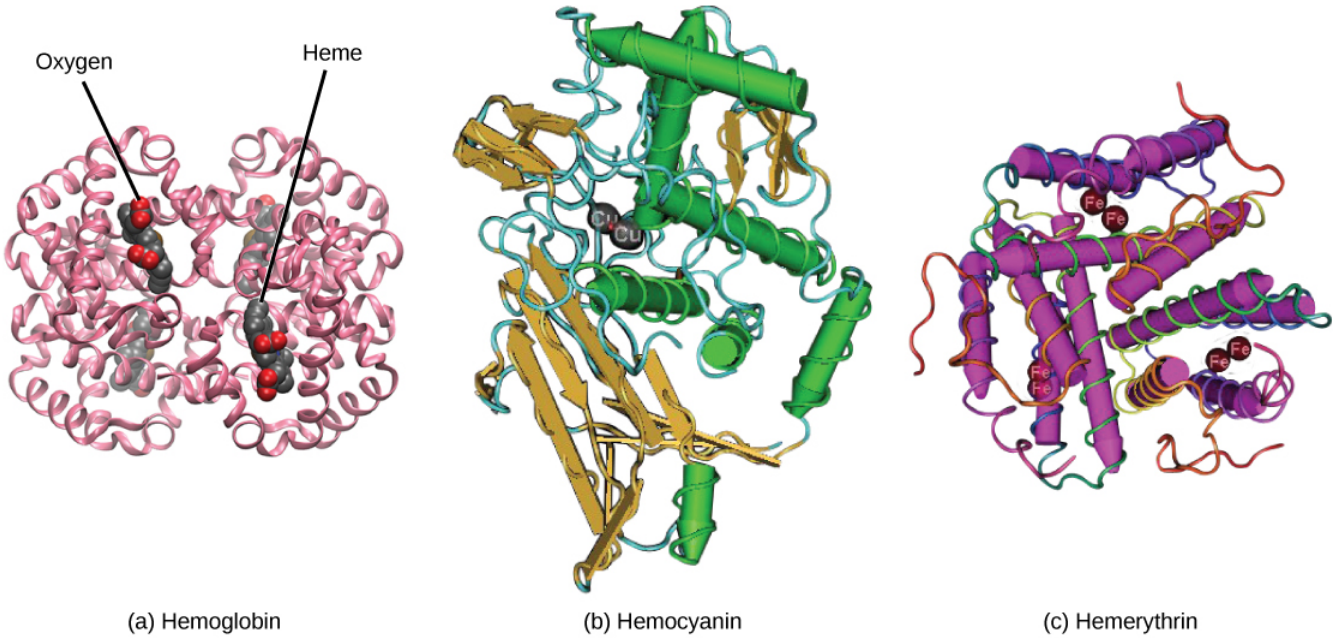


Figure 48.2.2: In most vertebrates, (a) hemoglobin delivers oxygen to the body and removes some carbon dioxide. Hemoglobin is composed of four protein subunits, two alpha chains and two beta chains, and a heme group that has iron associated with it. The iron reversibly associates with oxygen, and in so doing is oxidized from Fe^{2+} to Fe^{3+}. In most mollusks and some arthropods, (b) hemocyanin delivers oxygen. Unlike hemoglobin, hemolymph is not carried in blood cells, but floats free in the hemolymph. Copper instead of iron binds the oxygen, giving the hemolymph a blue-green color. In annelids, such as the earthworm, and some other invertebrates, (c) hemerythrin carries oxygen. Like hemoglobin, hemerythrin is carried in blood cells and has iron associated with it, but despite its name, hemerythrin does not contain heme.

The small size and large surface area of red blood cells allows for rapid diffusion of oxygen and carbon dioxide across the plasma membrane. In the lungs, carbon dioxide is released and oxygen is taken in by the blood. In the tissues, oxygen is released from the blood and carbon dioxide is bound for transport back to the lungs. Studies have found that hemoglobin also binds nitrous oxide (NO). NO is a vasodilator that relaxes the blood vessels and capillaries and may help with gas exchange and the passage of red blood cells through narrow vessels. Nitroglycerin, a heart medication for angina and heart attacks, is converted to NO to help relax the blood vessels and increase oxygen flow through the body.

A characteristic of red blood cells is their glycolipid and glycoprotein coating; these are lipids and proteins that have carbohydrate molecules attached. In humans, the surface glycoproteins and glycolipids on red blood cells vary between individuals, producing

the different blood types, such as A, B, and O. Red blood cells have an average life span of 120 days, at which time they are broken down and recycled in the liver and spleen by phagocytic macrophages, a type of white blood cell.

White Blood Cells

White blood cells, also called leukocytes (leuko = white), make up approximately one percent by volume of the cells in blood. The role of white blood cells is very different than that of red blood cells: they are primarily involved in the immune response to identify and target pathogens, such as invading bacteria, viruses, and other foreign organisms. White blood cells are formed continually; some only live for hours or days, but some live for years.

The morphology of white blood cells differs significantly from red blood cells. They have nuclei and do not contain hemoglobin. The different types of white blood cells are identified by their microscopic appearance after histologic staining, and each has a different specialized function. The two main groups, both illustrated in Figure **48.2.3** are the granulocytes, which include the neutrophils, eosinophils, and basophils, and the agranulocytes, which include the monocytes and lymphocytes.

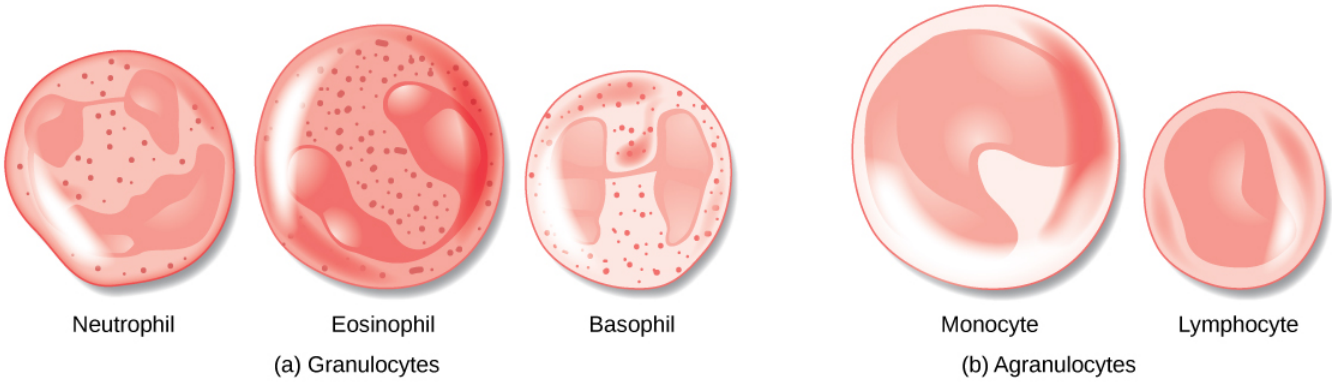


Figure **48.2.3**: (a) Granulocytes—including neutrophils, eosinophils and basophils—are characterized by a lobed nucleus and granular inclusions in the cytoplasm. Granulocytes are typically first-responders during injury or infection. (b) Agranulocytes include lymphocytes and monocytes. Lymphocytes, including B and T cells, are responsible for adaptive immune response. Monocytes differentiate into macrophages and dendritic cells, which in turn respond to infection or injury.

Granulocytes contain granules in their cytoplasm; the agranulocytes are so named because of the lack of granules in their cytoplasm. Some leukocytes become macrophages that either stay at the same site or move through the blood stream and gather at sites of infection or inflammation where they are attracted by chemical signals from foreign particles and damaged cells. Lymphocytes are the primary cells of the immune system and include B cells, T cells, and natural killer cells. B cells destroy bacteria and inactivate their toxins. They also produce antibodies. T cells attack viruses, fungi, some bacteria, transplanted cells, and cancer cells. T cells attack viruses by releasing toxins that kill the viruses. Natural killer cells attack a variety of infectious microbes and certain tumor cells.

One reason that HIV poses significant management challenges is because the virus directly targets T cells by gaining entry through a receptor. Once inside the cell, HIV then multiplies using the T cell's own genetic machinery. After the HIV virus replicates, it is transmitted directly from the infected T cell to macrophages. The presence of HIV can remain unrecognized for an extensive period of time before full disease symptoms develop.

Platelets and Coagulation Factors

Blood must clot to heal wounds and prevent excess blood loss. Small cell fragments called platelets (thrombocytes) are attracted to the wound site where they adhere by extending many projections and releasing their contents. These contents activate other platelets and also interact with other coagulation factors, which convert fibrinogen, a water-soluble protein present in blood serum into fibrin (a non-water soluble protein), causing the blood to clot. Many of the clotting factors require vitamin K to work, and vitamin K deficiency can lead to problems with blood clotting. Many platelets converge and stick together at the wound site forming a platelet plug (also called a fibrin clot), as illustrated in Figure **48.2.4**b. The plug or clot lasts for a number of days and stops the loss of blood. Platelets are formed from the disintegration of larger cells called megakaryocytes, like that shown in Figure **48.2.4**a. For each megakaryocyte, 2000–3000 platelets are formed with 150,000 to 400,000 platelets present in each cubic millimeter of blood. Each platelet is disc shaped and 2–4 μm in diameter. They contain many small vesicles but do not contain a nucleus.

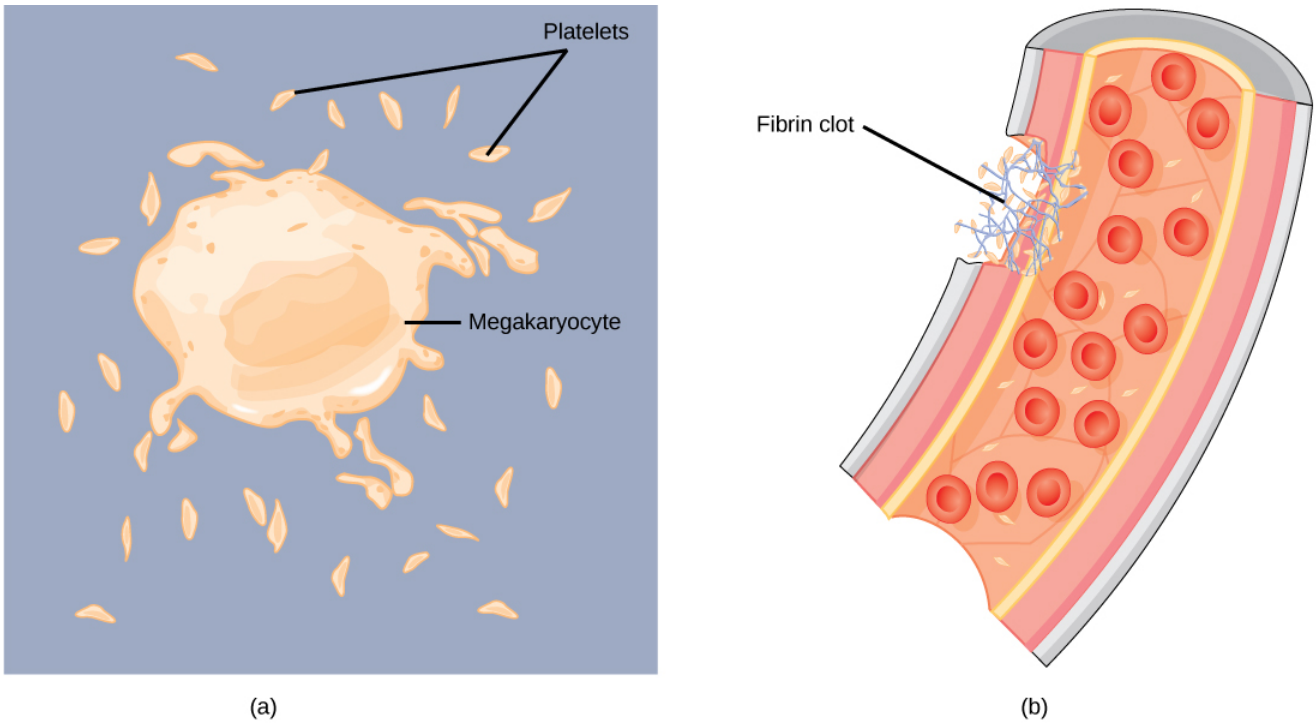


Figure 48.2.4: (a) Platelets are formed from large cells called megakaryocytes. The megakaryocyte breaks up into thousands of fragments that become platelets. (b) Platelets are required for clotting of the blood. The platelets collect at a wound site in conjunction with other clotting factors, such as fibrinogen, to form a fibrin clot that prevents blood loss and allows the wound to heal.

Plasma and Serum

The liquid component of blood is called plasma, and it is separated by spinning or centrifuging the blood at high rotations (3000 rpm or higher). The blood cells and platelets are separated by centrifugal forces to the bottom of a specimen tube. The upper liquid layer, the plasma, consists of 90 percent water along with various substances required for maintaining the body's pH, osmotic load, and for protecting the body. The plasma also contains the coagulation factors and antibodies.

The plasma component of blood without the coagulation factors is called the serum. Serum is similar to interstitial fluid in which the correct composition of key ions acting as electrolytes is essential for normal functioning of muscles and nerves. Other components in the serum include proteins that assist with maintaining pH and osmotic balance while giving viscosity to the blood. The serum also contains antibodies, specialized proteins that are important for defense against viruses and bacteria. Lipids, including cholesterol, are also transported in the serum, along with various other substances including nutrients, hormones, metabolic waste, plus external substances, such as, drugs, viruses, and bacteria.

Human serum albumin is the most abundant protein in human blood plasma and is synthesized in the liver. Albumin, which constitutes about half of the blood serum protein, transports hormones and fatty acids, buffers pH, and maintains osmotic pressures. Immunoglobin is a protein antibody produced in the mucosal lining and plays an important role in antibody mediated immunity.

Evolution Connection: Blood Types

Related to Proteins on the Surface of the Red Blood Cells Red blood cells are coated in antigens made of glycolipids and glycoproteins. The composition of these molecules is determined by genetics, which have evolved over time. In humans, the different surface antigens are grouped into 24 different blood groups with more than 100 different antigens on each red blood cell. The two most well known blood groups are the ABO, shown in Figure 48.2.5, and Rh systems. The surface antigens in the ABO blood group are glycolipids, called antigen A and antigen B. People with blood type A have antigen A, those with blood type B have antigen B, those with blood type AB have both antigens, and people with blood type O have neither antigen. Antibodies called agglutinougens are found in the blood plasma and react with the A or B antigens, if the two are mixed. When type A and type B blood are combined, agglutination (clumping) of the blood occurs because of antibodies in the plasma that bind with the opposing antigen; this causes clots that coagulate in the kidney causing kidney failure. Type O blood has neither

A or B antigens, and therefore, type O blood can be given to all blood types. Type O negative blood is the universal donor. Type AB positive blood is the universal acceptor because it has both A and B antigen. The ABO blood groups were discovered in 1900 and 1901 by Karl Landsteiner at the University of Vienna.

The Rh blood group was first discovered in Rhesus monkeys. Most people have the Rh antigen (Rh+) and do not have anti-Rh antibodies in their blood. The few people who do not have the Rh antigen and are Rh– can develop anti-Rh antibodies if exposed to Rh+ blood. This can happen after a blood transfusion or after an Rh– woman has an Rh+ baby. The first exposure does not usually cause a reaction; however, at the second exposure, enough antibodies have built up in the blood to produce a reaction that causes agglutination and breakdown of red blood cells. An injection can prevent this reaction.

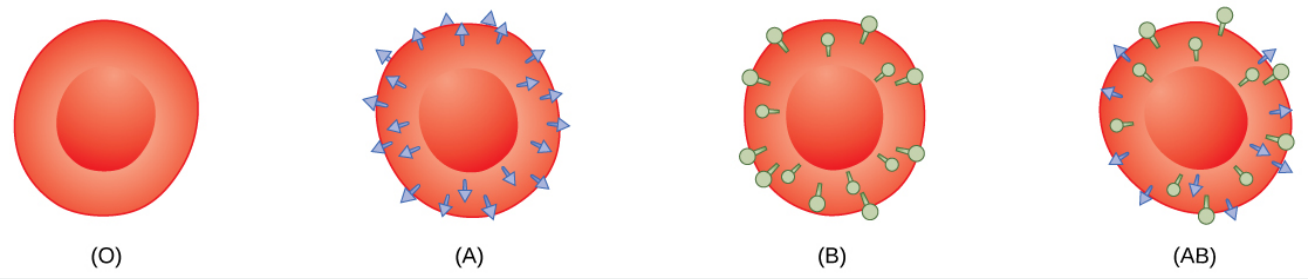


Figure **48.2.5**: Human red blood cells may have either type A or B glycoproteins on their surface, both glycoproteins combined (AB), or neither (O). The glycoproteins serve as antigens and can elicit an immune response in a person who receives a transfusion containing unfamiliar antigens. Type O blood, which has no A or B antigens, does not elicit an immune response when injected into a person of any blood type. Thus, O is considered the universal donor. Persons with type AB blood can accept blood from any blood type, and type AB is considered the universal acceptor.

Summary

Specific components of the blood include red blood cells, white blood cells, platelets, and the plasma, which contains coagulation factors and serum. Blood is important for regulation of the body's pH, temperature, osmotic pressure, the circulation of nutrients and removal of waste, the distribution of hormones from endocrine glands, and the elimination of excess heat; it also contains components for blood clotting. Red blood cells are specialized cells that contain hemoglobin and circulate through the body delivering oxygen to cells. White blood cells are involved in the immune response to identify and target invading bacteria, viruses, and other foreign organisms; they also recycle waste components, such as old red blood cells. Platelets and blood clotting factors cause the change of the soluble protein fibrinogen to the insoluble protein fibrin at a wound site forming a plug. Plasma consists of 90 percent water along with various substances, such as coagulation factors and antibodies. The serum is the plasma component of the blood without the coagulation factors.

Glossary

plasma
: liquid component of blood that is left after the cells are removed

platelet
: (also, thrombocyte) small cellular fragment that collects at wounds, cross-reacts with clotting factors, and forms a plug to prevent blood loss

red blood cell
: small (7–8 μm) biconcave cell without mitochondria (and in mammals without nuclei) that is packed with hemoglobin, giving the cell its red color; transports oxygen through the body

serum
: plasma without the coagulation factors

white blood cell

large (30 μm) cell with nuclei of which there are many types with different roles including the protection of the body from viruses and bacteria, and cleaning up dead cells and other waste

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48.3: Vertebrate Circulatory System

Skills to Develop

- Describe the structure of the heart and explain how cardiac muscle is different from other muscles
- Describe the cardiac cycle
- Explain the structure of arteries, veins, and capillaries, and how blood flows through the body

The heart is a complex muscle that pumps blood through the three divisions of the circulatory system: the coronary (vessels that serve the heart), pulmonary (heart and lungs), and systemic (systems of the body), as shown in Figure **48.3.1**. Coronary circulation intrinsic to the heart takes blood directly from the main artery (aorta) coming from the heart. For pulmonary and systemic circulation, the heart has to pump blood to the lungs or the rest of the body, respectively. In vertebrates, the lungs are relatively close to the heart in the thoracic cavity. The shorter distance to pump means that the muscle wall on the right side of the heart is not as thick as the left side which must have enough pressure to pump blood all the way to your big toe.

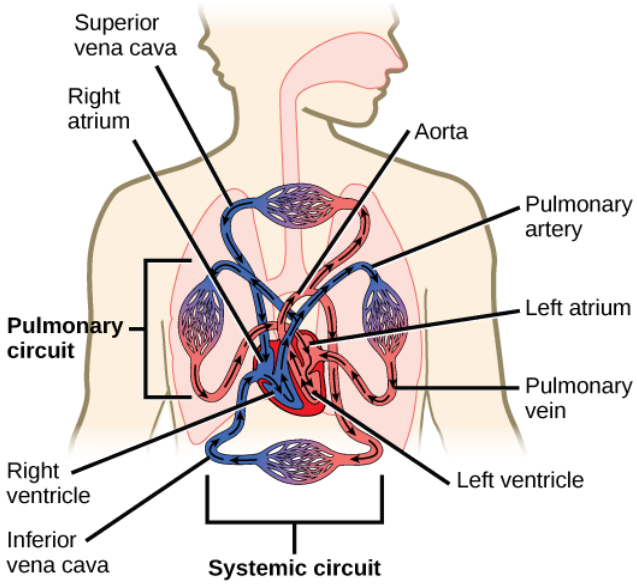


Figure **48.3.1**: The mammalian circulatory system is divided into three circuits: the systemic circuit, the pulmonary circuit, and the coronary circuit. Blood is pumped from veins of the systemic circuit into the right atrium of the heart, then into the right ventricle. Blood then enters the pulmonary circuit, and is oxygenated by the lungs. From the pulmonary circuit, blood re-enters the heart through the left atrium. From the left ventricle, blood re-enters the systemic circuit through the aorta and is distributed to the rest of the body. The coronary circuit, which provides blood to the heart, is not shown.

Exercise

Which of the following statements about the circulatory system is false?

A. Blood in the pulmonary vein is deoxygenated.
B. Blood in the inferior vena cava is deoxygenated.
C. Blood in the pulmonary artery is deoxygenated.
D. Blood in the aorta is oxygenated.

Answer

C

Structure of the Heart

The heart muscle is asymmetrical as a result of the distance blood must travel in the pulmonary and systemic circuits. Since the right side of the heart sends blood to the pulmonary circuit it is smaller than the left side which must send blood out to the whole

body in the systemic circuit, as shown in Figure **48.3.2**. In humans, the heart is about the size of a clenched fist; it is divided into four chambers: two atria and two ventricles. There is one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The atria are the chambers that receive blood, and the ventricles are the chambers that pump blood. The right atrium receives deoxygenated blood from the superior vena cava, which drains blood from the jugular vein that comes from the brain and from the veins that come from the arms, as well as from the inferior vena cava which drains blood from the veins that come from the lower organs and the legs. In addition, the right atrium receives blood from the coronary sinus which drains deoxygenated blood from the heart itself. This deoxygenated blood then passes to the right ventricle through the atrioventricular valve or the tricuspid valve, a flap of connective tissue that opens in only one direction to prevent the backflow of blood.

The valve separating the chambers on the left side of the heart valve is called the biscuspid or mitral valve. After it is filled, the right ventricle pumps the blood through the pulmonary arteries, by-passing the semilunar valve (or pulmonic valve) to the lungs for re-oxygenation. After blood passes through the pulmonary arteries, the right semilunar valves close preventing the blood from flowing backwards into the right ventricle. The left atrium then receives the oxygen-rich blood from the lungs via the pulmonary veins. This blood passes through the bicuspid valve or mitral valve (the atrioventricular valve on the left side of the heart) to the left ventricle where the blood is pumped out through aorta, the major artery of the body, taking oxygenated blood to the organs and muscles of the body. Once blood is pumped out of the left ventricle and into the aorta, the aortic semilunar valve (or aortic valve) closes preventing blood from flowing backward into the left ventricle. This pattern of pumping is referred to as double circulation and is found in all mammals.

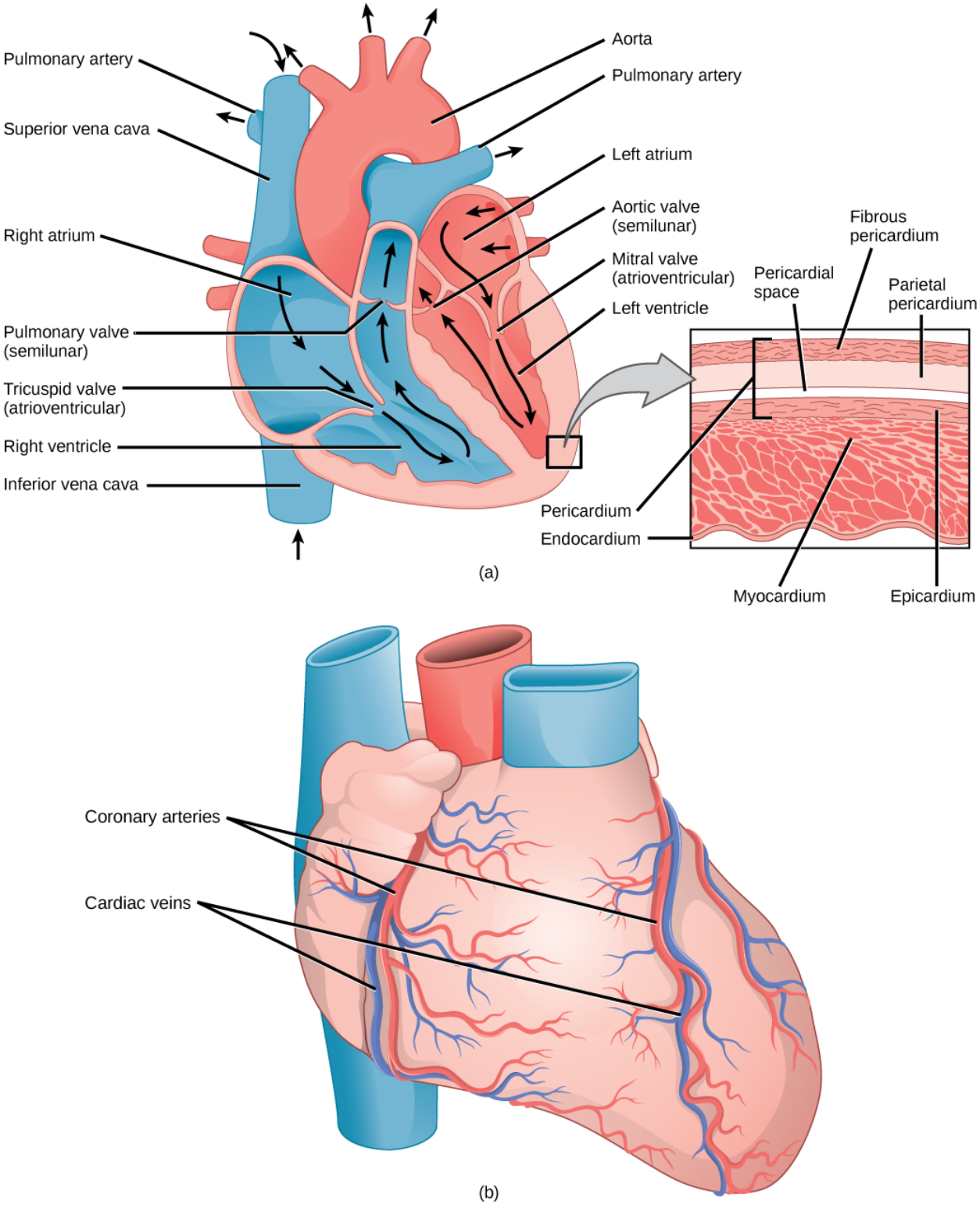


Figure **48.3.2**: (a) The heart is primarily made of a thick muscle layer, called the myocardium, surrounded by membranes. One-way valves separate the four chambers. (b) Blood vessels of the coronary system, including the coronary arteries and veins, keep the heart musculature oxygenated.

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Exercise

Which of the following statements about the heart is false?

A. The mitral valve separates the left ventricle from the left atrium.
B. Blood travels through the bicuspid valve to the left atrium.
C. Both the aortic and the pulmonary valves are semilunar valves.
D. The mitral valve is an atrioventricular valve.

Answer

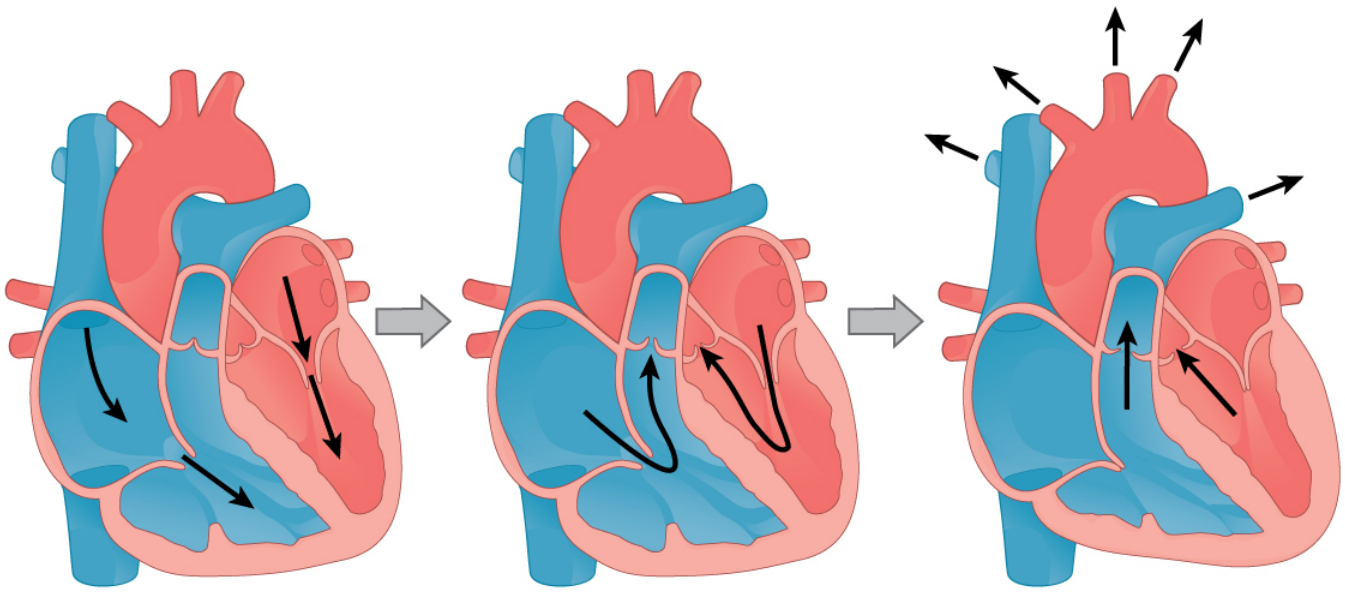
B

The heart is composed of three layers; the epicardium, the myocardium, and the endocardium, illustrated in Figure 48.3.2. The inner wall of the heart has a lining called the endocardium. The myocardium consists of the heart muscle cells that make up the middle layer and the bulk of the heart wall. The outer layer of cells is called the epicardium, of which the second layer is a membranous layered structure called the pericardium that surrounds and protects the heart; it allows enough room for vigorous pumping but also keeps the heart in place to reduce friction between the heart and other structures.

The heart has its own blood vessels that supply the heart muscle with blood. The coronary arteries branch from the aorta and surround the outer surface of the heart like a crown. They diverge into capillaries where the heart muscle is supplied with oxygen before converging again into the coronary veins to take the deoxygenated blood back to the right atrium where the blood will be re-oxygenated through the pulmonary circuit. The heart muscle will die without a steady supply of blood. Atherosclerosis is the blockage of an artery by the buildup of fatty plaques. Because of the size (narrow) of the coronary arteries and their function in serving the heart itself, atherosclerosis can be deadly in these arteries. The slowdown of blood flow and subsequent oxygen deprivation that results from atherosclerosis causes severe pain, known as angina, and complete blockage of the arteries will cause myocardial infarction: the death of cardiac muscle tissue, commonly known as a heart attack.

The Cardiac Cycle

The main purpose of the heart is to pump blood through the body; it does so in a repeating sequence called the cardiac cycle. The cardiac cycle is the coordination of the filling and emptying of the heart of blood by electrical signals that cause the heart muscles to contract and relax. The human heart beats over 100,000 times per day. In each cardiac cycle, the heart contracts (systole), pushing out the blood and pumping it through the body; this is followed by a relaxation phase (diastole), where the heart fills with blood, as illustrated in Figure 48.3.3. The atria contract at the same time, forcing blood through the atrioventricular valves into the ventricles. Closing of the atrioventricular valves produces a monosyllabic “lup” sound. Following a brief delay, the ventricles contract at the same time forcing blood through the semilunar valves into the aorta and the artery transporting blood to the lungs (via the pulmonary artery). Closing of the semilunar valves produces a monosyllabic “dup” sound.



(a) Cardiac diastole: all chambers are relaxed, and blood flows into the heart.

(b) Atrial systole, ventricular diastole: atria contract, pushing blood into the ventricles.

(c) Atrial diastole, ventricular systole: after the atria relax, the ventricles contract, pushing blood out of the heart.

Figure **48.3.3**: During (a) cardiac diastole, the heart muscle is relaxed and blood flows into the heart. During (b) atrial systole, the atria contract, pushing blood into the ventricles. During (c) atrial diastole, the ventricles contract, forcing blood out of the heart.

The pumping of the heart is a function of the cardiac muscle cells, or cardiomyocytes, that make up the heart muscle. Cardiomyocytes, shown in Figure **48.3.4**, are distinctive muscle cells that are striated like skeletal muscle but pump rhythmically and involuntarily like smooth muscle; they are connected by intercalated disks exclusive to cardiac muscle. They are self-stimulated for a period of time and isolated cardiomyocytes will beat if given the correct balance of nutrients and electrolytes.

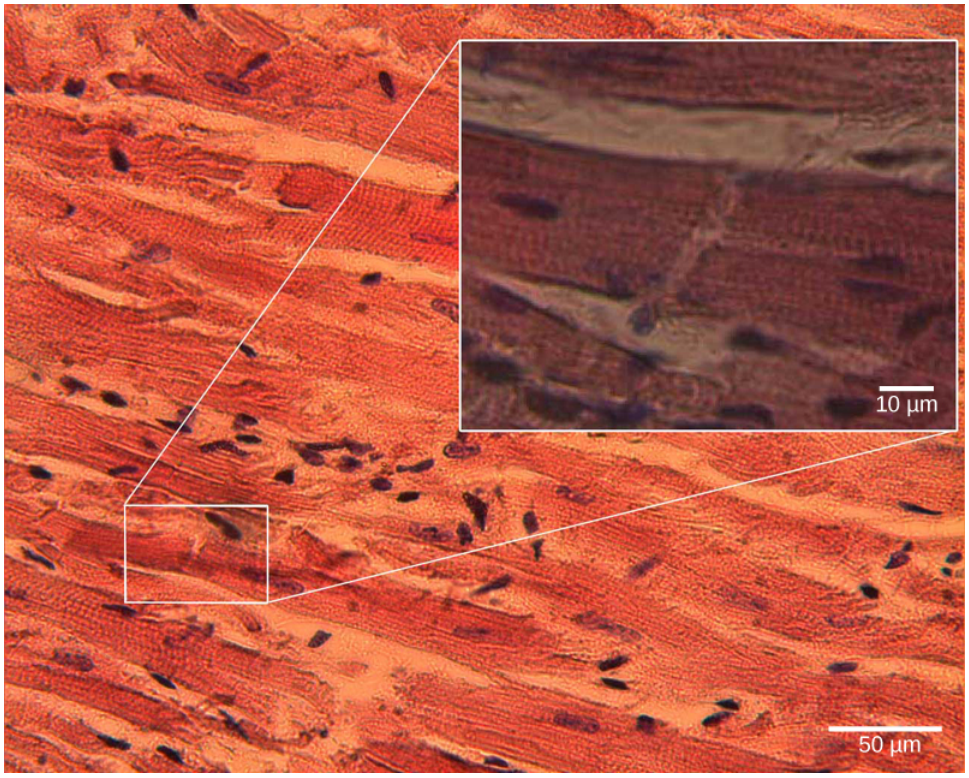


Figure 48.3.4: Cardiomyocytes are striated muscle cells found in cardiac tissue. (credit: modification of work by Dr. S. Girod, Anton Becker; scale-bar data from Matt Russell)

The autonomous beating of cardiac muscle cells is regulated by the heart's internal pacemaker that uses electrical signals to time the beating of the heart. The electrical signals and mechanical actions, illustrated in Figure 48.3.5, are intimately intertwined. The internal pacemaker starts at the sinoatrial (SA) node, which is located near the wall of the right atrium. Electrical charges spontaneously pulse from the SA node causing the two atria to contract in unison. The pulse reaches a second node, called the atrioventricular (AV) node, between the right atrium and right ventricle where it pauses for approximately 0.1 second before spreading to the walls of the ventricles. From the AV node, the electrical impulse enters the bundle of His, then to the left and right bundle branches extending through the interventricular septum. Finally, the Purkinje fibers conduct the impulse from the apex of the heart up the ventricular myocardium, and then the ventricles contract. This pause allows the atria to empty completely into the ventricles before the ventricles pump out the blood. The electrical impulses in the heart produce electrical currents that flow through the body and can be measured on the skin using electrodes. This information can be observed as an electrocardiogram (ECG)—a recording of the electrical impulses of the cardiac muscle.

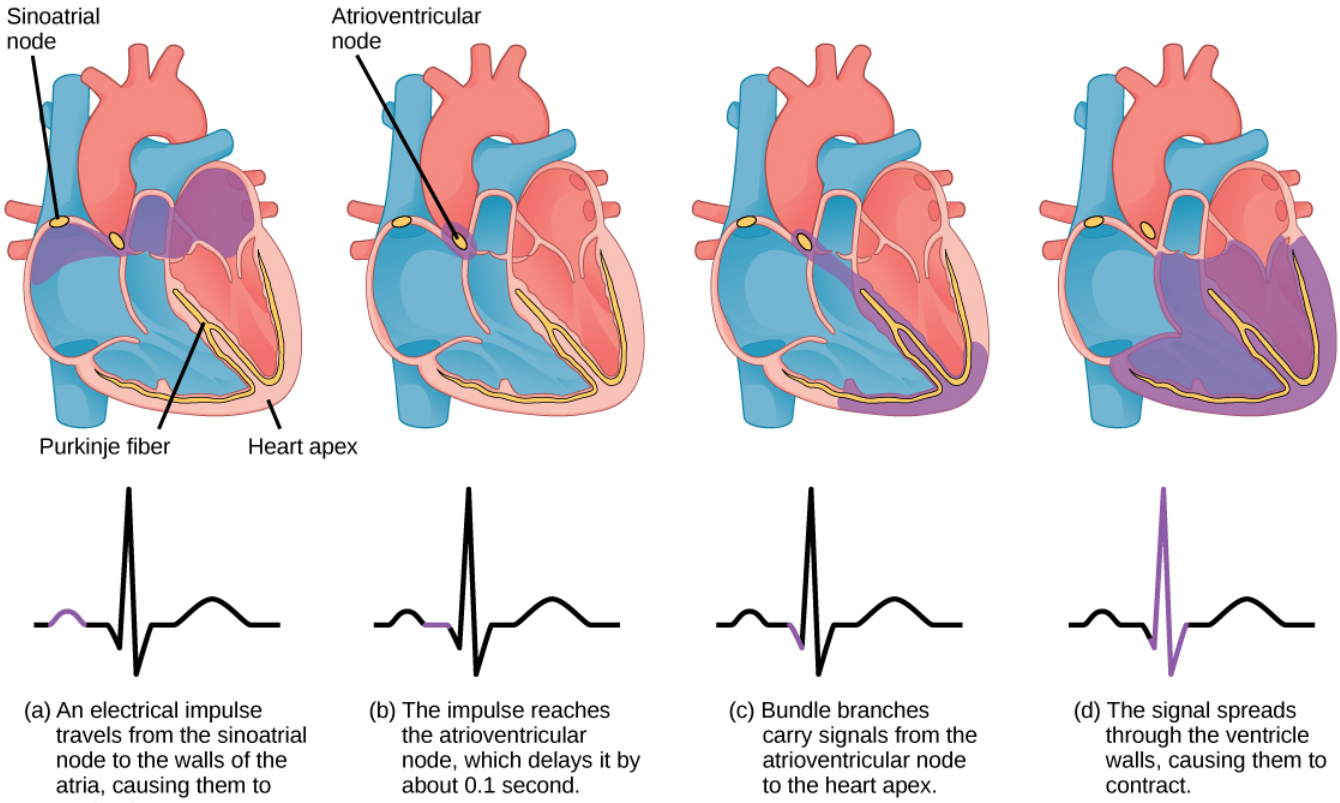
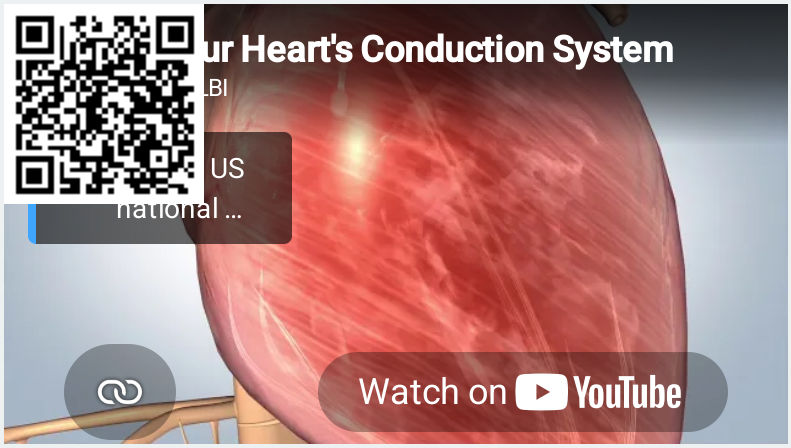


Figure 48.3.5: The beating of the heart is regulated by an electrical impulse that causes the characteristic reading of an ECG. The signal is initiated at the sinoatrial valve. The signal then (a) spreads to the atria, causing them to contract. The signal is (b) delayed at the atrioventricular node before it is passed on to the (c) heart apex. The delay allows the atria to relax before the (d) ventricles contract. The final part of the ECG cycle prepares the heart for the next beat.

Link to Learning



Visit this site and select the dropdown "Your Heart's Electrical System" to see the heart's "pacemaker" in action.

Arteries, Veins, and Capillaries

The blood from the heart is carried through the body by a complex network of blood vessels (Figure 48.3.6). Arteries take blood away from the heart. The main artery is the aorta that branches into major arteries that take blood to different limbs and organs. These major arteries include the carotid artery that takes blood to the brain, the brachial arteries that take blood to the arms, and the thoracic artery that takes blood to the thorax and then into the hepatic, renal, and gastric arteries for the liver, kidney, and stomach, respectively. The iliac artery takes blood to the lower limbs. The major arteries diverge into minor arteries, and then smaller vessels called arterioles, to reach more deeply into the muscles and organs of the body.

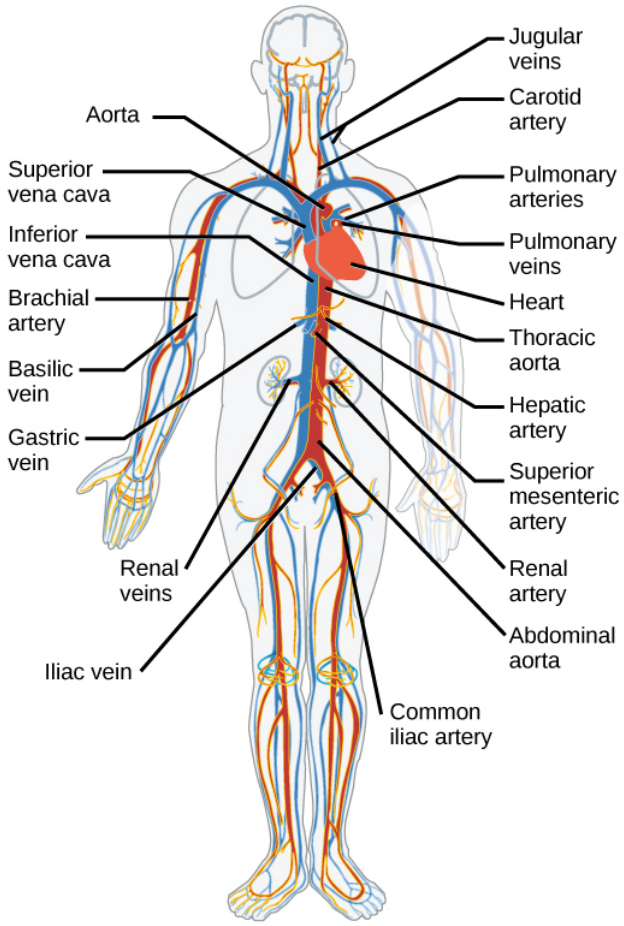


Figure **48.3.6**: The major human arteries and veins are shown. (credit: modification of work by Mariana Ruiz Villareal)

Arterioles diverge into capillary beds. Capillary beds contain a large number (10 to 100) of capillaries that branch among the cells and tissues of the body. Capillaries are narrow-diameter tubes that can fit red blood cells through in single file and are the sites for the exchange of nutrients, waste, and oxygen with tissues at the cellular level. Fluid also crosses into the interstitial space from the capillaries. The capillaries converge again into venules that connect to minor veins that finally connect to major veins that take blood high in carbon dioxide back to the heart. Veins are blood vessels that bring blood back to the heart. The major veins drain blood from the same organs and limbs that the major arteries supply. Fluid is also brought back to the heart via the lymphatic system.

The structure of the different types of blood vessels reflects their function or layers. There are three distinct layers, or tunics, that form the walls of blood vessels (Figure **48.3.7**). The first tunic is a smooth, inner lining of endothelial cells that are in contact with the red blood cells. The endothelial tunic is continuous with the endocardium of the heart. In capillaries, this single layer of cells is the location of diffusion of oxygen and carbon dioxide between the endothelial cells and red blood cells, as well as the exchange site via endocytosis and exocytosis. The movement of materials at the site of capillaries is regulated by vasoconstriction, narrowing of the blood vessels, and vasodilation, widening of the blood vessels; this is important in the overall regulation of blood pressure.

Veins and arteries both have two further tunics that surround the endothelium: the middle tunic is composed of smooth muscle and the outermost layer is connective tissue (collagen and elastic fibers). The elastic connective tissue stretches and supports the blood vessels, and the smooth muscle layer helps regulate blood flow by altering vascular resistance through vasoconstriction and vasodilation. The arteries have thicker smooth muscle and connective tissue than the veins to accommodate the higher pressure and speed of freshly pumped blood. The veins are thinner walled as the pressure and rate of flow are much lower. In addition, veins are structurally different than arteries in that veins have valves to prevent the backflow of blood. Because veins have to work against gravity to get blood back to the heart, contraction of skeletal muscle assists with the flow of blood back to the heart.

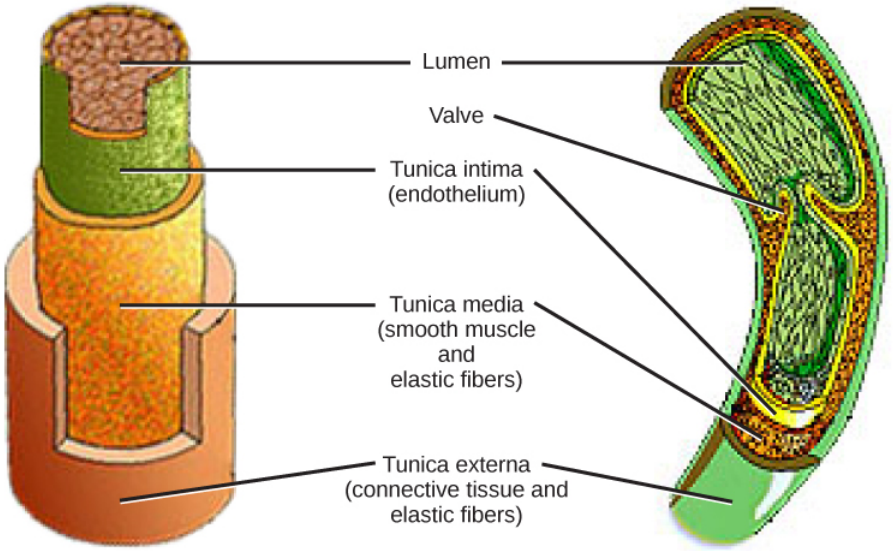


Figure 48.3.7: Arteries and veins consist of three layers: an outer tunica externa, a middle tunica media, and an inner tunica intima. Capillaries consist of a single layer of epithelial cells, the tunica intima. (credit: modification of work by NCI, NIH)

Summary

The heart muscle pumps blood through three divisions of the circulatory system: coronary, pulmonary, and systemic. There is one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The pumping of the heart is a function of cardiomyocytes, distinctive muscle cells that are striated like skeletal muscle but pump rhythmically and involuntarily like smooth muscle. The internal pacemaker starts at the sinoatrial node, which is located near the wall of the right atrium. Electrical charges pulse from the SA node causing the two atria to contract in unison; then the pulse reaches the atrioventricular node between the right atrium and right ventricle. A pause in the electric signal allows the atria to empty completely into the ventricles before the ventricles pump out the blood. The blood from the heart is carried through the body by a complex network of blood vessels; arteries take blood away from the heart, and veins bring blood back to the heart.

Glossary

angina
pain caused by partial blockage of the coronary arteries by the buildup of plaque and lack of oxygen to the heart muscle

aorta
major artery of the body that takes blood away from the heart

arteriole
small vessel that connects an artery to a capillary bed

artery
blood vessel that takes blood away from the heart

atherosclerosis
buildup of fatty plaques in the coronary arteries in the heart

atrioventricular valve
one-way membranous flap of connective tissue between the atrium and the ventricle in the right side of the heart; also known as tricuspid valve

bicuspid valve

(also, mitral valve; left atrioventricular valve) one-way membranous flap between the atrium and the ventricle in the left side of the heart

capillary
smallest blood vessel that allows the passage of individual blood cells and the site of diffusion of oxygen and nutrient exchange

capillary bed
large number of capillaries that converge to take blood to a particular organ or tissue

cardiac cycle
filling and emptying the heart of blood by electrical signals that cause the heart muscles to contract and relax

cardiomyocyte
specialized heart muscle cell that is striated but contracts involuntarily like smooth muscle

coronary artery
vessel that supplies the heart tissue with blood

coronary vein
vessel that takes blood away from the heart tissue back to the chambers in the heart

diastole
relaxation phase of the cardiac cycle when the heart is relaxed and the ventricles are filling with blood

electrocardiogram (ECG)
recording of the electrical impulses of the cardiac muscle

endocardium
innermost layer of tissue in the heart

epicardium
outermost tissue layer of the heart

inferior vena cava
drains blood from the veins that come from the lower organs and the legs

myocardial infarction
(also, heart attack) complete blockage of the coronary arteries and death of the cardiac muscle tissue

myocardium
heart muscle cells that make up the middle layer and the bulk of the heart wall

pericardium
membrane layer protecting the heart; also part of the epicardium

semilunar valve
membranous flap of connective tissue between the aorta and a ventricle of the heart (the aortic or pulmonary semilunar valves)

sinoatrial (SA) node
the heart’s internal pacemaker; located near the wall of the right atrium

superior vena cava
drains blood from the jugular vein that comes from the brain and from the veins that come from the arms

systole

contraction phase of cardiac cycle when the ventricles are pumping blood into the arteries

tricuspid valve

one-way membranous flap of connective tissue between the atrium and the ventricle in the right side of the heart; also known as atrioventricular valve

vasoconstriction

narrowing of a blood vessel

vasodilation

widening of a blood vessel

vein

blood vessel that brings blood back to the heart

vena cava

major vein of the body returning blood from the upper and lower parts of the body; see the superior vena cava and inferior vena cava

venule

blood vessel that connects a capillary bed to a vein

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48.4: Cardiac Cycle, Electrical Conduction, ECG, and Cardiac Output

Skills to Develop

- Describe the system of blood flow through the body
- Describe how blood pressure is regulated

Blood pressure (BP) is the pressure exerted by blood on the walls of a blood vessel that helps to push blood through the body. Systolic blood pressure measures the amount of pressure that blood exerts on vessels while the heart is beating. The optimal systolic blood pressure is 120 mmHg. Diastolic blood pressure measures the pressure in the vessels between heartbeats. The optimal diastolic blood pressure is 80 mmHg. Many factors can affect blood pressure, such as hormones, stress, exercise, eating, sitting, and standing. Blood flow through the body is regulated by the size of blood vessels, by the action of smooth muscle, by one-way valves, and by the fluid pressure of the blood itself.

How Blood Flows Through the Body

Blood is pushed through the body by the action of the pumping heart. With each rhythmic pump, blood is pushed under high pressure and velocity away from the heart, initially along the main artery, the aorta. In the aorta, the blood travels at 30 cm/sec. As blood moves into the arteries, arterioles, and ultimately to the capillary beds, the rate of movement slows dramatically to about 0.026 cm/sec, one-thousand times slower than the rate of movement in the aorta. While the diameter of each individual arteriole and capillary is far narrower than the diameter of the aorta, and according to the law of continuity, fluid should travel faster through a narrower diameter tube, the rate is actually slower due to the overall diameter of all the combined capillaries being far greater than the diameter of the individual aorta.

The slow rate of travel through the capillary beds, which reach almost every cell in the body, assists with gas and nutrient exchange and also promotes the diffusion of fluid into the interstitial space. After the blood has passed through the capillary beds to the venules, veins, and finally to the main venae cavae, the rate of flow increases again but is still much slower than the initial rate in the aorta. Blood primarily moves in the veins by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Because most veins must move blood against the pull of gravity, blood is prevented from flowing backward in the veins by one-way valves. Because skeletal muscle contraction aids in venous blood flow, it is important to get up and move frequently after long periods of sitting so that blood will not pool in the extremities.

Blood flow through the capillary beds is regulated depending on the body's needs and is directed by nerve and hormone signals. For example, after a large meal, most of the blood is diverted to the stomach by vasodilation of vessels of the digestive system and vasoconstriction of other vessels. During exercise, blood is diverted to the skeletal muscles through vasodilation while blood to the digestive system would be lessened through vasoconstriction. The blood entering some capillary beds is controlled by small muscles, called precapillary sphincters, illustrated in Figure **48.4.1**. If the sphincters are open, the blood will flow into the associated branches of the capillary blood. If all of the sphincters are closed, then the blood will flow directly from the arteriole to the venule through the thoroughfare channel (see Figure **48.4.1**). These muscles allow the body to precisely control when capillary beds receive blood flow. At any given moment only about 5-10% of our capillary beds actually have blood flowing through them.

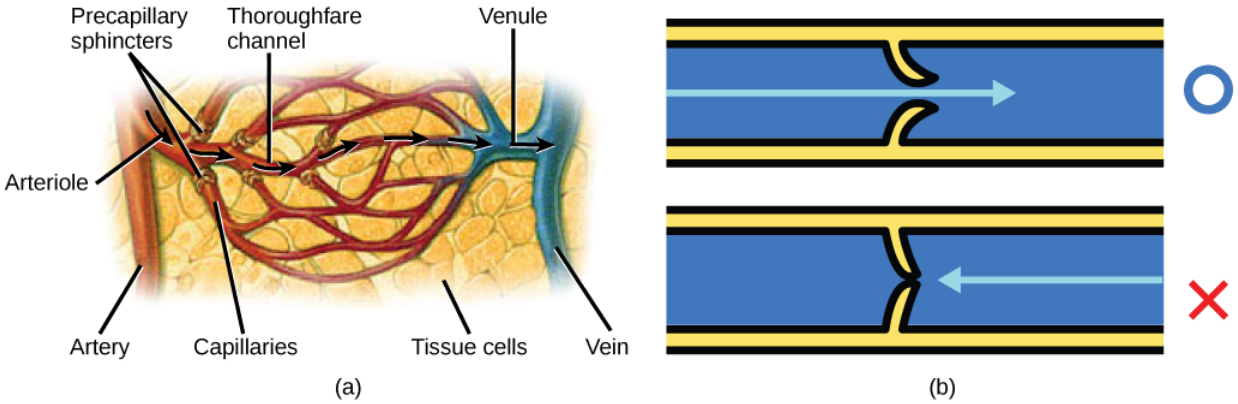


Figure 48.4.1: (a) Precapillary sphincters are rings of smooth muscle that regulate the flow of blood through capillaries; they help control the location of blood flow to where it is needed. (b) Valves in the veins prevent blood from moving backward. (credit a: modification of work by NCI)

Exercise

Varicose veins are veins that become enlarged because the valves no longer close properly, allowing blood to flow backward. Varicose veins are often most prominent on the legs. Why do you think this is the case?

Answer

Blood in the legs is farthest away from the heart and has to flow up to reach it.

Link to Learning



The circulatory system consisting of the heart, arteries, capillaries, and veins, is the pumping mechanism that transports blood throughout the body. Watch this video to see the circulatory system's blood flow.

Proteins and other large solutes cannot leave the capillaries. The loss of the watery plasma creates a hyperosmotic solution within the capillaries, especially near the venules. This causes about 85% of the plasma that leaves the capillaries to eventually diffuses back into the capillaries near the venules. The remaining 15% of blood plasma drains out from the interstitial fluid into nearby lymphatic vessels (Figure 48.4.2). The fluid in the lymph is similar in composition to the interstitial fluid. The lymph fluid passes through lymph nodes before it returns to the heart via the vena cava. Lymph nodes are specialized organs that filter the lymph by percolation through a maze of connective tissue filled with white blood cells. The white blood cells remove infectious agents, such as bacteria and viruses, to clean the lymph before it returns to the bloodstream. After it is cleaned, the lymph returns to the heart by the action of smooth muscle pumping, skeletal muscle action, and one-way valves joining the returning blood near the junction of the venae cavae entering the right atrium of the heart.

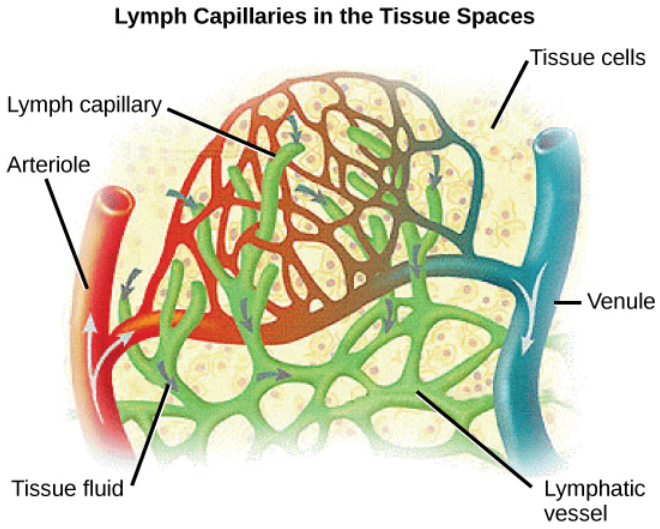


Figure **48.4.2**: Fluid from the capillaries moves into the interstitial space and lymph capillaries by diffusion down a pressure gradient and also by osmosis. Out of 7,200 liters of fluid pumped by the average heart in a day, over 1,500 liters is filtered. (credit: modification of work by NCI, NIH)

Evolution Connection: Vertebrate Diversity in Blood Circulation

Blood circulation has evolved differently in vertebrates and may show variation in different animals for the required amount of pressure, organ and vessel location, and organ size. Animals with longs necks and those that live in cold environments have distinct blood pressure adaptations.

Long necked animals, such as giraffes, need to pump blood upward from the heart against gravity. The blood pressure required from the pumping of the left ventricle would be equivalent to 250 mm Hg (mm Hg = millimeters of mercury, a unit of pressure) to reach the height of a giraffe's head, which is 2.5 meters higher than the heart. However, if checks and balances were not in place, this blood pressure would damage the giraffe's brain, particularly if it was bending down to drink. These checks and balances include valves and feedback mechanisms that reduce the rate of cardiac output. Long-necked dinosaurs such as the sauropods had to pump blood even higher, up to ten meters above the heart. This would have required a blood pressure of more than 600 mm Hg, which could only have been achieved by an enormous heart. Evidence for such an enormous heart does not exist and mechanisms to reduce the blood pressure required include the slowing of metabolism as these animals grew larger. It is likely that they did not routinely feed on tree tops but grazed on the ground.

Living in cold water, whales need to maintain the temperature in their blood. This is achieved by the veins and arteries being close together so that heat exchange can occur. This mechanism is called a countercurrent heat exchanger. The blood vessels and the whole body are also protected by thick layers of blubber to prevent heat loss. In land animals that live in cold environments, thick fur and hibernation are used to retain heat and slow metabolism.

Blood Pressure

The pressure of the blood flow in the body is produced by the hydrostatic pressure of the fluid (blood) against the walls of the blood vessels. Fluid will move from areas of high to low hydrostatic pressures. In the arteries, the hydrostatic pressure near the heart is very high and blood flows to the arterioles where the rate of flow is slowed by the narrow openings of the arterioles. During systole, when new blood is entering the arteries, the artery walls stretch to accommodate the increase of pressure of the extra blood; during diastole, the walls return to normal because of their elastic properties. The blood pressure of the systole phase and the diastole phase, graphed in Figure **48.4.3**, gives the two pressure readings for blood pressure. For example, 120/80 indicates a reading of 120 mm Hg during the systole and 80 mm Hg during diastole. Throughout the cardiac cycle, the blood continues to empty into the arterioles at a relatively even rate. This resistance to blood flow is called peripheral resistance.

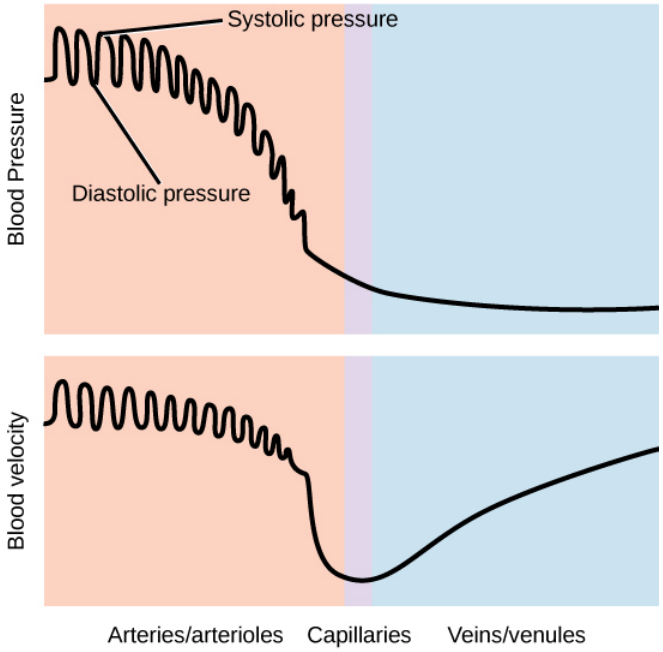


Figure **48.4.3**: Blood pressure is related to the blood velocity in the arteries and arterioles. In the capillaries and veins, the blood pressure continues to decease but velocity increases.

Blood Pressure Regulation

Cardiac output is the volume of blood pumped by the heart in one minute. It is calculated by multiplying the number of heart contractions that occur per minute (heart rate) times the stroke volume (the volume of blood pumped into the aorta per contraction of the left ventricle). Therefore, cardiac output can be increased by increasing heart rate, as when exercising. However, cardiac output can also be increased by increasing stroke volume, such as if the heart contracts with greater strength. Stroke volume can also be increased by speeding blood circulation through the body so that more blood enters the heart between contractions. During heavy exertion, the blood vessels relax and increase in diameter, offsetting the increased heart rate and ensuring adequate oxygenated blood gets to the muscles. Stress triggers a decrease in the diameter of the blood vessels, consequently increasing blood pressure. These changes can also be caused by nerve signals or hormones, and even standing up or lying down can have a great effect on blood pressure.

Summary

Blood primarily moves through the body by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Blood is prevented from flowing backward in the veins by one-way valves. Blood flow through the capillary beds is controlled by precapillary sphincters to increase and decrease flow depending on the body's needs and is directed by nerve and hormone signals. Lymph vessels take fluid that has leaked out of the blood to the lymph nodes where it is cleaned before returning to the heart. During systole, blood enters the arteries, and the artery walls stretch to accommodate the extra blood. During diastole, the artery walls return to normal. The blood pressure of the systole phase and the diastole phase gives the two pressure readings for blood pressure.

Glossary

blood pressure (BP)
pressure of blood in the arteries that helps to push blood through the body

cardiac output
the volume of blood pumped by the heart in one minute as a product of heart rate multiplied by stroke volume

lymph node
specialized organ that contains a large number of macrophages that clean the lymph before the fluid is returned to the heart

peripheral resistance

resistance of the artery and blood vessel walls to the pressure placed on them by the force of the heart pumping

precapillary sphincter

small muscle that controls blood circulation in the capillary beds

stroke volume

the volume of blood pumped into the aorta per contraction of the left ventricle

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48.5: Blood Pressure and Blood Vessels

Skills to Develop

- Describe the system of blood flow through the body
- Describe how blood pressure is regulated

Blood pressure (BP) is the pressure exerted by blood on the walls of a blood vessel that helps to push blood through the body. Systolic blood pressure measures the amount of pressure that blood exerts on vessels while the heart is beating. The optimal systolic blood pressure is 120 mmHg. Diastolic blood pressure measures the pressure in the vessels between heartbeats. The optimal diastolic blood pressure is 80 mmHg. Many factors can affect blood pressure, such as hormones, stress, exercise, eating, sitting, and standing. Blood flow through the body is regulated by the size of blood vessels, by the action of smooth muscle, by one-way valves, and by the fluid pressure of the blood itself.

How Blood Flows Through the Body

Blood is pushed through the body by the action of the pumping heart. With each rhythmic pump, blood is pushed under high pressure and velocity away from the heart, initially along the main artery, the aorta. In the aorta, the blood travels at 30 cm/sec. As blood moves into the arteries, arterioles, and ultimately to the capillary beds, the rate of movement slows dramatically to about 0.026 cm/sec, one-thousand times slower than the rate of movement in the aorta. While the diameter of each individual arteriole and capillary is far narrower than the diameter of the aorta, and according to the law of continuity, fluid should travel faster through a narrower diameter tube, the rate is actually slower due to the overall diameter of all the combined capillaries being far greater than the diameter of the individual aorta.

The slow rate of travel through the capillary beds, which reach almost every cell in the body, assists with gas and nutrient exchange and also promotes the diffusion of fluid into the interstitial space. After the blood has passed through the capillary beds to the venules, veins, and finally to the main venae cavae, the rate of flow increases again but is still much slower than the initial rate in the aorta. Blood primarily moves in the veins by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Because most veins must move blood against the pull of gravity, blood is prevented from flowing backward in the veins by one-way valves. Because skeletal muscle contraction aids in venous blood flow, it is important to get up and move frequently after long periods of sitting so that blood will not pool in the extremities.

Blood flow through the capillary beds is regulated depending on the body's needs and is directed by nerve and hormone signals. For example, after a large meal, most of the blood is diverted to the stomach by vasodilation of vessels of the digestive system and vasoconstriction of other vessels. During exercise, blood is diverted to the skeletal muscles through vasodilation while blood to the digestive system would be lessened through vasoconstriction. The blood entering some capillary beds is controlled by small muscles, called precapillary sphincters, illustrated in Figure **48.5.1**. If the sphincters are open, the blood will flow into the associated branches of the capillary blood. If all of the sphincters are closed, then the blood will flow directly from the arteriole to the venule through the thoroughfare channel (see Figure **48.5.1**). These muscles allow the body to precisely control when capillary beds receive blood flow. At any given moment only about 5-10% of our capillary beds actually have blood flowing through them.

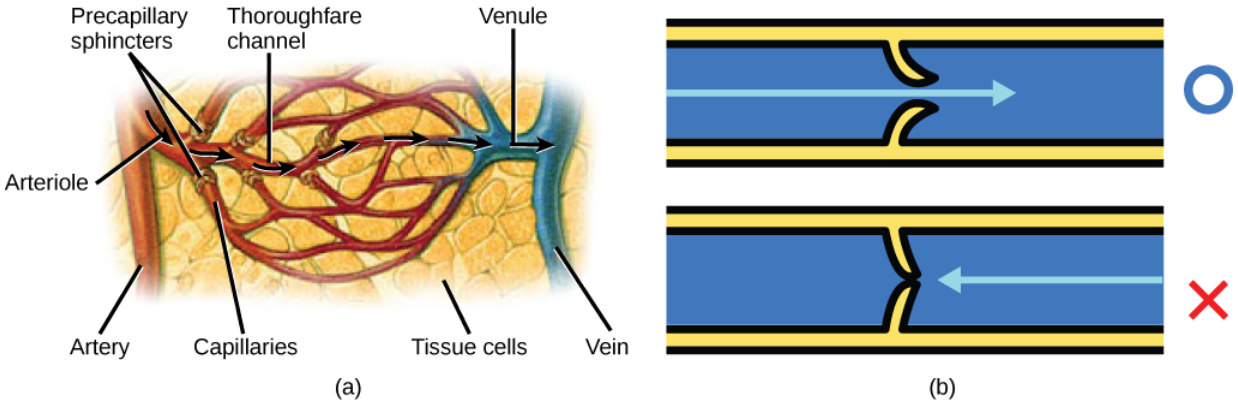


Figure 48.5.1: (a) Precapillary sphincters are rings of smooth muscle that regulate the flow of blood through capillaries; they help control the location of blood flow to where it is needed. (b) Valves in the veins prevent blood from moving backward. (credit a: modification of work by NCI)

Exercise

Varicose veins are veins that become enlarged because the valves no longer close properly, allowing blood to flow backward. Varicose veins are often most prominent on the legs. Why do you think this is the case?

Answer

Blood in the legs is farthest away from the heart and has to flow up to reach it.

Link to Learning



The circulatory system consisting of the heart, arteries, capillaries, and veins, is the pumping mechanism that transports blood throughout the body. Watch this video to see the circulatory system's blood flow.

Proteins and other large solutes cannot leave the capillaries. The loss of the watery plasma creates a hyperosmotic solution within the capillaries, especially near the venules. This causes about 85% of the plasma that leaves the capillaries to eventually diffuses back into the capillaries near the venules. The remaining 15% of blood plasma drains out from the interstitial fluid into nearby lymphatic vessels (Figure 48.5.2). The fluid in the lymph is similar in composition to the interstitial fluid. The lymph fluid passes through lymph nodes before it returns to the heart via the vena cava. Lymph nodes are specialized organs that filter the lymph by percolation through a maze of connective tissue filled with white blood cells. The white blood cells remove infectious agents, such as bacteria and viruses, to clean the lymph before it returns to the bloodstream. After it is cleaned, the lymph returns to the heart by the action of smooth muscle pumping, skeletal muscle action, and one-way valves joining the returning blood near the junction of the venae cavae entering the right atrium of the heart.

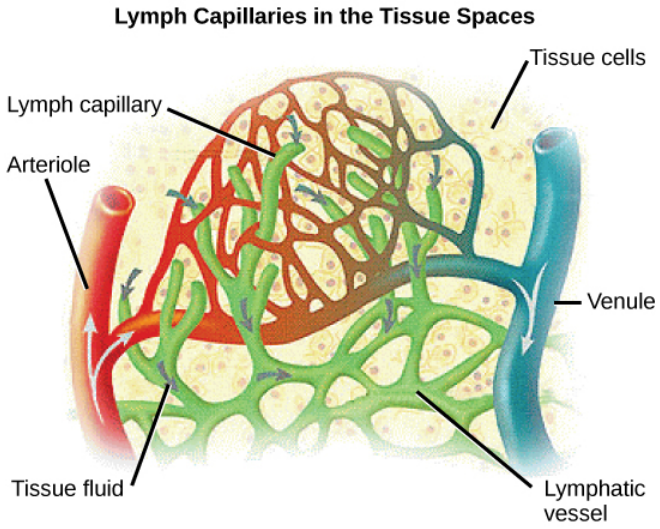


Figure **48.5.2**: Fluid from the capillaries moves into the interstitial space and lymph capillaries by diffusion down a pressure gradient and also by osmosis. Out of 7,200 liters of fluid pumped by the average heart in a day, over 1,500 liters is filtered. (credit: modification of work by NCI, NIH)

Evolution Connection: Vertebrate Diversity in Blood Circulation

Blood circulation has evolved differently in vertebrates and may show variation in different animals for the required amount of pressure, organ and vessel location, and organ size. Animals with longs necks and those that live in cold environments have distinct blood pressure adaptations.

Long necked animals, such as giraffes, need to pump blood upward from the heart against gravity. The blood pressure required from the pumping of the left ventricle would be equivalent to 250 mm Hg (mm Hg = millimeters of mercury, a unit of pressure) to reach the height of a giraffe's head, which is 2.5 meters higher than the heart. However, if checks and balances were not in place, this blood pressure would damage the giraffe's brain, particularly if it was bending down to drink. These checks and balances include valves and feedback mechanisms that reduce the rate of cardiac output. Long-necked dinosaurs such as the sauropods had to pump blood even higher, up to ten meters above the heart. This would have required a blood pressure of more than 600 mm Hg, which could only have been achieved by an enormous heart. Evidence for such an enormous heart does not exist and mechanisms to reduce the blood pressure required include the slowing of metabolism as these animals grew larger. It is likely that they did not routinely feed on tree tops but grazed on the ground.

Living in cold water, whales need to maintain the temperature in their blood. This is achieved by the veins and arteries being close together so that heat exchange can occur. This mechanism is called a countercurrent heat exchanger. The blood vessels and the whole body are also protected by thick layers of blubber to prevent heat loss. In land animals that live in cold environments, thick fur and hibernation are used to retain heat and slow metabolism.

Blood Pressure

The pressure of the blood flow in the body is produced by the hydrostatic pressure of the fluid (blood) against the walls of the blood vessels. Fluid will move from areas of high to low hydrostatic pressures. In the arteries, the hydrostatic pressure near the heart is very high and blood flows to the arterioles where the rate of flow is slowed by the narrow openings of the arterioles. During systole, when new blood is entering the arteries, the artery walls stretch to accommodate the increase of pressure of the extra blood; during diastole, the walls return to normal because of their elastic properties. The blood pressure of the systole phase and the diastole phase, graphed in Figure **48.5.3**, gives the two pressure readings for blood pressure. For example, 120/80 indicates a reading of 120 mm Hg during the systole and 80 mm Hg during diastole. Throughout the cardiac cycle, the blood continues to empty into the arterioles at a relatively even rate. This resistance to blood flow is called peripheral resistance.

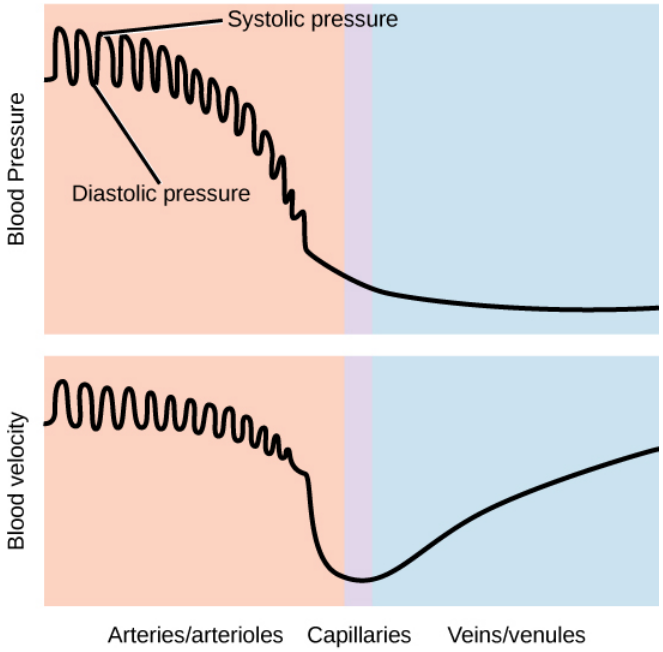


Figure 48.5.3: Blood pressure is related to the blood velocity in the arteries and arterioles. In the capillaries and veins, the blood pressure continues to decease but velocity increases.

Blood Pressure Regulation

Cardiac output is the volume of blood pumped by the heart in one minute. It is calculated by multiplying the number of heart contractions that occur per minute (heart rate) times the stroke volume (the volume of blood pumped into the aorta per contraction of the left ventricle). Therefore, cardiac output can be increased by increasing heart rate, as when exercising. However, cardiac output can also be increased by increasing stroke volume, such as if the heart contracts with greater strength. Stroke volume can also be increased by speeding blood circulation through the body so that more blood enters the heart between contractions. During heavy exertion, the blood vessels relax and increase in diameter, offsetting the increased heart rate and ensuring adequate oxygenated blood gets to the muscles. Stress triggers a decrease in the diameter of the blood vessels, consequently increasing blood pressure. These changes can also be caused by nerve signals or hormones, and even standing up or lying down can have a great effect on blood pressure.

Summary

Blood primarily moves through the body by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Blood is prevented from flowing backward in the veins by one-way valves. Blood flow through the capillary beds is controlled by precapillary sphincters to increase and decrease flow depending on the body's needs and is directed by nerve and hormone signals. Lymph vessels take fluid that has leaked out of the blood to the lymph nodes where it is cleaned before returning to the heart. During systole, blood enters the arteries, and the artery walls stretch to accommodate the extra blood. During diastole, the artery walls return to normal. The blood pressure of the systole phase and the diastole phase gives the two pressure readings for blood pressure.

Glossary

blood pressure (BP)
pressure of blood in the arteries that helps to push blood through the body

cardiac output
the volume of blood pumped by the heart in one minute as a product of heart rate multiplied by stroke volume

lymph node
specialized organ that contains a large number of macrophages that clean the lymph before the fluid is returned to the heart

peripheral resistance

resistance of the artery and blood vessel walls to the pressure placed on them by the force of the heart pumping

precapillary sphincter

small muscle that controls blood circulation in the capillary beds

stroke volume

the volume of blood pumped into the aorta per contraction of the left ventricle

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CHAPTER OVERVIEW

49: Osmotic Regulation and the Urinary System

49.1: Osmolarity and Osmotic Balance

49.2: Nitrogenous Wastes- Ammonia, Urea, and Uric Acid

49.3: Osmoregulatory Organs

49.4: Evolution of the Vertebrate Kidney

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49.6: Hormonal Control of Osmoregulatory Functions

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49.1: Osmolarity and Osmotic Balance

Skills to Develop

- Define osmosis and explain its role within molecules
- Explain why osmoregulation and osmotic balance are important body functions
- Describe active transport mechanisms
- Explain osmolarity and the way in which it is measured
- Describe osmoregulators or osmoconformers and how these tools allow animals to adapt to different environments

Osmosis is the diffusion of water across a membrane in response to osmotic pressure caused by an imbalance of molecules on either side of the membrane. Osmoregulation is the process of maintenance of salt and water balance (osmotic balance) across membranes within the body's fluids, which are composed of water, plus electrolytes and non-electrolytes. An electrolyte is a solute that dissociates into ions when dissolved in water. A non-electrolyte, in contrast, doesn't dissociate into ions during water dissolution. Both electrolytes and non-electrolytes contribute to the osmotic balance. The body's fluids include blood plasma, the cytosol within cells, and interstitial fluid, the fluid that exists in the spaces between cells and tissues of the body. The membranes of the body (such as the pleural, serous, and cell membranes) are semi-permeable membranes. Semi-permeable membranes are permeable (or permissive) to certain types of solutes and water. Solutions on two sides of a semi-permeable membrane tend to equalize in solute concentration by movement of solutes and/or water across the membrane. As seen in Figure **49.1.1**, a cell placed in water tends to swell due to gain of water from the hypotonic or "low salt" environment. A cell placed in a solution with higher salt concentration, on the other hand, tends to make the membrane shrivel up due to loss of water into the hypertonic or "high salt" environment. Isotonic cells have an equal concentration of solutes inside and outside the cell; this equalizes the osmotic pressure on either side of the cell membrane which is a semi-permeable membrane.

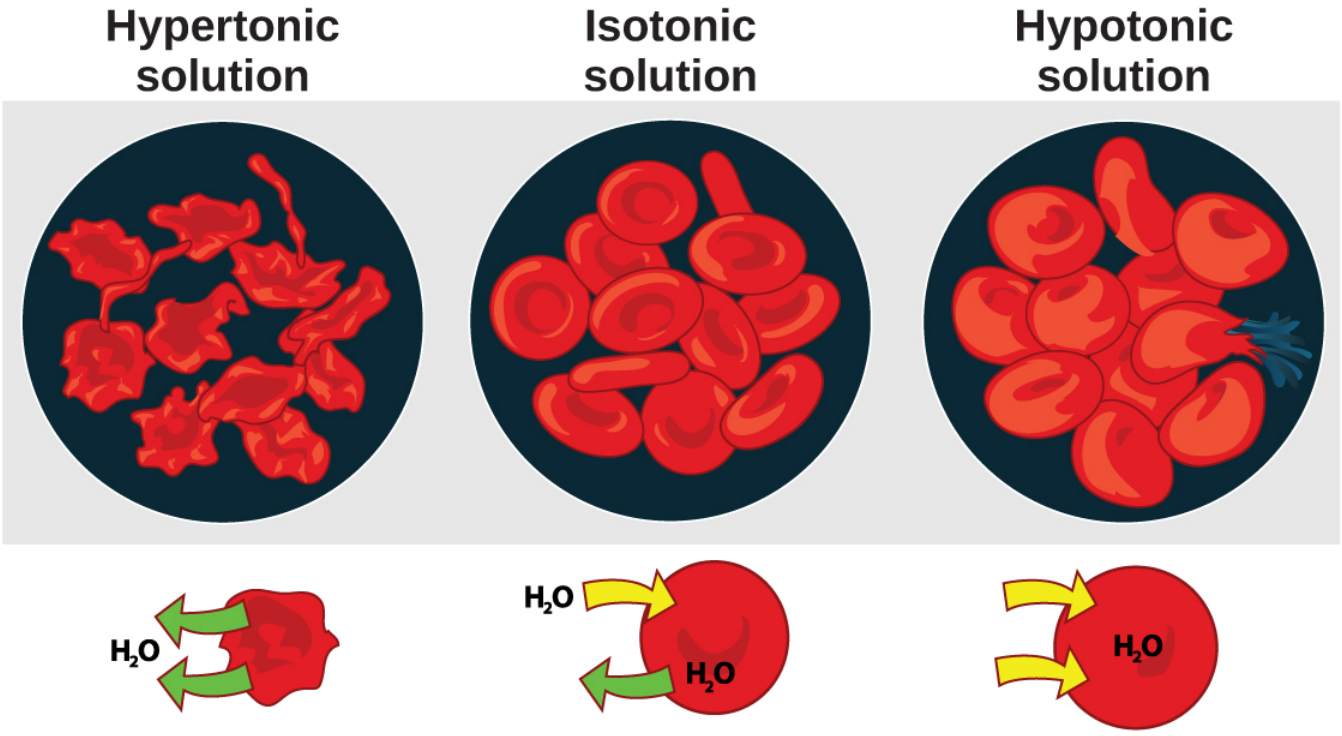


Figure **49.1.1**: Cells placed in a hypertonic environment tend to shrink due to loss of water. In a hypotonic environment, cells tend to swell due to intake of water. The blood maintains an isotonic environment so that cells neither shrink nor swell. (credit: Mariana Ruiz Villareal)

The body does not exist in isolation. There is a constant input of water and electrolytes into the system. While osmoregulation is achieved across membranes within the body, excess electrolytes and wastes are transported to the kidneys and excreted, helping to maintain osmotic balance.

Need for Osmoregulation

Biological systems constantly interact and exchange water and nutrients with the environment by way of consumption of food and water and through excretion in the form of sweat, urine, and feces. Without a mechanism to regulate osmotic pressure, or when a disease damages this mechanism, there is a tendency to accumulate toxic waste and water, which can have dire consequences.

Mammalian systems have evolved to regulate not only the overall osmotic pressure across membranes, but also specific concentrations of important electrolytes in the three major fluid compartments: blood plasma, extracellular fluid, and intracellular fluid. Since osmotic pressure is regulated by the movement of water across membranes, the volume of the fluid compartments can also change temporarily. Because blood plasma is one of the fluid components, osmotic pressures have a direct bearing on blood pressure.

Transport of Electrolytes across Cell Membranes

Electrolytes, such as sodium chloride, ionize in water, meaning that they dissociate into their component ions. In water, sodium chloride (NaCl), dissociates into the sodium ion (Na^+) and the chloride ion ($Cl^–$). The most important ions, whose concentrations are very closely regulated in body fluids, are the cations sodium (Na^+), potassium (K^+), calcium (Ca^{+2}), magnesium (Mg^{+2}), and the anions chloride (Cl^-), carbonate (CO_3^{-2}), bicarbonate (HCO_3^-), and phosphate(PO_3^-). Electrolytes are lost from the body during urination and perspiration. For this reason, athletes are encouraged to replace electrolytes and fluids during periods of increased activity and perspiration.

Osmotic pressure is influenced by the concentration of solutes in a solution. It is directly proportional to the number of solute atoms or molecules and not dependent on the size of the solute molecules. Because electrolytes dissociate into their component ions, they, in essence, add more solute particles into the solution and have a greater effect on osmotic pressure, per mass than compounds that do not dissociate in water, such as glucose.

Water can pass through membranes by passive diffusion. If electrolyte ions could passively diffuse across membranes, it would be impossible to maintain specific concentrations of ions in each fluid compartment therefore they require special mechanisms to cross the semi-permeable membranes in the body. This movement can be accomplished by facilitated diffusion and active transport. Facilitated diffusion requires protein-based channels for moving the solute. Active transport requires energy in the form of ATP conversion, carrier proteins, or pumps in order to move ions against the concentration gradient.

Concept of Osmolality and Milliequivalent

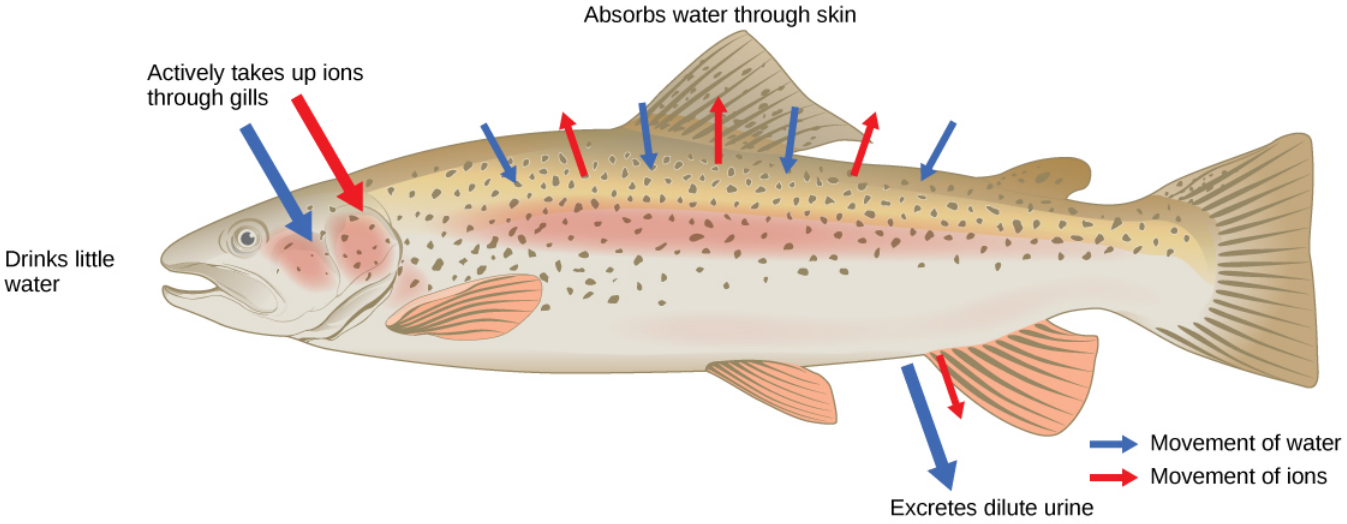
In order to calculate osmotic pressure, it is necessary to understand how solute concentrations are measured. The unit for measuring solutes is the mole. One mole is defined as the gram molecular weight of the solute. For example, the molecular weight of sodium chloride is 58.44. Thus, one mole of sodium chloride weighs 58.44 grams. The molarity of a solution is the number of moles of solute per liter of solution. The molality of a solution is the number of moles of solute per kilogram of solvent. If the solvent is water, one kilogram of water is equal to one liter of water. While molarity and molality are used to express the concentration of solutions, electrolyte concentrations are usually expressed in terms of milliequivalents per liter (mEq/L): the mEq/L is equal to the ion concentration (in millimoles) multiplied by the number of electrical charges on the ion. The unit of milliequivalent takes into consideration the ions present in the solution (since electrolytes form ions in aqueous solutions) and the charge on the ions.

Thus, for ions that have a charge of one, one milliequivalent is equal to one millimole. For ions that have a charge of two (like calcium), one milliequivalent is equal to 0.5 millimoles. Another unit for the expression of electrolyte concentration is the milliosmole (mOsm), which is the number of milliequivalents of solute per kilogram of solvent. Body fluids are usually maintained within the range of 280 to 300 mOsm.

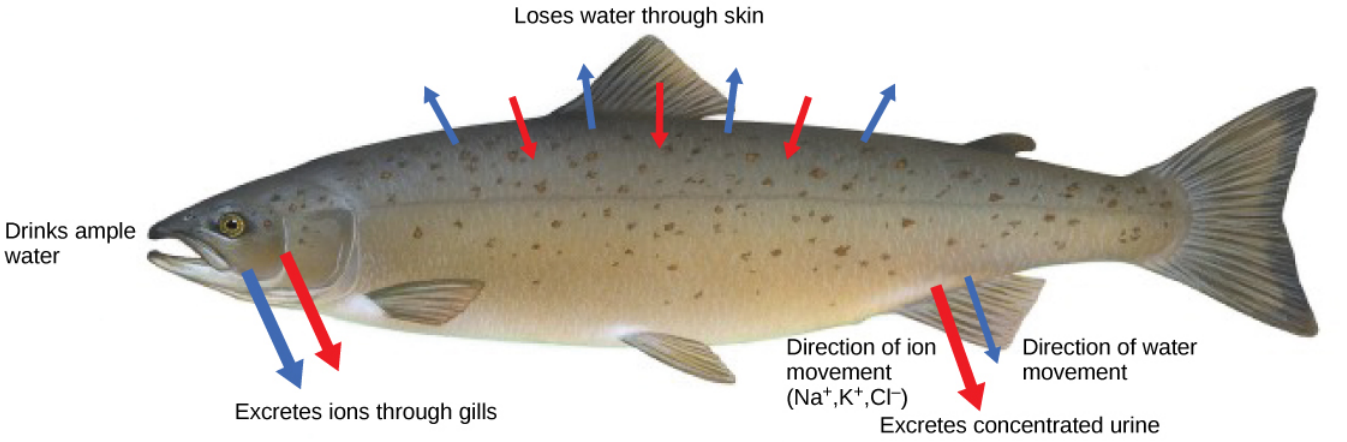
Osmoregulators and Osmoconformers

Persons lost at sea without any fresh water to drink are at risk of severe dehydration because the human body cannot adapt to drinking seawater, which is hypertonic in comparison to body fluids. Organisms such as goldfish that can tolerate only a relatively narrow range of salinity are referred to as stenohaline. About 90 percent of all bony fish are restricted to either freshwater or seawater. They are incapable of osmotic regulation in the opposite environment. It is possible, however, for a few fishes like salmon to spend part of their life in fresh water and part in sea water. Organisms like the salmon and molly that can tolerate a relatively wide range of salinity are referred to as euryhaline organisms. This is possible because some fish have evolved

osmoregulatory mechanisms to survive in all kinds of aquatic environments. When they live in fresh water, their bodies tend to take up water because the environment is relatively hypotonic, as illustrated in Figure 49.1.2a. In such hypotonic environments, these fish do not drink much water. Instead, they pass a lot of very dilute urine, and they achieve electrolyte balance by active transport of salts through the gills. When they move to a hypertonic marine environment, these fish start drinking sea water; they excrete the excess salts through their gills and their urine, as illustrated in Figure 49.1.2b. Most marine invertebrates, on the other hand, may be isotonic with sea water (osmoconformers). Their body fluid concentrations conform to changes in seawater concentration. Cartilaginous fishes' salt composition of the blood is similar to bony fishes; however, the blood of sharks contains the organic compounds urea and trimethylamine oxide (TMAO). This does not mean that their electrolyte composition is similar to that of sea water. They achieve isotonicity with the sea by storing large concentrations of urea. These animals that secrete urea are called ureotelic animals. TMAO stabilizes proteins in the presence of high urea levels, preventing the disruption of peptide bonds that would occur in other animals exposed to similar levels of urea. Sharks are cartilaginous fish with a rectal gland to secrete salt and assist in osmoregulation.



(a) Osmoregulation in a freshwater environment



(b) Osmoregulation in a saltwater environment

Figure 49.1.2: Fish are osmoregulators, but must use different mechanisms to survive in (a) freshwater or (b) saltwater environments. (credit: modification of work by Duane Raver, NOAA)

Career Connection: Dialysis Technician

Dialysis is a medical process of removing wastes and excess water from the blood by diffusion and ultrafiltration. When kidney function fails, dialysis must be done to artificially rid the body of wastes. This is a vital process to keep patients alive.

In some cases, the patients undergo artificial dialysis until they are eligible for a kidney transplant. In others who are not candidates for kidney transplants, dialysis is a life-long necessity.

Dialysis technicians typically work in hospitals and clinics. While some roles in this field include equipment development and maintenance, most dialysis technicians work in direct patient care. Their on-the-job duties, which typically occur under the direct supervision of a registered nurse, focus on providing dialysis treatments. This can include reviewing patient history and current condition, assessing and responding to patient needs before and during treatment, and monitoring the dialysis process. Treatment may include taking and reporting a patient's vital signs and preparing solutions and equipment to ensure accurate and sterile procedures.

Summary

Solute concentrations across a semi-permeable membranes influence the movement of water and solutes across the membrane. It is the number of solute molecules and not the molecular size that is important in osmosis. Osmoregulation and osmotic balance are important bodily functions, resulting in water and salt balance. Not all solutes can pass through a semi-permeable membrane. Osmosis is the movement of water across the membrane. Osmosis occurs to equalize the number of solute molecules across a semi-permeable membrane by the movement of water to the side of higher solute concentration. Facilitated diffusion utilizes protein channels to move solute molecules from areas of higher to lower concentration while active transport mechanisms are required to move solutes against concentration gradients. Osmolarity is measured in units of milliequivalents or milliosmoles, both of which take into consideration the number of solute particles and the charge on them. Fish that live in fresh water or saltwater adapt by being osmoregulators or osmoconformers.

Glossary

electrolyte
: solute that breaks down into ions when dissolved in water

molality
: number of moles of solute per kilogram of solvent

molarity
: number of moles of solute per liter of solution

mole
: gram equivalent of the molecular weight of a substance

non-electrolyte
: solute that does not break down into ions when dissolved in water

osmoconformer
: organism that changes its tonicity based on its environment

osmoregulation
: mechanism by which water and solute concentrations are maintained at desired levels

osmoregulator
: organism that maintains its tonicity irrespective of its environment

osmotic balance
: balance of the amount of water and salt input and output to and from a biological system without disturbing the desired osmotic pressure and solute concentration in every compartment

osmotic pressure
: pressure exerted on a membrane to equalize solute concentration on either side

semi-permeable membrane

membrane that allows only certain solutes to pass through

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49.2: Nitrogenous Wastes- Ammonia, Urea, and Uric Acid

Skills to Develop

- Compare and contrast the way in which aquatic animals and terrestrial animals can eliminate toxic ammonia from their systems
- Compare the major byproduct of ammonia metabolism in vertebrate animals to that of birds, insects, and reptiles

Of the four major macromolecules in biological systems, both proteins and nucleic acids contain nitrogen. During the catabolism, or breakdown, of nitrogen-containing macromolecules, carbon, hydrogen, and oxygen are extracted and stored in the form of carbohydrates and fats. Excess nitrogen is excreted from the body. Nitrogenous wastes tend to form toxic ammonia, which raises the pH of body fluids. The formation of ammonia itself requires energy in the form of ATP and large quantities of water to dilute it out of a biological system. Animals that live in aquatic environments tend to release ammonia into the water. Animals that excrete ammonia are said to be ammonotelic. Terrestrial organisms have evolved other mechanisms to excrete nitrogenous wastes. The animals must detoxify ammonia by converting it into a relatively nontoxic form such as urea or uric acid. Mammals, including humans, produce urea, whereas reptiles and many terrestrial invertebrates produce uric acid. Animals that secrete urea as the primary nitrogenous waste material are called ureotelic animals.

Nitrogenous Waste in Terrestrial Animals: The Urea Cycle

The urea cycle is the primary mechanism by which mammals convert ammonia to urea. Urea is made in the liver and excreted in urine. The overall chemical reaction by which ammonia is converted to urea is 2 NH_3 (ammonia) + CO_2 + 3 ATP + H_2O → H_2N-CO-NH_2 (urea) + 2 ADP + 4 P_i + AMP.

The urea cycle utilizes five intermediate steps, catalyzed by five different enzymes, to convert ammonia to urea, as shown in Figure 49.2.1. The amino acid L-ornithine gets converted into different intermediates before being regenerated at the end of the urea cycle. Hence, the urea cycle is also referred to as the ornithine cycle. The enzyme ornithine transcarbamylase catalyzes a key step in the urea cycle and its deficiency can lead to accumulation of toxic levels of ammonia in the body. The first two reactions occur in the mitochondria and the last three reactions occur in the cytosol. Urea concentration in the blood, called blood urea nitrogen or BUN, is used as an indicator of kidney function.

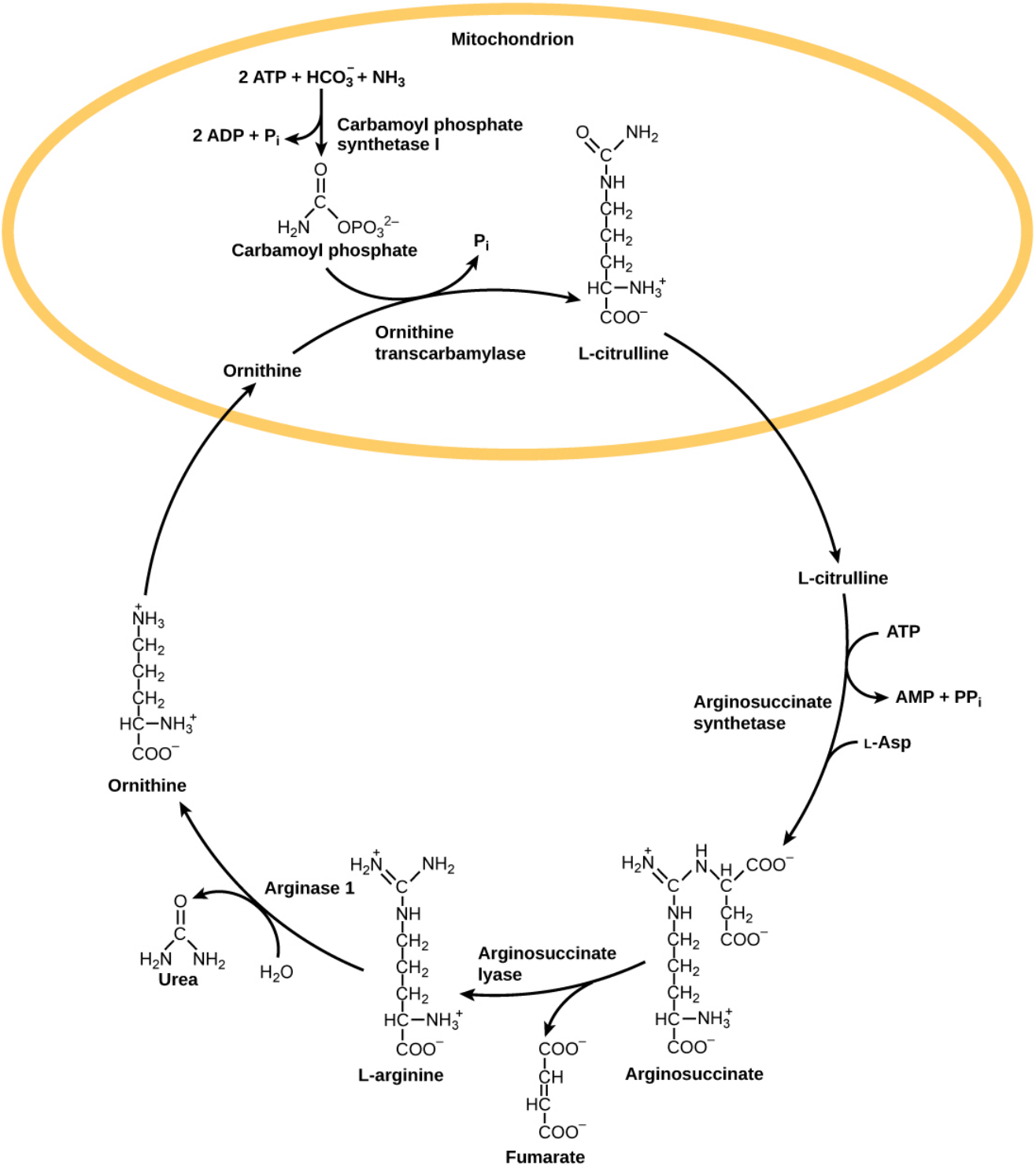


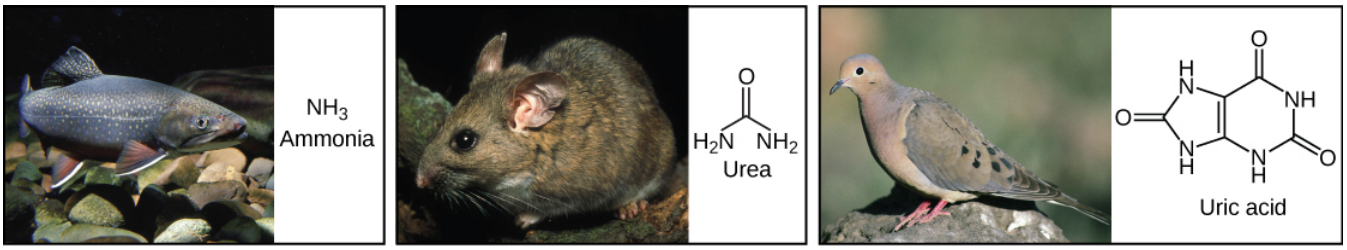
Figure **49.2.1**: The urea cycle converts ammonia to urea.

Evolution Connection: Excretion of Nitrogenous Waste

The theory of evolution proposes that life started in an aquatic environment. It is not surprising to see that biochemical pathways like the urea cycle evolved to adapt to a changing environment when terrestrial life forms evolved. Arid conditions probably led to the evolution of the uric acid pathway as a means of conserving water.

Nitrogenous Waste in Birds and Reptiles: Uric Acid

Birds, reptiles, and most terrestrial arthropods convert toxic ammonia to uric acid or the closely related compound guanine (guano) instead of urea. Mammals also form some uric acid during breakdown of nucleic acids. Uric acid is a compound similar to purines found in nucleic acids. It is water insoluble and tends to form a white paste or powder; it is excreted by birds, insects, and reptiles. Conversion of ammonia to uric acid requires more energy and is much more complex than conversion of ammonia to urea Figure 49.2.2.



(a) Many invertebrates and aquatic species excrete ammonia.

(b) Mammals, many adult amphibians, and some marine species excrete urea.

(c) Insects, land snails, birds, and many reptiles excrete uric acid.

Figure 49.2.2: Nitrogenous waste is excreted in different forms by different species. These include (a) ammonia, (b) urea, and (c) uric acid. (credit a: modification of work by Eric Engbretson, USFWS; credit b: modification of work by B. "Moose" Peterson, USFWS; credit c: modification of work by Dave Menke, USFWS)

Everyday Connection: Gout

Mammals use uric acid crystals as an antioxidant in their cells. However, too much uric acid tends to form kidney stones and may also cause a painful condition called gout, where uric acid crystals accumulate in the joints, as illustrated in Figure 49.2.3. Food choices that reduce the amount of nitrogenous bases in the diet help reduce the risk of gout. For example, tea, coffee, and chocolate have purine-like compounds, called xanthines, and should be avoided by people with gout and kidney stones.



Figure 49.2.3: Gout causes the inflammation visible in this person's left big toe joint. (credit: "Gonzosft"/Wikimedia Commons)

Summary

Ammonia is the waste produced by metabolism of nitrogen-containing compounds like proteins and nucleic acids. While aquatic animals can easily excrete ammonia into their watery surroundings, terrestrial animals have evolved special mechanisms to eliminate the toxic ammonia from their systems. Urea is the major byproduct of ammonia metabolism in vertebrate animals. Uric acid is the major byproduct of ammonia metabolism in birds, terrestrial arthropods, and reptiles.

Glossary

ammonia

compound made of one nitrogen atom and three hydrogen atoms

ammonotelic

describes an animal that excretes ammonia as the primary waste material

antioxidant
agent that prevents cell destruction by reactive oxygen species

blood urea nitrogen (BUN)
estimate of urea in the blood and an indicator of kidney function

urea cycle
pathway by which ammonia is converted to urea

ureotelic
describes animals that secrete urea as the primary nitrogenous waste material

uric acid
byproduct of ammonia metabolism in birds, insects, and reptiles

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49.3: Osmoregulatory Organs

Skills to Develop

- Explain how the kidneys serve as the main osmoregulatory organs in mammalian systems
- Describe the structure of the kidneys and the functions of the parts of the kidney
- Describe how the nephron is the functional unit of the kidney and explain how it actively filters blood and generates urine
- Detail the three steps in the formation of urine: glomerular filtration, tubular reabsorption, and tubular secretion

Although the kidneys are the major osmoregulatory organ, the skin and lungs also play a role in the process. Water and electrolytes are lost through sweat glands in the skin, which helps moisturize and cool the skin surface, while the lungs expel a small amount of water in the form of mucous secretions and via evaporation of water vapor.

Kidneys: The Main Osmoregulatory Organ

The kidneys, illustrated in Figure **49.3.1**, are a pair of bean-shaped structures that are located just below and posterior to the liver in the peritoneal cavity. The adrenal glands sit on top of each kidney and are also called the suprarenal glands. Kidneys filter blood and purify it. All the blood in the human body is filtered many times a day by the kidneys; these organs use up almost 25 percent of the oxygen absorbed through the lungs to perform this function. Oxygen allows the kidney cells to efficiently manufacture chemical energy in the form of ATP through aerobic respiration. The filtrate coming out of the kidneys is called urine.

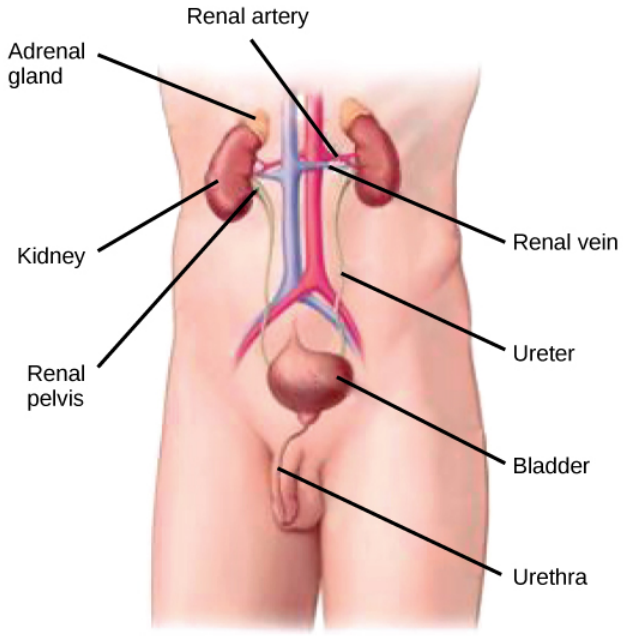


Figure **49.3.1**: Kidneys filter the blood, producing urine that is stored in the bladder prior to elimination through the urethra. (credit: modification of work by NCI)

Kidney Structure

Externally, the kidneys are surrounded by three layers, illustrated in Figure **49.3.2**. The outermost layer is a tough connective tissue layer called the renal fascia. The second layer is called the perirenal fat capsule, which helps anchor the kidneys in place. The third and innermost layer is the renal capsule. Internally, the kidney has three regions—an outer cortex, a medulla in the middle, and the renal pelvis in the region called the hilum of the kidney. The hilum is the concave part of the bean-shape where blood vessels and nerves enter and exit the kidney; it is also the point of exit for the ureters. The renal cortex is granular due to the presence of nephrons—the functional unit of the kidney. The medulla consists of multiple pyramidal tissue masses, called the renal pyramids. In between the pyramids are spaces called renal columns through which the blood vessels pass. The tips of the pyramids, called renal papillae, point toward the renal pelvis. There are, on average, eight renal pyramids in each kidney. The renal pyramids along with the adjoining cortical region are called the lobes of the kidney. The renal pelvis leads to the ureter on the outside of the kidney.

On the inside of the kidney, the renal pelvis branches out into two or three extensions called the major calyces, which further branch into the minor calyces. The ureters are urine-bearing tubes that exit the kidney and empty into the urinary bladder.

Art Connection

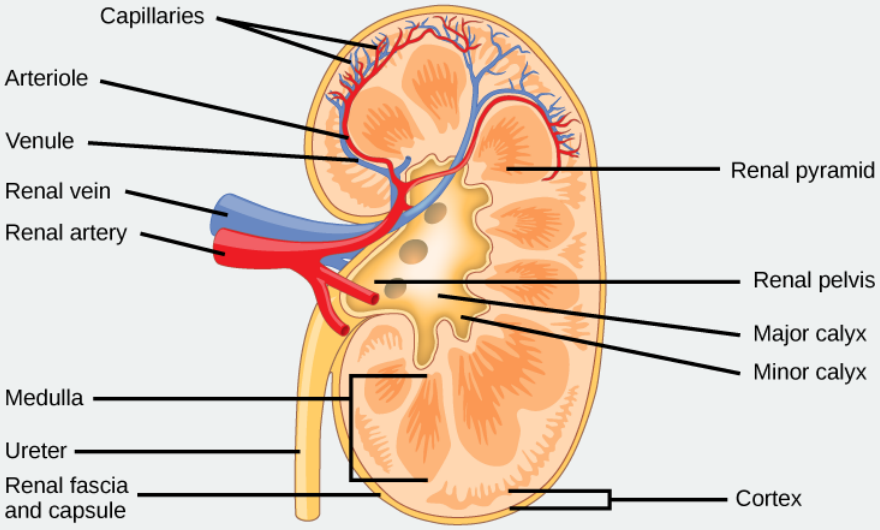


Figure 49.3.2: The internal structure of the kidney is shown. (credit: modification of work by NCI)

Which of the following statements about the kidney is false?

A. The renal pelvis drains into the ureter.
B. The renal pyramids are in the medulla.
C. The cortex covers the capsule.
D. Nephrons are in the renal cortex.

Because the kidney filters blood, its network of blood vessels is an important component of its structure and function. The arteries, veins, and nerves that supply the kidney enter and exit at the renal hilum. Renal blood supply starts with the branching of the aorta into the renal arteries (which are each named based on the region of the kidney they pass through) and ends with the exiting of the renal veins to join the inferior vena cava. The renal arteries split into several segmental arteries upon entering the kidneys. Each segmental artery splits further into several interlobar arteries and enters the renal columns, which supply the renal lobes. The interlobar arteries split at the junction of the renal cortex and medulla to form the arcuate arteries. The arcuate “bow shaped” arteries form arcs along the base of the medullary pyramids. Cortical radiate arteries, as the name suggests, radiate out from the arcuate arteries. The cortical radiate arteries branch into numerous afferent arterioles, and then enter the capillaries supplying the nephrons. Veins trace the path of the arteries and have similar names, except there are no segmental veins.

As mentioned previously, the functional unit of the kidney is the nephron, illustrated in Figure 49.3.3. Each kidney is made up of over one million nephrons that dot the renal cortex, giving it a granular appearance when sectioned sagittally. There are two types of nephrons—cortical nephrons (85 percent), which are deep in the renal cortex, and juxtamedullary nephrons (15 percent), which lie in the renal cortex close to the renal medulla. A nephron consists of three parts—a renal corpuscle, a renal tubule, and the associated capillary network, which originates from the cortical radiate arteries.

Art Connection

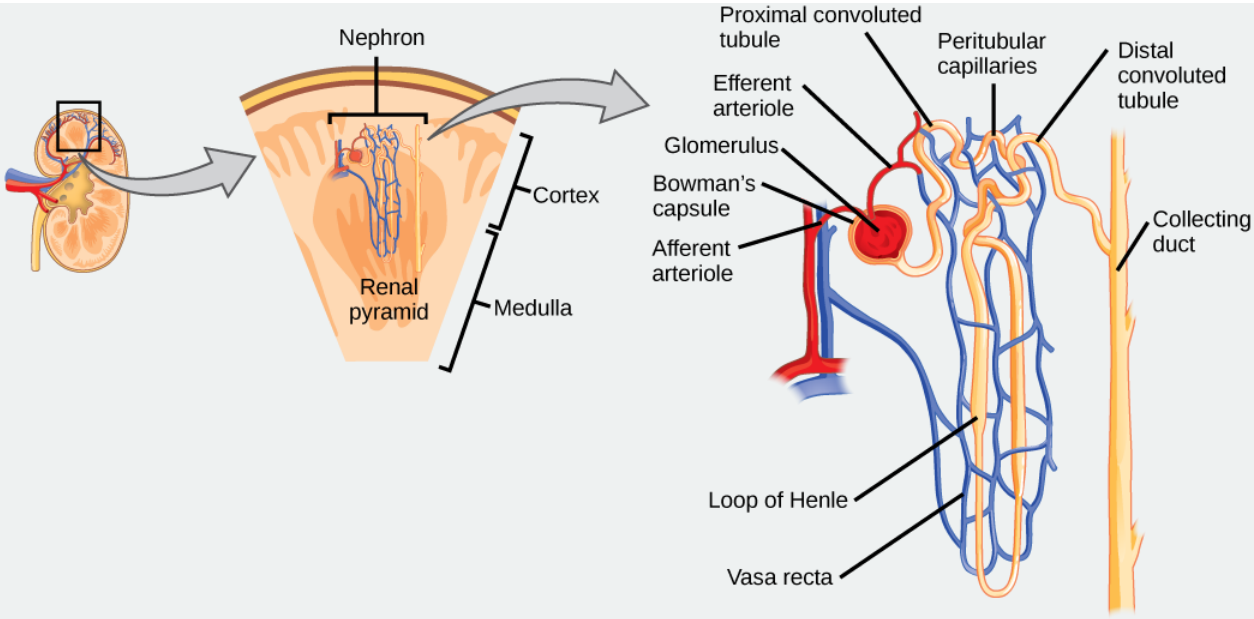


Figure **49.3.3**: The nephron is the functional unit of the kidney. The glomerulus and convoluted tubules are located in the kidney cortex, while collecting ducts are located in the pyramids of the medulla. (credit: modification of work by NIDDK)

Which of the following statements about the nephron is false?

A. The collecting duct empties into the distal convoluted tubule.
B. The Bowman's capsule surrounds the glomerulus.
C. The loop of Henle is between the proximal and distal convoluted tubules.
D. The loop of Henle empties into the distal convoluted tubule.

Renal Corpuscle

The renal corpuscle, located in the renal cortex, is made up of a network of capillaries known as the glomerulus and the capsule, a cup-shaped chamber that surrounds it, called the glomerular or Bowman's capsule.

Renal Tubule

The renal tubule is a long and convoluted structure that emerges from the glomerulus and can be divided into three parts based on function. The first part is called the proximal convoluted tubule (PCT) due to its proximity to the glomerulus; it stays in the renal cortex. The second part is called the loop of Henle, or nephritic loop, because it forms a loop (with descending and ascending limbs) that goes through the renal medulla. The third part of the renal tubule is called the distal convoluted tubule (DCT) and this part is also restricted to the renal cortex. The DCT, which is the last part of the nephron, connects and empties its contents into collecting ducts that line the medullary pyramids. The collecting ducts amass contents from multiple nephrons and fuse together as they enter the papillae of the renal medulla.

Capillary Network within the Nephron

The capillary network that originates from the renal arteries supplies the nephron with blood that needs to be filtered. The branch that enters the glomerulus is called the afferent arteriole. The branch that exits the glomerulus is called the efferent arteriole. Within the glomerulus, the network of capillaries is called the glomerular capillary bed. Once the efferent arteriole exits the glomerulus, it forms the peritubular capillary network, which surrounds and interacts with parts of the renal tubule. In cortical nephrons, the peritubular capillary network surrounds the PCT and DCT. In juxtamedullary nephrons, the peritubular capillary network forms a network around the loop of Henle and is called the vasa recta.

Kidney Function and Physiology

Kidneys filter blood in a three-step process. First, the nephrons filter blood that runs through the capillary network in the glomerulus. Almost all solutes, except for proteins, are filtered out into the glomerulus by a process called glomerular filtration.

Second, the filtrate is collected in the renal tubules. Most of the solutes get reabsorbed in the PCT by a process called tubular reabsorption. In the loop of Henle, the filtrate continues to exchange solutes and water with the renal medulla and the peritubular capillary network. Water is also reabsorbed during this step. Then, additional solutes and wastes are secreted into the kidney tubules during tubular secretion, which is, in essence, the opposite process to tubular reabsorption. The collecting ducts collect filtrate coming from the nephrons and fuse in the medullary papillae. From here, the papillae deliver the filtrate, now called urine, into the minor calyces that eventually connect to the ureters through the renal pelvis. This entire process is illustrated in Figure **49.3.4**.

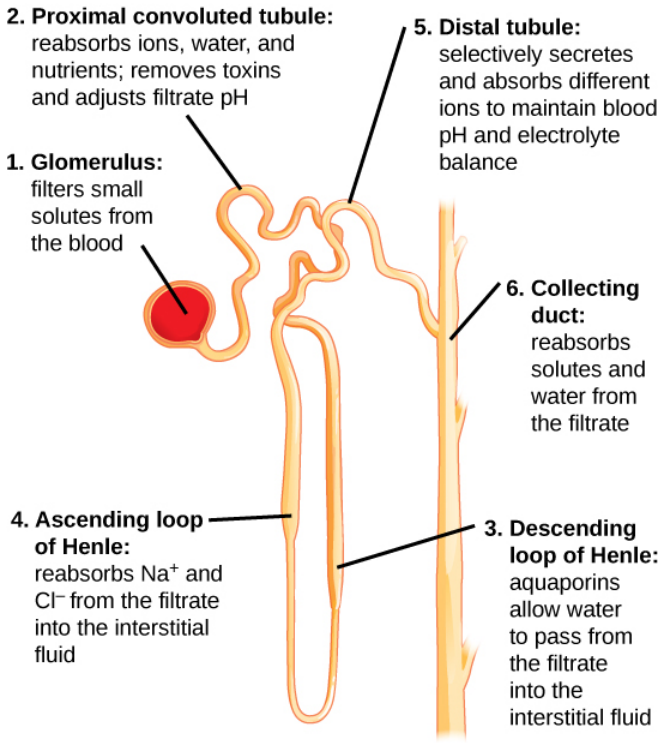


Figure **49.3.4**: Each part of the nephron performs a different function in filtering waste and maintaining homeostatic balance. (1) The glomerulus forces small solutes out of the blood by pressure. (2) The proximal convoluted tubule reabsorbs ions, water, and nutrients from the filtrate into the interstitial fluid, and actively transports toxins and drugs from the interstitial fluid into the filtrate. The proximal convoluted tubule also adjusts blood pH by selectively secreting ammonia (NH_3) into the filtrate, where it reacts with H^+ to form NH_4^+. The more acidic the filtrate, the more ammonia is secreted. (3) The descending loop of Henle is lined with cells containing aquaporins that allow water to pass from the filtrate into the interstitial fluid. (4) In the thin part of the ascending loop of Henle, Na^+ and Cl^- ions diffuse into the interstitial fluid. In the thick part, these same ions are actively transported into the interstitial fluid. Because salt but not water is lost, the filtrate becomes more dilute as it travels up the limb. (5) In the distal convoluted tubule, K^+ and H^+ ions are selectively secreted into the filtrate, while Na^+, Cl^-, and HCO_3^- ions are reabsorbed to maintain pH and electrolyte balance in the blood. (6) The collecting duct reabsorbs solutes and water from the filtrate, forming dilute urine. (credit: modification of work by NIDDK)

Glomerular Filtration

Glomerular filtration filters out most of the solutes due to high blood pressure and specialized membranes in the afferent arteriole. The blood pressure in the glomerulus is maintained independent of factors that affect systemic blood pressure. The “leaky” connections between the endothelial cells of the glomerular capillary network allow solutes to pass through easily. All solutes in the glomerular capillaries, except for macromolecules like proteins, pass through by passive diffusion. There is no energy requirement at this stage of the filtration process. Glomerular filtration rate (GFR) is the volume of glomerular filtrate formed per minute by the kidneys. GFR is regulated by multiple mechanisms and is an important indicator of kidney function.

Link to Learning

To learn more about the vascular system of kidneys, click through this review and the steps of blood flow.

Tubular Reabsorption and Secretion

Tubular reabsorption occurs in the PCT part of the renal tubule. Almost all nutrients are reabsorbed, and this occurs either by passive or active transport. Reabsorption of water and some key electrolytes are regulated and can be influenced by hormones. Sodium (Na^+) is the most abundant ion and most of it is reabsorbed by active transport and then transported to the peritubular capillaries. Because Na^+ is actively transported out of the tubule, water follows it to even out the osmotic pressure. Water is also independently reabsorbed into the peritubular capillaries due to the presence of aquaporins, or water channels, in the PCT. This occurs due to the low blood pressure and high osmotic pressure in the peritubular capillaries. However, every solute has a transport maximum and the excess is not reabsorbed.

In the loop of Henle, the permeability of the membrane changes. The descending limb is permeable to water, not solutes; the opposite is true for the ascending limb. Additionally, the loop of Henle invades the renal medulla, which is naturally high in salt concentration and tends to absorb water from the renal tubule and concentrate the filtrate. The osmotic gradient increases as it moves deeper into the medulla. Because two sides of the loop of Henle perform opposing functions, as illustrated in Figure **49.3.5**, it acts as a countercurrent multiplier. The vasa recta around it acts as the countercurrent exchanger.

Art Connection

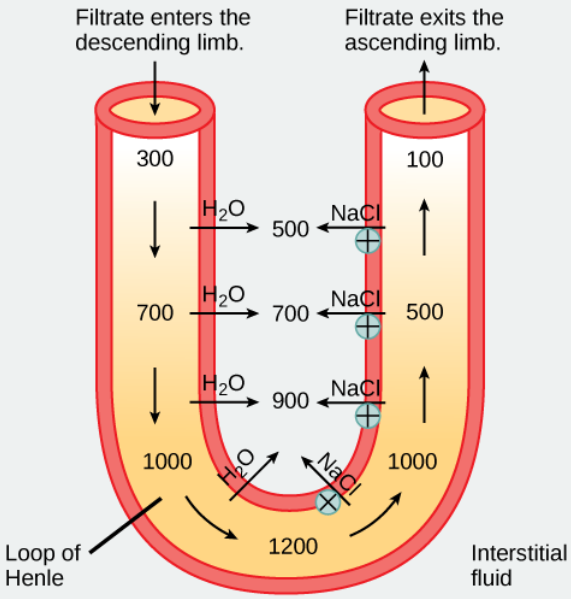


Figure **49.3.5**: The loop of Henle acts as a countercurrent multiplier that uses energy to create concentration gradients. The descending limb is water permeable. Water flows from the filtrate to the interstitial fluid, so osmolality inside the limb increases as it descends into the renal medulla. At the bottom, the osmolality is higher inside the loop than in the interstitial fluid. Thus, as filtrate enters the ascending limb, Na^+ and Cl^- ions exit through ion channels present in the cell membrane. Further up, Na^+ is actively transported out of the filtrate and Cl^- follows. Osmolarity is given in units of milliosmoles per liter (mOsm/L).

Loop diuretics are drugs sometimes used to treat hypertension. These drugs inhibit the reabsorption of Na^+ and Cl^- ions by the ascending limb of the loop of Henle. A side effect is that they increase urination. Why do you think this is the case?

By the time the filtrate reaches the DCT, most of the urine and solutes have been reabsorbed. If the body requires additional water, all of it can be reabsorbed at this point. Further reabsorption is controlled by hormones, which will be discussed in a later section. Excretion of wastes occurs due to lack of reabsorption combined with tubular secretion. Undesirable products like metabolic wastes, urea, uric acid, and certain drugs, are excreted by tubular secretion. Most of the tubular secretion happens in the DCT, but some occurs in the early part of the collecting duct. Kidneys also maintain an acid-base balance by secreting excess H^+ ions.

Although parts of the renal tubules are named proximal and distal, in a cross-section of the kidney, the tubules are placed close together and in contact with each other and the glomerulus. This allows for exchange of chemical messengers between the different cell types. For example, the DCT ascending limb of the loop of Henle has masses of cells called macula densa, which are in contact with cells of the afferent arterioles called juxtaglomerular cells. Together, the macula densa and juxtaglomerular cells form the juxtaglomerular complex (JGC). The JGC is an endocrine structure that secretes the enzyme renin and the hormone erythropoietin. When hormones trigger the macula densa cells in the DCT due to variations in blood volume, blood pressure, or electrolyte balance, these cells can immediately communicate the problem to the capillaries in the afferent and efferent arterioles, which can constrict or relax to change the glomerular filtration rate of the kidneys.

Career Connection: Nephrologist

A nephrologist studies and deals with diseases of the kidneys—both those that cause kidney failure (such as diabetes) and the conditions that are produced by kidney disease (such as hypertension). Blood pressure, blood volume, and changes in electrolyte balance come under the purview of a nephrologist.

Nephrologists usually work with other physicians who refer patients to them or consult with them about specific diagnoses and treatment plans. Patients are usually referred to a nephrologist for symptoms such as blood or protein in the urine, very high blood pressure, kidney stones, or renal failure.

Nephrology is a subspecialty of internal medicine. To become a nephrologist, medical school is followed by additional training to become certified in internal medicine. An additional two or more years is spent specifically studying kidney disorders and their accompanying effects on the body.

Summary

The kidneys are the main osmoregulatory organs in mammalian systems; they function to filter blood and maintain the osmolarity of body fluids at 300 mOsm. They are surrounded by three layers and are made up internally of three distinct regions—the cortex, medulla, and pelvis.

The blood vessels that transport blood into and out of the kidneys arise from and merge with the aorta and inferior vena cava, respectively. The renal arteries branch out from the aorta and enter the kidney where they further divide into segmental, interlobar, arcuate, and cortical radiate arteries.

The nephron is the functional unit of the kidney, which actively filters blood and generates urine. The nephron is made up of the renal corpuscle and renal tubule. Cortical nephrons are found in the renal cortex, while juxtamedullary nephrons are found in the renal cortex close to the renal medulla. The nephron filters and exchanges water and solutes with two sets of blood vessels and the tissue fluid in the kidneys.

There are three steps in the formation of urine: glomerular filtration, which occurs in the glomerulus; tubular reabsorption, which occurs in the renal tubules; and tubular secretion, which also occurs in the renal tubules.

Art Connections

Figure 49.3.2: Which of the following statements about the kidney is false?

A. The renal pelvis drains into the ureter.
B. The renal pyramids are in the medulla.
C. The cortex covers the capsule.
D. Nephrons are in the renal cortex.

Answer

C

Figure 49.3.3: Which of the following statements about the nephron is false?

A. The collecting duct empties into the distal convoluted tubule.
B. The Bowman's capsule surrounds the glomerulus.
C. The loop of Henle is between the proximal and distal convoluted tubules.
D. The loop of Henle empties into the distal convoluted tubule.

Answer

A

Figure 49.3.5: Loop diuretics are drugs sometimes used to treat hypertension. These drugs inhibit the reabsorption of Na^+ and Cl^- ions by the ascending limb of the loop of Henle. A side effect is that they increase urination. Why do you think this is the case?

Answer

Loop diuretics decrease the excretion of salt into the renal medulla, thereby reducing its osmolality. As a result, less water is excreted into the medulla by the descending limb, and more water is excreted as urine.

Glossary

afferent arteriole
arteriole that branches from the cortical radiate artery and enters the glomerulus

arcuate artery
artery that branches from the interlobar artery and arches over the base of the renal pyramids

ascending limb
part of the loop of Henle that ascends from the renal medulla to the renal cortex

Bowman's capsule
structure that encloses the glomerulus

calyx
structure that connects the renal pelvis to the renal medulla

cortex (animal)
outer layer of an organ like the kidney or adrenal gland

cortical nephron
nephron that lies in the renal cortex

cortical radiate artery
artery that radiates from the arcuate arteries into the renal cortex

countercurrent exchanger
peritubular capillary network that allows exchange of solutes and water from the renal tubules

countercurrent multiplier
osmotic gradient in the renal medulla that is responsible for concentration of urine

descending limb
part of the loop of Henle that descends from the renal cortex into the renal medulla

distal convoluted tubule (DCT)
part of the renal tubule that is the most distant from the glomerulus

efferent arteriole
arteriole that exits from the glomerulus

glomerular filtration
filtration of blood in the glomerular capillary network into the glomerulus

glomerular filtration rate (GFR)
amount of filtrate formed by the glomerulus per minute

glomerulus (renal)
part of the renal corpuscle that contains the capillary network

hilum
region in the renal pelvis where blood vessels, nerves, and ureters bunch before entering or exiting the kidney

inferior vena cava
one of the main veins in the human body

interlobar artery
artery that branches from the segmental artery and travels in between the renal lobes

juxtaglomerular cell
cell in the afferent and efferent arterioles that responds to stimuli from the macula densa

juxtamedullary nephron
nephron that lies in the cortex but close to the renal medulla

kidney
organ that performs excretory and osmoregulatory functions

lobes of the kidney
renal pyramid along with the adjoining cortical region

loop of Henle
part of the renal tubule that loops into the renal medulla

macula densa
group of cells that senses changes in sodium ion concentration; present in parts of the renal tubule and collecting ducts

medulla
middle layer of an organ like the kidney or adrenal gland

nephron
functional unit of the kidney

perirenal fat capsule
fat layer that suspends the kidneys

peritubular capillary network
capillary network that surrounds the renal tubule after the efferent artery exits the glomerulus

proximal convoluted tubule (PCT)
part of the renal tubule that lies close to the glomerulus

renal artery
branch of the artery that enters the kidney

renal capsule
layer that encapsulates the kidneys

renal column
area of the kidney through which the interlobar arteries travel in the process of supplying blood to the renal lobes

renal corpuscle
glomerulus and the Bowman's capsule together

renal fascia
connective tissue that supports the kidneys

renal pelvis
region in the kidney where the calyces join the ureters

renal pyramid
conical structure in the renal medulla

renal tubule
tubule of the nephron that arises from the glomerulus

renal vein
branch of a vein that exits the kidney and joins the inferior vena cava

segmental artery
artery that branches from the renal artery

transport maximum
maximum amount of solute that can be transported out of the renal tubules during reabsorption

tubular reabsorption
reclamation of water and solutes that got filtered out in the glomerulus

tubular secretion
process of secretion of wastes that do not get reabsorbed

ureter
urine-bearing tube coming out of the kidney; carries urine to the bladder

urinary bladder
structure that the ureters empty the urine into; stores urine

urine
filtrate produced by kidneys that gets excreted out of the body

vasa recta
peritubular network that surrounds the loop of Henle of the juxtamedullary nephrons

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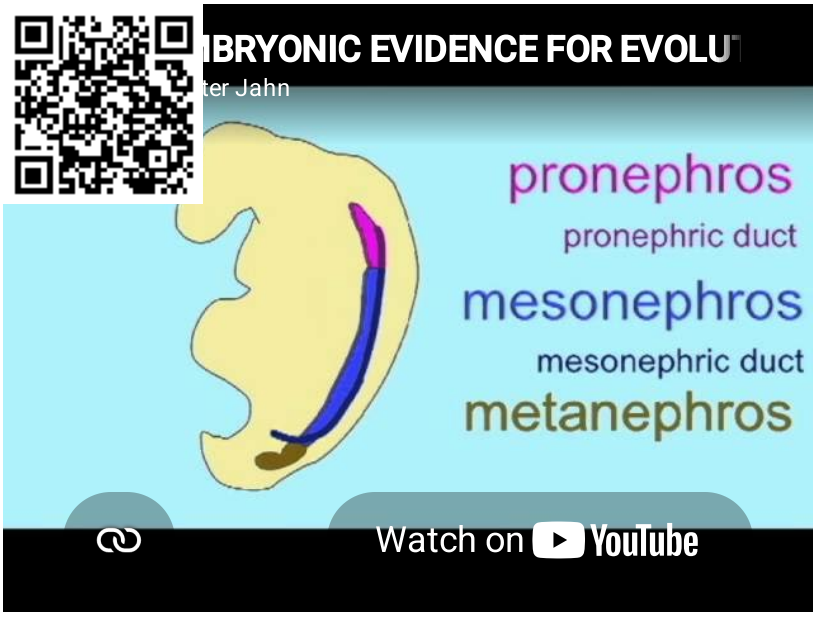
49.4: Evolution of the Vertebrate Kidney

Evolutionary pressure and the need to regulate body fluid homeostasis have led to pre-adaptation of the vertebrate kidneys to different environment conditions and to development of three kidney forms: the pronephros, mesonephros and metanephros. The kidneys of amniotes are unique compared to other internal organs, since three different kidneys are sequentially developed during embryogenesis, replacing each other and reflecting the evolution of the kidneys in vertebrates.[28]

At the very beginning of vertebrates, when they evolved from marine chordates, their evolution probably took place in fresh or slightly saline water. There is a hypothesis according to which marine fish received their kidneys after a previous adaptation of the kidneys to fresh water. As a result, early vertebrates developed renal glomeruli capable of filtering blood and perhaps tubules that reabsorbed ions. Excretion of excess water from the body is the main characteristic of the pronephros in the case of species in which it develops into a functional excretory organ. In some species, the pronephros is functional during the embryonic stage of development, representing the first stage of kidney development, after which the mesonephros develops. The mesonephros probably appeared in the course of evolution in response to the increase in body mass of vertebrates, which also led to an increase in blood pressure.

The evolution of the kidneys, along with the evolution of the lungs, allowed vertebrates called amniotes to live and reproduce in terrestrial environment. Metanephros, the permanent kidney of amniotes, has the unique ability to efficiently retain water in the body. In addition to water conservation, terrestrial life also required maintenance of salt levels in the body along with the excretion of waste products. The first class of animals to become fully terrestrial without a larval stage were the reptiles, which were the first amniotes. The kidney takes a key role in maintenance of the constant internal environment. The relative ionic composition of the extracellular fluid is similar between marine fish and all subsequent species. Therefore, it can be said that the kidneys made it possible to preserve approximately the same composition of extracellular fluid in vertebrates as it was in the primordial ocean.

Text excerpted from Wikipedia https://en.wikipedia.org/wiki/Kidney_(vertebrates) Accessed 14 November 2023



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49.5: The Mammalian Kidney

Skills to Develop

- Explain how the kidneys serve as the main osmoregulatory organs in mammalian systems
- Describe the structure of the kidneys and the functions of the parts of the kidney
- Describe how the nephron is the functional unit of the kidney and explain how it actively filters blood and generates urine
- Detail the three steps in the formation of urine: glomerular filtration, tubular reabsorption, and tubular secretion

Although the kidneys are the major osmoregulatory organ, the skin and lungs also play a role in the process. Water and electrolytes are lost through sweat glands in the skin, which helps moisturize and cool the skin surface, while the lungs expel a small amount of water in the form of mucous secretions and via evaporation of water vapor.

Kidneys: The Main Osmoregulatory Organ

The kidneys, illustrated in Figure **49.5.1**, are a pair of bean-shaped structures that are located just below and posterior to the liver in the peritoneal cavity. The adrenal glands sit on top of each kidney and are also called the suprarenal glands. Kidneys filter blood and purify it. All the blood in the human body is filtered many times a day by the kidneys; these organs use up almost 25 percent of the oxygen absorbed through the lungs to perform this function. Oxygen allows the kidney cells to efficiently manufacture chemical energy in the form of ATP through aerobic respiration. The filtrate coming out of the kidneys is called urine.

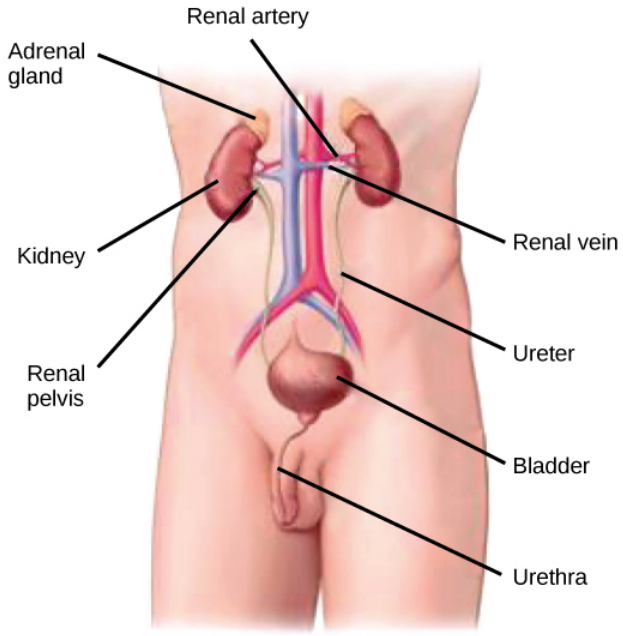


Figure **49.5.1**: Kidneys filter the blood, producing urine that is stored in the bladder prior to elimination through the urethra. (credit: modification of work by NCI)

Kidney Structure

Externally, the kidneys are surrounded by three layers, illustrated in Figure **49.5.2**. The outermost layer is a tough connective tissue layer called the renal fascia. The second layer is called the perirenal fat capsule, which helps anchor the kidneys in place. The third and innermost layer is the renal capsule. Internally, the kidney has three regions—an outer cortex, a medulla in the middle, and the renal pelvis in the region called the hilum of the kidney. The hilum is the concave part of the bean-shape where blood vessels and nerves enter and exit the kidney; it is also the point of exit for the ureters. The renal cortex is granular due to the presence of nephrons—the functional unit of the kidney. The medulla consists of multiple pyramidal tissue masses, called the renal pyramids. In between the pyramids are spaces called renal columns through which the blood vessels pass. The tips of the pyramids, called renal papillae, point toward the renal pelvis. There are, on average, eight renal pyramids in each kidney. The renal pyramids along with the adjoining cortical region are called the lobes of the kidney. The renal pelvis leads to the ureter on the outside of the kidney.

On the inside of the kidney, the renal pelvis branches out into two or three extensions called the major calyces, which further branch into the minor calyces. The ureters are urine-bearing tubes that exit the kidney and empty into the urinary bladder.

Art Connection

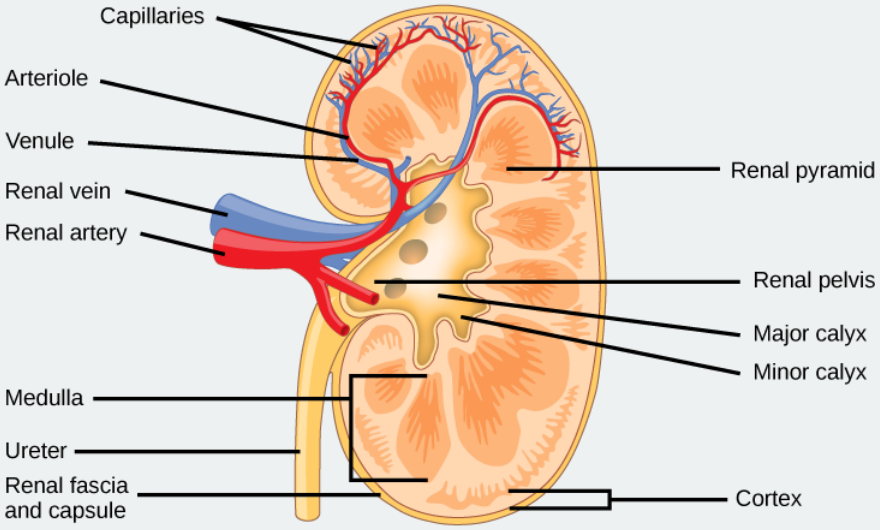


Figure 49.5.2: The internal structure of the kidney is shown. (credit: modification of work by NCI)

Which of the following statements about the kidney is false?

A. The renal pelvis drains into the ureter.
B. The renal pyramids are in the medulla.
C. The cortex covers the capsule.
D. Nephrons are in the renal cortex.

Because the kidney filters blood, its network of blood vessels is an important component of its structure and function. The arteries, veins, and nerves that supply the kidney enter and exit at the renal hilum. Renal blood supply starts with the branching of the aorta into the renal arteries (which are each named based on the region of the kidney they pass through) and ends with the exiting of the renal veins to join the inferior vena cava. The renal arteries split into several segmental arteries upon entering the kidneys. Each segmental artery splits further into several interlobar arteries and enters the renal columns, which supply the renal lobes. The interlobar arteries split at the junction of the renal cortex and medulla to form the arcuate arteries. The arcuate “bow shaped” arteries form arcs along the base of the medullary pyramids. Cortical radiate arteries, as the name suggests, radiate out from the arcuate arteries. The cortical radiate arteries branch into numerous afferent arterioles, and then enter the capillaries supplying the nephrons. Veins trace the path of the arteries and have similar names, except there are no segmental veins.

As mentioned previously, the functional unit of the kidney is the nephron, illustrated in Figure 49.5.3. Each kidney is made up of over one million nephrons that dot the renal cortex, giving it a granular appearance when sectioned sagittally. There are two types of nephrons—cortical nephrons (85 percent), which are deep in the renal cortex, and juxtamedullary nephrons (15 percent), which lie in the renal cortex close to the renal medulla. A nephron consists of three parts—a renal corpuscle, a renal tubule, and the associated capillary network, which originates from the cortical radiate arteries.

Art Connection

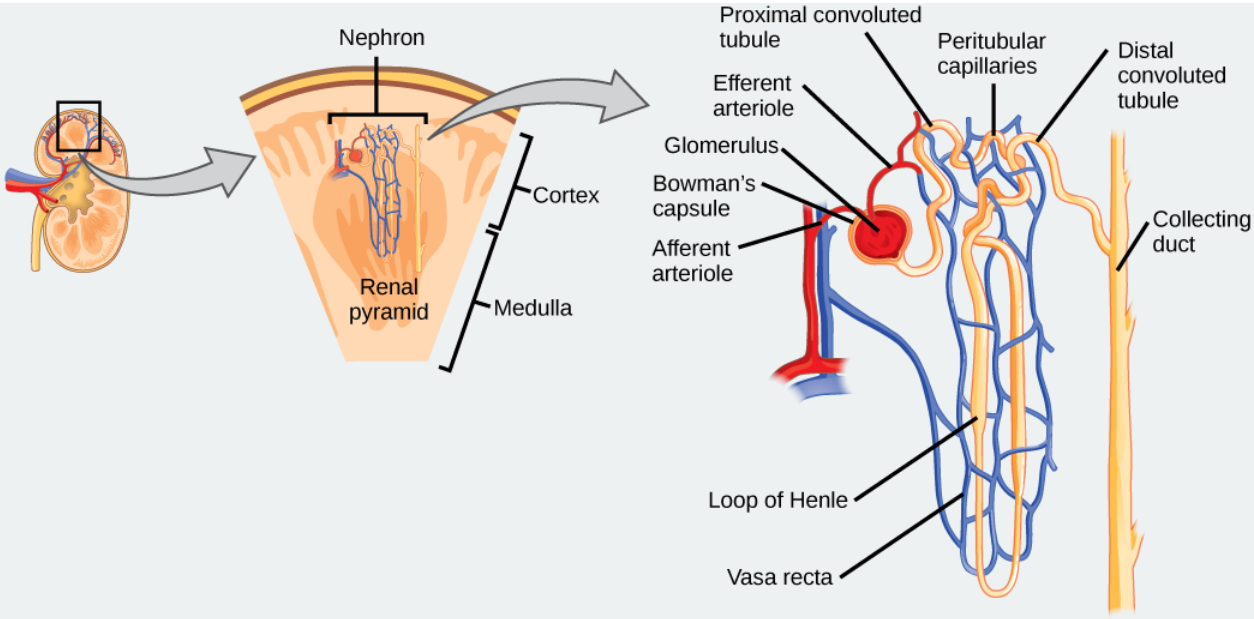


Figure **49.5.3**: The nephron is the functional unit of the kidney. The glomerulus and convoluted tubules are located in the kidney cortex, while collecting ducts are located in the pyramids of the medulla. (credit: modification of work by NIDDK)

Which of the following statements about the nephron is false?

A. The collecting duct empties into the distal convoluted tubule.
B. The Bowman's capsule surrounds the glomerulus.
C. The loop of Henle is between the proximal and distal convoluted tubules.
D. The loop of Henle empties into the distal convoluted tubule.

Renal Corpuscle

The renal corpuscle, located in the renal cortex, is made up of a network of capillaries known as the glomerulus and the capsule, a cup-shaped chamber that surrounds it, called the glomerular or Bowman's capsule.

Renal Tubule

The renal tubule is a long and convoluted structure that emerges from the glomerulus and can be divided into three parts based on function. The first part is called the proximal convoluted tubule (PCT) due to its proximity to the glomerulus; it stays in the renal cortex. The second part is called the loop of Henle, or nephritic loop, because it forms a loop (with descending and ascending limbs) that goes through the renal medulla. The third part of the renal tubule is called the distal convoluted tubule (DCT) and this part is also restricted to the renal cortex. The DCT, which is the last part of the nephron, connects and empties its contents into collecting ducts that line the medullary pyramids. The collecting ducts amass contents from multiple nephrons and fuse together as they enter the papillae of the renal medulla.

Capillary Network within the Nephron

The capillary network that originates from the renal arteries supplies the nephron with blood that needs to be filtered. The branch that enters the glomerulus is called the afferent arteriole. The branch that exits the glomerulus is called the efferent arteriole. Within the glomerulus, the network of capillaries is called the glomerular capillary bed. Once the efferent arteriole exits the glomerulus, it forms the peritubular capillary network, which surrounds and interacts with parts of the renal tubule. In cortical nephrons, the peritubular capillary network surrounds the PCT and DCT. In juxtamedullary nephrons, the peritubular capillary network forms a network around the loop of Henle and is called the vasa recta.

Kidney Function and Physiology

Kidneys filter blood in a three-step process. First, the nephrons filter blood that runs through the capillary network in the glomerulus. Almost all solutes, except for proteins, are filtered out into the glomerulus by a process called glomerular filtration.

Second, the filtrate is collected in the renal tubules. Most of the solutes get reabsorbed in the PCT by a process called tubular reabsorption. In the loop of Henle, the filtrate continues to exchange solutes and water with the renal medulla and the peritubular capillary network. Water is also reabsorbed during this step. Then, additional solutes and wastes are secreted into the kidney tubules during tubular secretion, which is, in essence, the opposite process to tubular reabsorption. The collecting ducts collect filtrate coming from the nephrons and fuse in the medullary papillae. From here, the papillae deliver the filtrate, now called urine, into the minor calyces that eventually connect to the ureters through the renal pelvis. This entire process is illustrated in Figure **49.5.4**.

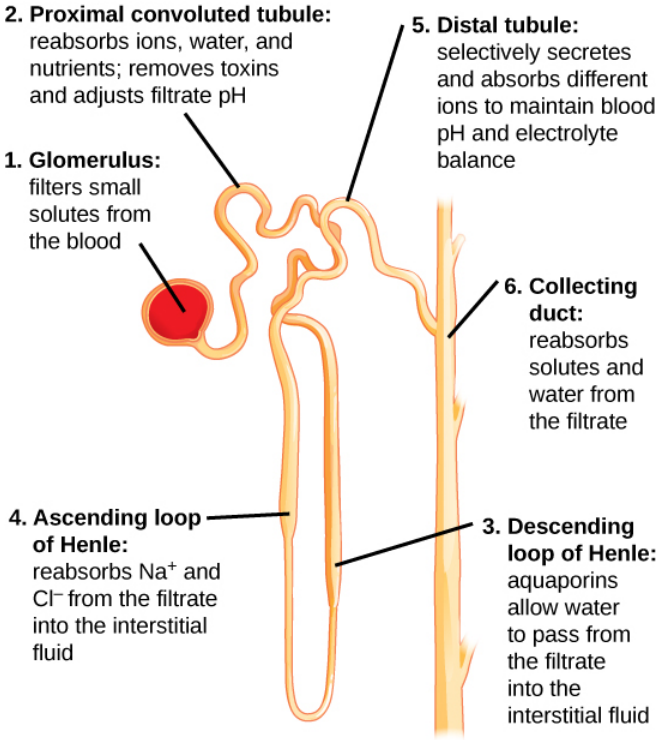


Figure **49.5.4**: Each part of the nephron performs a different function in filtering waste and maintaining homeostatic balance. (1) The glomerulus forces small solutes out of the blood by pressure. (2) The proximal convoluted tubule reabsorbs ions, water, and nutrients from the filtrate into the interstitial fluid, and actively transports toxins and drugs from the interstitial fluid into the filtrate. The proximal convoluted tubule also adjusts blood pH by selectively secreting ammonia (NH_3) into the filtrate, where it reacts with H^+ to form NH_4^+. The more acidic the filtrate, the more ammonia is secreted. (3) The descending loop of Henle is lined with cells containing aquaporins that allow water to pass from the filtrate into the interstitial fluid. (4) In the thin part of the ascending loop of Henle, Na^+ and Cl^- ions diffuse into the interstitial fluid. In the thick part, these same ions are actively transported into the interstitial fluid. Because salt but not water is lost, the filtrate becomes more dilute as it travels up the limb. (5) In the distal convoluted tubule, K^+ and H^+ ions are selectively secreted into the filtrate, while Na^+, Cl^-, and HCO_3^- ions are reabsorbed to maintain pH and electrolyte balance in the blood. (6) The collecting duct reabsorbs solutes and water from the filtrate, forming dilute urine. (credit: modification of work by NIDDK)

Glomerular Filtration

Glomerular filtration filters out most of the solutes due to high blood pressure and specialized membranes in the afferent arteriole. The blood pressure in the glomerulus is maintained independent of factors that affect systemic blood pressure. The “leaky” connections between the endothelial cells of the glomerular capillary network allow solutes to pass through easily. All solutes in the glomerular capillaries, except for macromolecules like proteins, pass through by passive diffusion. There is no energy requirement at this stage of the filtration process. Glomerular filtration rate (GFR) is the volume of glomerular filtrate formed per minute by the kidneys. GFR is regulated by multiple mechanisms and is an important indicator of kidney function.

Link to Learning

To learn more about the vascular system of kidneys, click through this review and the steps of blood flow.

Tubular Reabsorption and Secretion

Tubular reabsorption occurs in the PCT part of the renal tubule. Almost all nutrients are reabsorbed, and this occurs either by passive or active transport. Reabsorption of water and some key electrolytes are regulated and can be influenced by hormones. Sodium (Na^+) is the most abundant ion and most of it is reabsorbed by active transport and then transported to the peritubular capillaries. Because Na^+ is actively transported out of the tubule, water follows it to even out the osmotic pressure. Water is also independently reabsorbed into the peritubular capillaries due to the presence of aquaporins, or water channels, in the PCT. This occurs due to the low blood pressure and high osmotic pressure in the peritubular capillaries. However, every solute has a transport maximum and the excess is not reabsorbed.

In the loop of Henle, the permeability of the membrane changes. The descending limb is permeable to water, not solutes; the opposite is true for the ascending limb. Additionally, the loop of Henle invades the renal medulla, which is naturally high in salt concentration and tends to absorb water from the renal tubule and concentrate the filtrate. The osmotic gradient increases as it moves deeper into the medulla. Because two sides of the loop of Henle perform opposing functions, as illustrated in Figure **49.5.5**, it acts as a countercurrent multiplier. The vasa recta around it acts as the countercurrent exchanger.

Art Connection

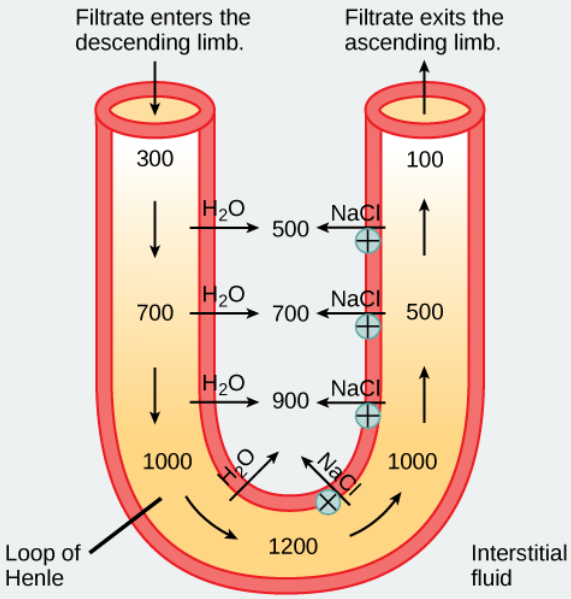


Figure **49.5.5**: The loop of Henle acts as a countercurrent multiplier that uses energy to create concentration gradients. The descending limb is water permeable. Water flows from the filtrate to the interstitial fluid, so osmolality inside the limb increases as it descends into the renal medulla. At the bottom, the osmolality is higher inside the loop than in the interstitial fluid. Thus, as filtrate enters the ascending limb, Na^+ and Cl^- ions exit through ion channels present in the cell membrane. Further up, Na^+ is actively transported out of the filtrate and Cl^- follows. Osmolarity is given in units of milliosmoles per liter (mOsm/L).

Loop diuretics are drugs sometimes used to treat hypertension. These drugs inhibit the reabsorption of Na^+ and Cl^- ions by the ascending limb of the loop of Henle. A side effect is that they increase urination. Why do you think this is the case?

By the time the filtrate reaches the DCT, most of the urine and solutes have been reabsorbed. If the body requires additional water, all of it can be reabsorbed at this point. Further reabsorption is controlled by hormones, which will be discussed in a later section. Excretion of wastes occurs due to lack of reabsorption combined with tubular secretion. Undesirable products like metabolic wastes, urea, uric acid, and certain drugs, are excreted by tubular secretion. Most of the tubular secretion happens in the DCT, but some occurs in the early part of the collecting duct. Kidneys also maintain an acid-base balance by secreting excess H^+ ions.

Although parts of the renal tubules are named proximal and distal, in a cross-section of the kidney, the tubules are placed close together and in contact with each other and the glomerulus. This allows for exchange of chemical messengers between the different cell types. For example, the DCT ascending limb of the loop of Henle has masses of cells called macula densa, which are in contact with cells of the afferent arterioles called juxtaglomerular cells. Together, the macula densa and juxtaglomerular cells form the juxtaglomerular complex (JGC). The JGC is an endocrine structure that secretes the enzyme renin and the hormone erythropoietin. When hormones trigger the macula densa cells in the DCT due to variations in blood volume, blood pressure, or electrolyte balance, these cells can immediately communicate the problem to the capillaries in the afferent and efferent arterioles, which can constrict or relax to change the glomerular filtration rate of the kidneys.

Career Connection: Nephrologist

A nephrologist studies and deals with diseases of the kidneys—both those that cause kidney failure (such as diabetes) and the conditions that are produced by kidney disease (such as hypertension). Blood pressure, blood volume, and changes in electrolyte balance come under the purview of a nephrologist.

Nephrologists usually work with other physicians who refer patients to them or consult with them about specific diagnoses and treatment plans. Patients are usually referred to a nephrologist for symptoms such as blood or protein in the urine, very high blood pressure, kidney stones, or renal failure.

Nephrology is a subspecialty of internal medicine. To become a nephrologist, medical school is followed by additional training to become certified in internal medicine. An additional two or more years is spent specifically studying kidney disorders and their accompanying effects on the body.

Summary

The kidneys are the main osmoregulatory organs in mammalian systems; they function to filter blood and maintain the osmolarity of body fluids at 300 mOsm. They are surrounded by three layers and are made up internally of three distinct regions—the cortex, medulla, and pelvis.

The blood vessels that transport blood into and out of the kidneys arise from and merge with the aorta and inferior vena cava, respectively. The renal arteries branch out from the aorta and enter the kidney where they further divide into segmental, interlobar, arcuate, and cortical radiate arteries.

The nephron is the functional unit of the kidney, which actively filters blood and generates urine. The nephron is made up of the renal corpuscle and renal tubule. Cortical nephrons are found in the renal cortex, while juxtamedullary nephrons are found in the renal cortex close to the renal medulla. The nephron filters and exchanges water and solutes with two sets of blood vessels and the tissue fluid in the kidneys.

There are three steps in the formation of urine: glomerular filtration, which occurs in the glomerulus; tubular reabsorption, which occurs in the renal tubules; and tubular secretion, which also occurs in the renal tubules.

Art Connections

Figure 49.5.2: Which of the following statements about the kidney is false?

A. The renal pelvis drains into the ureter.
B. The renal pyramids are in the medulla.
C. The cortex covers the capsule.
D. Nephrons are in the renal cortex.

Answer

C

Figure 49.5.3: Which of the following statements about the nephron is false?

A. The collecting duct empties into the distal convoluted tubule.
B. The Bowman's capsule surrounds the glomerulus.
C. The loop of Henle is between the proximal and distal convoluted tubules.
D. The loop of Henle empties into the distal convoluted tubule.

Answer

A

Figure 49.5.5: Loop diuretics are drugs sometimes used to treat hypertension. These drugs inhibit the reabsorption of Na^+ and Cl^- ions by the ascending limb of the loop of Henle. A side effect is that they increase urination. Why do you think this is the case?

Answer

Loop diuretics decrease the excretion of salt into the renal medulla, thereby reducing its osmolality. As a result, less water is excreted into the medulla by the descending limb, and more water is excreted as urine.

Glossary

afferent arteriole
arteriole that branches from the cortical radiate artery and enters the glomerulus

arcuate artery
artery that branches from the interlobar artery and arches over the base of the renal pyramids

ascending limb
part of the loop of Henle that ascends from the renal medulla to the renal cortex

Bowman's capsule
structure that encloses the glomerulus

calyx
structure that connects the renal pelvis to the renal medulla

cortex (animal)
outer layer of an organ like the kidney or adrenal gland

cortical nephron
nephron that lies in the renal cortex

cortical radiate artery
artery that radiates from the arcuate arteries into the renal cortex

countercurrent exchanger
peritubular capillary network that allows exchange of solutes and water from the renal tubules

countercurrent multiplier
osmotic gradient in the renal medulla that is responsible for concentration of urine

descending limb
part of the loop of Henle that descends from the renal cortex into the renal medulla

distal convoluted tubule (DCT)
part of the renal tubule that is the most distant from the glomerulus

efferent arteriole
arteriole that exits from the glomerulus

glomerular filtration
filtration of blood in the glomerular capillary network into the glomerulus

glomerular filtration rate (GFR)
amount of filtrate formed by the glomerulus per minute

glomerulus (renal)
part of the renal corpuscle that contains the capillary network

hilum
region in the renal pelvis where blood vessels, nerves, and ureters bunch before entering or exiting the kidney

inferior vena cava
one of the main veins in the human body

interlobar artery
artery that branches from the segmental artery and travels in between the renal lobes

juxtaglomerular cell
cell in the afferent and efferent arterioles that responds to stimuli from the macula densa

juxtamedullary nephron
nephron that lies in the cortex but close to the renal medulla

kidney
organ that performs excretory and osmoregulatory functions

lobes of the kidney
renal pyramid along with the adjoining cortical region

loop of Henle
part of the renal tubule that loops into the renal medulla

macula densa
group of cells that senses changes in sodium ion concentration; present in parts of the renal tubule and collecting ducts

medulla
middle layer of an organ like the kidney or adrenal gland

nephron
functional unit of the kidney

perirenal fat capsule
fat layer that suspends the kidneys

peritubular capillary network
capillary network that surrounds the renal tubule after the efferent artery exits the glomerulus

proximal convoluted tubule (PCT)
part of the renal tubule that lies close to the glomerulus

renal artery
branch of the artery that enters the kidney

renal capsule
layer that encapsulates the kidneys

renal column
area of the kidney through which the interlobar arteries travel in the process of supplying blood to the renal lobes

renal corpuscle
glomerulus and the Bowman's capsule together

renal fascia
connective tissue that supports the kidneys

renal pelvis
region in the kidney where the calyces join the ureters

renal pyramid
conical structure in the renal medulla

renal tubule
tubule of the nephron that arises from the glomerulus

renal vein
branch of a vein that exits the kidney and joins the inferior vena cava

segmental artery
artery that branches from the renal artery

transport maximum
maximum amount of solute that can be transported out of the renal tubules during reabsorption

tubular reabsorption
reclamation of water and solutes that got filtered out in the glomerulus

tubular secretion
process of secretion of wastes that do not get reabsorbed

ureter
urine-bearing tube coming out of the kidney; carries urine to the bladder

urinary bladder
structure that the ureters empty the urine into; stores urine

urine
filtrate produced by kidneys that gets excreted out of the body

vasa recta
peritubular network that surrounds the loop of Henle of the juxtamedullary nephrons

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49.6: Hormonal Control of Osmoregulatory Functions

Skills to Develop

- Explain how hormonal cues help the kidneys synchronize the osmotic needs of the body
- Describe how hormones like epinephrine, norepinephrine, renin-angiotensin, aldosterone, anti-diuretic hormone, and atrial natriuretic peptide help regulate waste elimination, maintain correct osmolarity, and perform other osmoregulatory functions

While the kidneys operate to maintain osmotic balance and blood pressure in the body, they also act in concert with hormones. Hormones are small molecules that act as messengers within the body. Hormones are typically secreted from one cell and travel in the bloodstream to affect a target cell in another portion of the body. Different regions of the nephron bear specialized cells that have receptors to respond to chemical messengers and hormones. Table **49.6.1** summarizes the hormones that control the osmoregulatory functions.

Table 49.6.1: Hormones That Affect Osmoregulation

Hormone	Where produced	Function
Epinephrine and Norepinephrine	Adrenal medulla	Can decrease kidney function temporarily by vasoconstriction
Renin	Kidney nephrons	Increases blood pressure by acting on angiotensinogen
Angiotensin	Liver	Angiotensin II affects multiple processes and increases blood pressure
Aldosterone	Adrenal cortex	Prevents loss of sodium and water
Anti-diuretic hormone (vasopressin)	Hypothalamus (stored in the posterior pituitary)	Prevents water loss
Atrial natriuretic peptide	Heart atrium	Decreases blood pressure by acting as a vasodilator and increasing glomerular filtration rate; decreases sodium reabsorption in kidneys

Epinephrine and Norepinephrine

Epinephrine and norepinephrine are released by the adrenal medulla and nervous system respectively. They are the flight/fight hormones that are released when the body is under extreme stress. During stress, much of the body's energy is used to combat imminent danger. Kidney function is halted temporarily by epinephrine and norepinephrine. These hormones function by acting directly on the smooth muscles of blood vessels to constrict them. Once the afferent arterioles are constricted, blood flow into the nephrons stops. These hormones go one step further and trigger the renin-angiotensin-aldosterone system.

Renin-Angiotensin-Aldosterone

The renin-angiotensin-aldosterone system, illustrated in Figure **49.6.1** proceeds through several steps to produce angiotensin II, which acts to stabilize blood pressure and volume. Renin (secreted by a part of the juxtaglomerular complex) is produced by the granular cells of the afferent and efferent arterioles. Thus, the kidneys control blood pressure and volume directly. Renin acts on angiotensinogen, which is made in the liver and converts it to angiotensin I. Angiotensin converting enzyme (ACE) converts angiotensin I to angiotensin II. Angiotensin II raises blood pressure by constricting blood vessels. It also triggers the release of the mineralocorticoid aldosterone from the adrenal cortex, which in turn stimulates the renal tubules to reabsorb more sodium. Angiotensin II also triggers the release of anti-diuretic hormone (ADH) from the hypothalamus, leading to water retention in the kidneys. It acts directly on the nephrons and decreases glomerular filtration rate. Medically, blood pressure can be controlled by drugs that inhibit ACE (called ACE inhibitors).

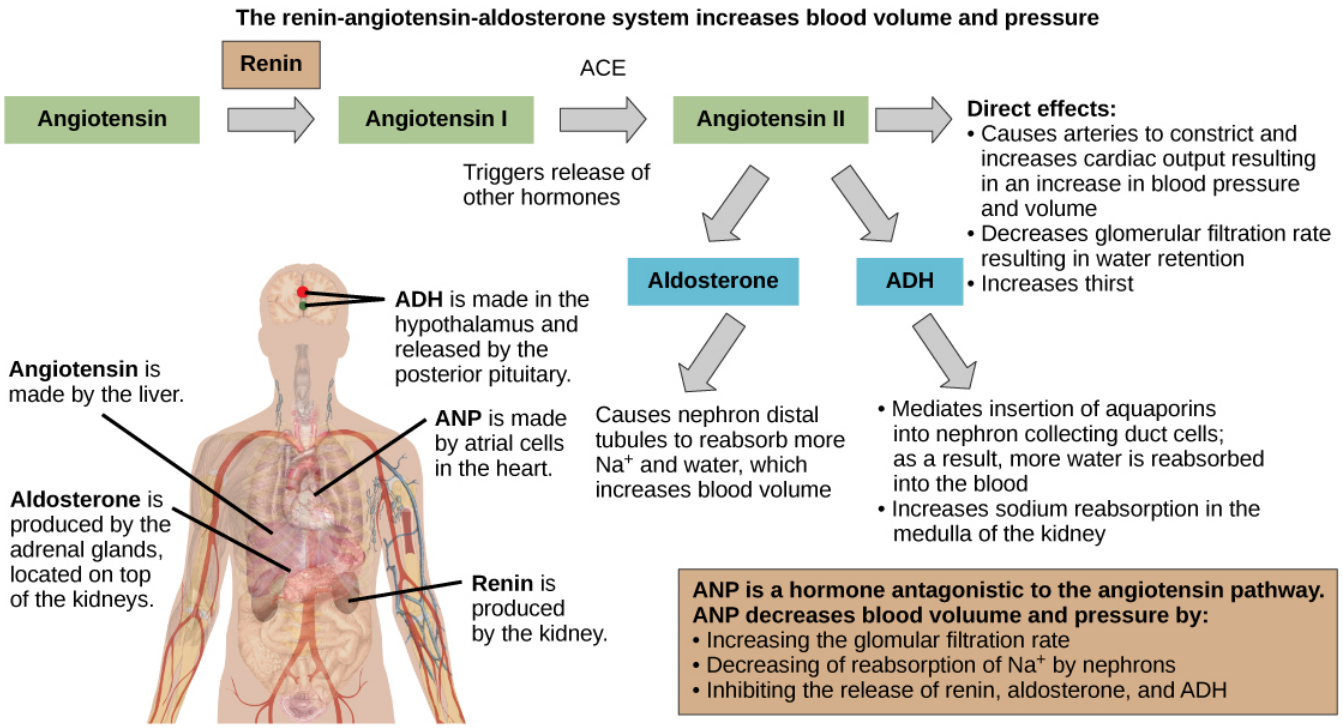


Figure **49.6.1**: The renin-angiotensin-aldosterone system increases blood pressure and volume. The hormone ANP has antagonistic effects. (credit: modification of work by Mikael Häggström)

Mineralocorticoids

Mineralocorticoids are hormones synthesized by the adrenal cortex that affect osmotic balance. Aldosterone is a mineralocorticoid that regulates sodium levels in the blood. Almost all of the sodium in the blood is reclaimed by the renal tubules under the influence of aldosterone. Because sodium is always reabsorbed by active transport and water follows sodium to maintain osmotic balance, aldosterone manages not only sodium levels but also the water levels in body fluids. In contrast, the aldosterone also stimulates potassium secretion concurrently with sodium reabsorption. In contrast, absence of aldosterone means that no sodium gets reabsorbed in the renal tubules and all of it gets excreted in the urine. In addition, the daily dietary potassium load is not secreted and the retention of K^+ can cause a dangerous increase in plasma K^+ concentration. Patients who have Addison's disease have a failing adrenal cortex and cannot produce aldosterone. They lose sodium in their urine constantly, and if the supply is not replenished, the consequences can be fatal.

Antidiurectic Hormone

As previously discussed, antidiuretic hormone or ADH (also called vasopressin), as the name suggests, helps the body conserve water when body fluid volume, especially that of blood, is low. It is formed by the hypothalamus and is stored and released from the posterior pituitary. It acts by inserting aquaporins in the collecting ducts and promotes reabsorption of water. ADH also acts as a vasoconstrictor and increases blood pressure during hemorrhaging.

Atrial Natriuretic Peptide Hormone

The atrial natriuretic peptide (ANP) lowers blood pressure by acting as a vasodilator. It is released by cells in the atrium of the heart in response to high blood pressure and in patients with sleep apnea. ANP affects salt release, and because water passively follows salt to maintain osmotic balance, it also has a diuretic effect. ANP also prevents sodium reabsorption by the renal tubules, decreasing water reabsorption (thus acting as a diuretic) and lowering blood pressure. Its actions suppress the actions of aldosterone, ADH, and renin.

Summary

Hormonal cues help the kidneys synchronize the osmotic needs of the body. Hormones like epinephrine, norepinephrine, renin-angiotensin, aldosterone, anti-diuretic hormone, and atrial natriuretic peptide help regulate the needs of the body as well as the

communication between the different organ systems.

Glossary

angiotensin converting enzyme (ACE)
enzyme that converts angiotensin I to angiotensin II

angiotensin I
product in the renin-angiotensin-aldosterone pathway

angiotensin II
molecule that affects different organs to increase blood pressure

anti-diuretic hormone (ADH)
hormone that prevents the loss of water

renin-angiotensin-aldosterone
biochemical pathway that activates angiotensin II, which increases blood pressure

vasodilator
compound that increases the diameter of blood vessels

vasopressin
another name for anti-diuretic hormone

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CHAPTER OVERVIEW

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50.1: Innate Immunity

50.2: Adaptive Immunity

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50.1: Innate Immunity

Skills to Develop

- Describe physical and chemical immune barriers
- Explain immediate and induced innate immune responses
- Discuss natural killer cells
- Describe major histocompatibility class I molecules
- Summarize how the proteins in a complement system function to destroy extracellular pathogens

The immune system comprises both innate and adaptive immune responses. Innate immunity occurs naturally because of genetic factors or physiology; it is not induced by infection or vaccination but works to reduce the workload for the adaptive immune response. Both the innate and adaptive levels of the immune response involve secreted proteins, receptor-mediated signaling, and intricate cell-to-cell communication. The innate immune system developed early in animal evolution, roughly a billion years ago, as an essential response to infection. Innate immunity has a limited number of specific targets: any pathogenic threat triggers a consistent sequence of events that can identify the type of pathogen and either clear the infection independently or mobilize a highly specialized adaptive immune response. For example, tears and mucus secretions contain microbicidal factors.

Physical and Chemical Barriers

Before any immune factors are triggered, the skin functions as a continuous, impassable barrier to potentially infectious pathogens. Pathogens are killed or inactivated on the skin by desiccation (drying out) and by the skin's acidity. In addition, beneficial microorganisms that coexist on the skin compete with invading pathogens, preventing infection. Regions of the body that are not protected by skin (such as the eyes and mucus membranes) have alternative methods of defense, such as tears and mucus secretions that trap and rinse away pathogens, and cilia in the nasal passages and respiratory tract that push the mucus with the pathogens out of the body. Throughout the body are other defenses, such as the low pH of the stomach (which inhibits the growth of pathogens), blood proteins that bind and disrupt bacterial cell membranes, and the process of urination (which flushes pathogens from the urinary tract).

Despite these barriers, pathogens may enter the body through skin abrasions or punctures, or by collecting on mucosal surfaces in large numbers that overcome the mucus or cilia. Some pathogens have evolved specific mechanisms that allow them to overcome physical and chemical barriers. When pathogens do enter the body, the innate immune system responds with inflammation, pathogen engulfment, and secretion of immune factors and proteins.

Pathogen Recognition

An infection may be intracellular or extracellular, depending on the pathogen. All viruses infect cells and replicate within those cells (intracellularly), whereas bacteria and other parasites may replicate intracellularly or extracellularly, depending on the species. The innate immune system must respond accordingly: by identifying the extracellular pathogen and/or by identifying host cells that have already been infected. When a pathogen enters the body, cells in the blood and lymph detect the specific pathogen-associated molecular patterns (PAMPs) on the pathogen's surface. PAMPs are carbohydrate, polypeptide, and nucleic acid "signatures" that are expressed by viruses, bacteria, and parasites but which differ from molecules on host cells. The immune system has specific cells, described in Figure 50.1.1 and shown in Figure 50.1.2, with receptors that recognize these PAMPs. A macrophage is a large phagocytic cell that engulfs foreign particles and pathogens. Macrophages recognize PAMPs via complementary pattern recognition receptors (PRRs). PRRs are molecules on macrophages and dendritic cells which are in contact with the external environment. A monocyte is a type of white blood cell that circulates in the blood and lymph and differentiates into macrophages after it moves into infected tissue. Dendritic cells bind molecular signatures of pathogens and promote pathogen engulfment and destruction. Toll-like receptors (TLRs) are a type of PRR that recognizes molecules that are shared by pathogens but distinguishable from host molecules). TLRs are present in invertebrates as well as vertebrates, and appear to be one of the most ancient components of the immune system. TLRs have also been identified in the mammalian nervous system.

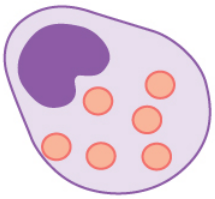
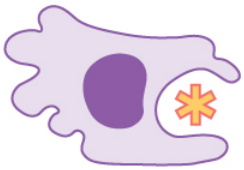
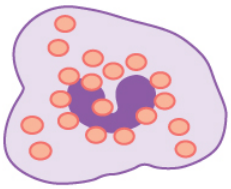
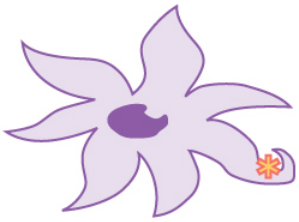
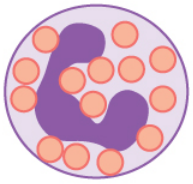
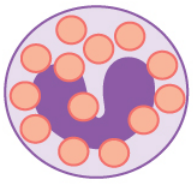
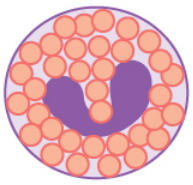
Cell type	Characteristics	Location	Image
Mast cell	Dilates blood vessels and induces inflammation through release of histamines and heparin. Recruits macrophages and neutrophils. Involved in wound healing and defense against pathogens but can also be responsible for allergic reactions.	Connective tissues, mucous membranes	
Macrophage	Phagocytic cell that consumes foreign pathogens and cancer cells. Stimulates response of other immune cells.	Migrates from blood vessels into tissues.	
Natural killer cell	Kills tumor cells and virus-infected cells.	Circulates in blood and migrates into tissues.	
Dendritic cell	Presents antigens on its surface, thereby triggering adaptive immunity.	Present in epithelial tissue, including skin, lung and tissues of the digestive tract. Migrates to lymph nodes upon activation.	
Monocyte	Differentiates into macrophages and dendritic cells in response to inflammation.	Stored in spleen, moves through blood vessels to infected tissues.	
Neutrophil	First responders at the site of infection or trauma, this abundant phagocytic cell represents 50-60 percent of all leukocytes. Releases toxins that kill or inhibit bacteria and fungi and recruits other immune cells to the site of infection.	Migrates from blood vessels into tissues.	
Basophil	Responsible for defense against parasites. Releases histamines that cause inflammation and may be responsible for allergic reactions.	Circulates in blood and migrates to tissues.	
Eosinophil	Releases toxins that kill bacteria and parasites but also causes tissue damage.	Circulates in blood and migrates to tissues.	

Figure **50.1.1**: The characteristics and location of cells involved in the innate immune system are described. (credit: modification of work by NIH)

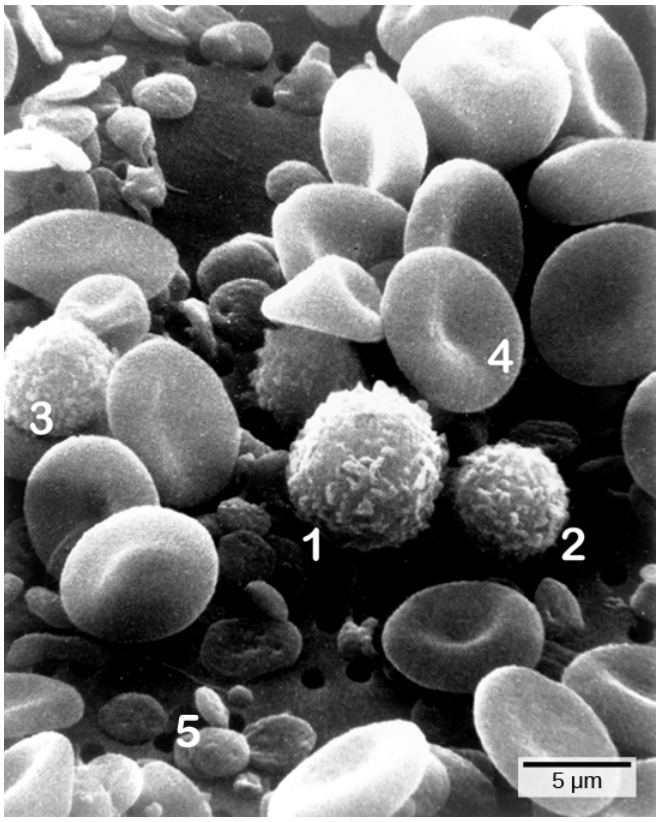


Figure 50.1.2: Cells of the blood include (1) monocytes, (2) lymphocytes, (3) neutrophils, (4) red blood cells, and (5) platelets. Note the very similar morphologies of the leukocytes (1, 2, 3). (credit: modification of work by Bruce Wetzel, Harry Schaefer, NCI; scale-bar data from Matt Russell)

Cytokine Release Affect

The binding of PRRs with PAMPs triggers the release of cytokines, which signal that a pathogen is present and needs to be destroyed along with any infected cells. A cytokine is a chemical messenger that regulates cell differentiation (form and function), proliferation (production), and gene expression to affect immune responses. At least 40 types of cytokines exist in humans that differ in terms of the cell type that produces them, the cell type that responds to them, and the changes they produce. One type cytokine, interferon, is illustrated in Figure 50.1.3.

One subclass of cytokines is the interleukin (IL), so named because they mediate interactions between leukocytes (white blood cells). Interleukins are involved in bridging the innate and adaptive immune responses. In addition to being released from cells after PAMP recognition, cytokines are released by the infected cells which bind to nearby uninfected cells and induce those cells to release cytokines, which results in a cytokine burst.

A second class of early-acting cytokines is interferons, which are released by infected cells as a warning to nearby uninfected cells. One of the functions of an interferon is to inhibit viral replication. They also have other important functions, such as tumor surveillance. Interferons work by signaling neighboring uninfected cells to destroy RNA and reduce protein synthesis, signaling neighboring infected cells to undergo apoptosis (programmed cell death), and activating immune cells.

In response to interferons, uninfected cells alter their gene expression, which increases the cells' resistance to infection. One effect of interferon-induced gene expression is a sharply reduced cellular protein synthesis. Virally infected cells produce more viruses by synthesizing large quantities of viral proteins. Thus, by reducing protein synthesis, a cell becomes resistant to viral infection.

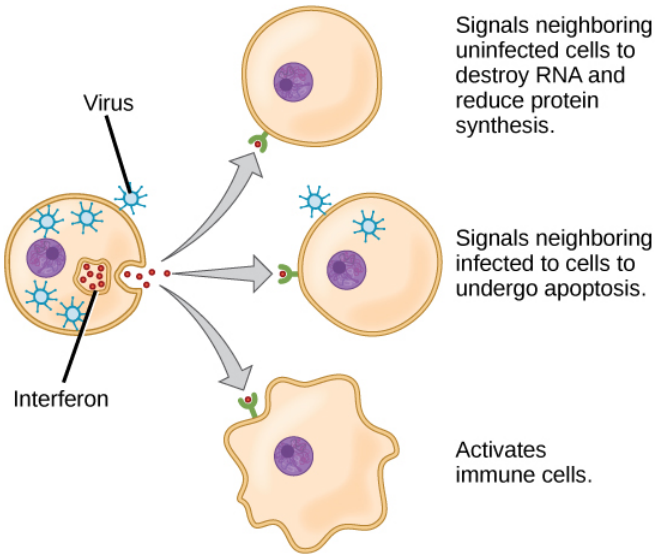


Figure **50.1.3**: Interferons are cytokines that are released by a cell infected with a virus. Response of neighboring cells to interferon helps stem the infection.

Phagocytosis and Inflammation

The first cytokines to be produced are pro-inflammatory; that is, they encourage inflammation, the localized redness, swelling, heat, and pain that result from the movement of leukocytes and fluid through increasingly permeable capillaries to a site of infection. The population of leukocytes that arrives at an infection site depends on the nature of the infecting pathogen. Both macrophages and dendritic cells engulf pathogens and cellular debris through phagocytosis. A neutrophil is also a phagocytic leukocyte that engulfs and digests pathogens. Neutrophils, shown in Figure **50.1.1**, are the most abundant leukocytes of the immune system. Neutrophils have a nucleus with two to five lobes, and they contain organelles, called lysosomes, that digest engulfed pathogens. An eosinophil is a leukocyte that works with other eosinophils to surround a parasite; it is involved in the allergic response and in protection against helminthes (parasitic worms).

Neutrophils and eosinophils are particularly important leukocytes that engulf large pathogens, such as bacteria and fungi. A mast cell is a leukocyte that produces inflammatory molecules, such as histamine, in response to large pathogens. A basophil is a leukocyte that, like a neutrophil, releases chemicals to stimulate the inflammatory response as illustrated in Figure **50.1.4**. Basophils are also involved in allergy and hypersensitivity responses and induce specific types of inflammatory responses. Eosinophils and basophils produce additional inflammatory mediators to recruit more leukocytes. A hypersensitive immune response to harmless antigens, such as in pollen, often involves the release of histamine by basophils and mast cells.

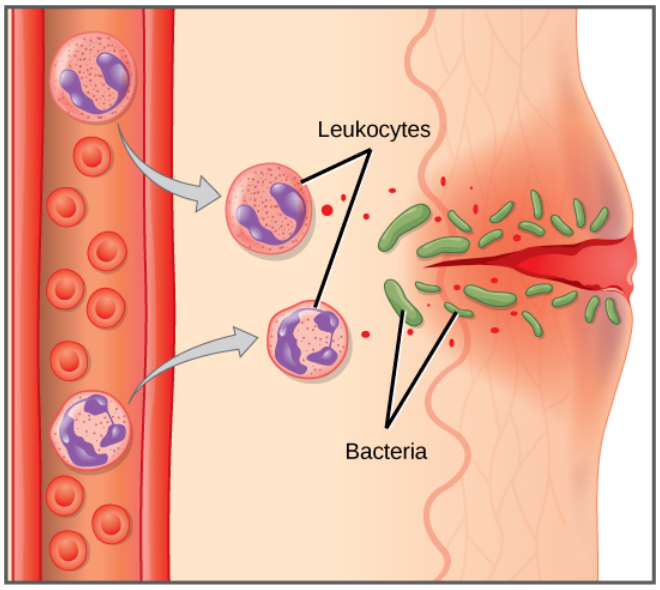


Figure 50.1.4: In response to a cut, mast cells secrete histamines that cause nearby capillaries to dilate. Neutrophils and monocytes leave the capillaries. Monocytes mature into macrophages. Neutrophils, dendritic cells and macrophages release chemicals to stimulate the inflammatory response. Neutrophils and macrophages also consume invading bacteria by phagocytosis.

Cytokines also send feedback to cells of the nervous system to bring about the overall symptoms of feeling sick, which include lethargy, muscle pain, and nausea. These effects may have evolved because the symptoms encourage the individual to rest and prevent them from spreading the infection to others. Cytokines also increase the core body temperature, causing a fever, which causes the liver to withhold iron from the blood. Without iron, certain pathogens, such as some bacteria, are unable to replicate; this is called nutritional immunity.

Natural Killer Cells

Lymphocytes are leukocytes that are histologically identifiable by their large, darkly staining nuclei; they are small cells with very little cytoplasm, as shown in Figure 50.1.5. Infected cells are identified and destroyed by natural killer (NK) cells, lymphocytes that can kill cells infected with viruses or tumor cells (abnormal cells that uncontrollably divide and invade other tissue). T cells and B cells of the adaptive immune system also are classified as lymphocytes. T cells are lymphocytes that mature in the thymus gland, and B cells are lymphocytes that mature in the bone marrow. NK cells identify intracellular infections, especially from viruses, by the altered expression of major histocompatibility class (MHC) I molecules on the surface of infected cells. MHC I molecules are proteins on the surfaces of all nucleated cells, thus they are scarce on red blood cells and platelets which are non-nucleated. The function of MHC I molecules is to display fragments of proteins from the infectious agents within the cell to T-cells; healthy cells will be ignored, while “non-self” or foreign proteins will be attacked by the immune system. MHC II molecules are found mainly on cells containing antigens (“non-self proteins”) and on lymphocytes. MHC II molecules interact with helper T-cells to trigger the appropriate immune response, which may include the inflammatory response.

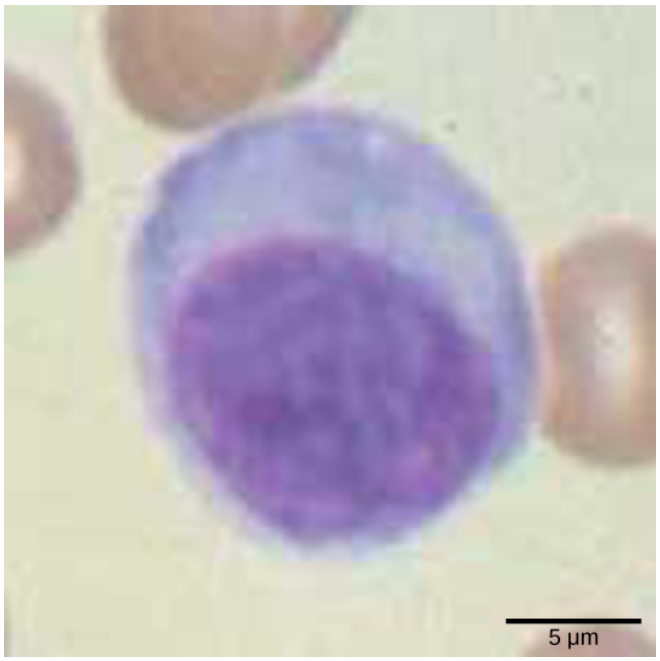


Figure **50.1.5**: Lymphocytes, such as NK cells, are characterized by their large nuclei that actively absorb Wright stain and therefore appear dark colored under a microscope.

An infected cell (or a tumor cell) is usually incapable of synthesizing and displaying MHC I molecules appropriately. The metabolic resources of cells infected by some viruses produce proteins that interfere with MHC I processing and/or trafficking to the cell surface. The reduced MHC I on host cells varies from virus to virus and results from active inhibitors being produced by the viruses. This process can deplete host MHC I molecules on the cell surface, which NK cells detect as “unhealthy” or “abnormal” while searching for cellular MHC I molecules. Similarly, the dramatically altered gene expression of tumor cells leads to expression of extremely deformed or absent MHC I molecules that also signal “unhealthy” or “abnormal.”

NK cells are always active; an interaction with normal, intact MHC I molecules on a healthy cell disables the killing sequence, and the NK cell moves on. After the NK cell detects an infected or tumor cell, its cytoplasm secretes granules comprised of perforin, a destructive protein that creates a pore in the target cell. Granzymes are released along with the perforin in the immunological synapse. A granzyme is a protease that digests cellular proteins and induces the target cell to undergo programmed cell death, or apoptosis. Phagocytic cells then digest the cell debris left behind. NK cells are constantly patrolling the body and are an effective mechanism for controlling potential infections and preventing cancer progression.

Complement

An array of approximately 20 types of soluble proteins, called a complement system, functions to destroy extracellular pathogens. Cells of the liver and macrophages synthesize complement proteins continuously; these proteins are abundant in the blood serum and are capable of responding immediately to infecting microorganisms. The complement system is so named because it is complementary to the antibody response of the adaptive immune system. Complement proteins bind to the surfaces of microorganisms and are particularly attracted to pathogens that are already bound by antibodies. Binding of complement proteins occurs in a specific and highly regulated sequence, with each successive protein being activated by cleavage and/or structural changes induced upon binding of the preceding protein(s). After the first few complement proteins bind, a cascade of sequential binding events follows in which the pathogen rapidly becomes coated in complement proteins.

Complement proteins perform several functions. The proteins serve as a marker to indicate the presence of a pathogen to phagocytic cells, such as macrophages and B cells, and enhance engulfment; this process is called opsonization. Certain complement proteins can combine to form attack complexes that open pores in microbial cell membranes. These structures destroy pathogens by causing their contents to leak, as illustrated in Figure **50.1.6**.

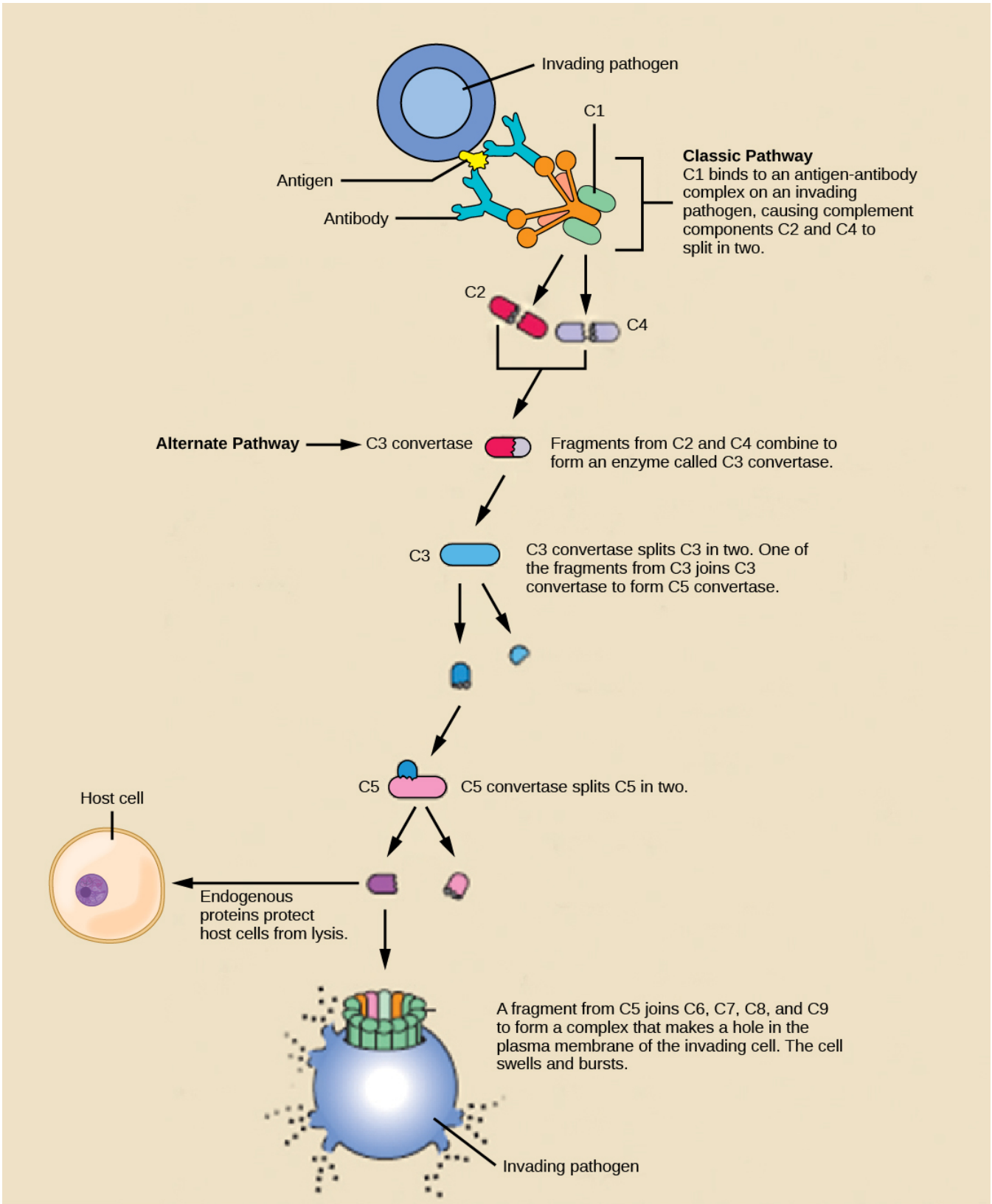


Figure **50.1.6**: The classic pathway for the complement cascade involves the attachment of several initial complement proteins to an antibody-bound pathogen followed by rapid activation and binding of many more complement proteins and the creation of destructive pores in the microbial cell envelope and cell wall. The alternate pathway does not involve antibody activation. Rather, C3 convertase spontaneously breaks down C3. Endogenous regulatory proteins prevent the complement complex from binding to host cells. Pathogens lacking these regulatory proteins are lysed. (credit: modification of work by NIH)

Summary

The innate immune system serves as a first responder to pathogenic threats that bypass natural physical and chemical barriers of the body. Using a combination of cellular and molecular attacks, the innate immune system identifies the nature of a pathogen and responds with inflammation, phagocytosis, cytokine release, destruction by NK cells, and/or a complement system. When innate mechanisms are insufficient to clear an infection, the adaptive immune response is informed and mobilized.

Glossary

basophil
leukocyte that releases chemicals usually involved in the inflammatory response

B cell
lymphocyte that matures in the bone marrow and differentiates into antibody-secreting plasma cells

complement system
array of approximately 20 soluble proteins of the innate immune system that enhance phagocytosis, bore holes in pathogens, and recruit lymphocytes; enhances the adaptive response when antibodies are produced

cytokine
chemical messenger that regulates cell differentiation, proliferation, gene expression, and cell trafficking to effect immune responses

eosinophil
leukocyte that responds to parasites and is involved in the allergic response

granzyme
protease that enters target cells through perforin and induces apoptosis in the target cells; used by NK cells and killer T cells

inflammation
localized redness, swelling, heat, and pain that results from the movement of leukocytes and fluid through opened capillaries to a site of infection

innate immunity
immunity that occurs naturally because of genetic factors or physiology, and is not induced by infection or vaccination

interferon
cytokine that inhibits viral replication and modulates the immune response

lymphocyte
leukocyte that is histologically identifiable by its large nuclei; it is a small cell with very little cytoplasm

macrophage
large phagocytic cell that engulfs foreign particles and pathogens

major histocompatibility class (MHC) I/II molecule
protein found on the surface of all nucleated cells (I) or specifically on antigen-presenting cells (II) that signals to immune cells whether the cell is healthy/normal or is infected/cancerous; it provides the appropriate template into which antigens can be loaded for recognition by lymphocytes

mast cell
leukocyte that produces inflammatory molecules, such as histamine, in response to large pathogens and allergens

monocyte

type of white blood cell that circulates in the blood and lymph and differentiates into macrophages after it moves into infected tissue

natural killer (NK) cell
lymphocyte that can kill cells infected with viruses or tumor cells

neutrophil
phagocytic leukocyte that engulfs and digests pathogens

opsonization
process that enhances phagocytosis using proteins to indicate the presence of a pathogen to phagocytic cells

pathogen-associated molecular pattern (PAMP)
carbohydrate, polypeptide, and nucleic acid “signature” that is expressed by viruses, bacteria, and parasites but differs from molecules on host cells

pattern recognition receptor (PRR)
molecule on macrophages and dendritic cells that binds molecular signatures of pathogens and promotes pathogen engulfment and destruction

perforin
destructive protein that creates a pore in the target cell; used by NK cells and killer T cells

T cell
lymphocyte that matures in the thymus gland; one of the main cells involved in the adaptive immune system

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50.2: Adaptive Immunity

Skills to Develop

- Explain adaptive immunity
- Compare and contrast adaptive and innate immunity
- Describe cell-mediated immune response and humoral immune response
- Describe immune tolerance

The adaptive, or acquired, immune response takes days or even weeks to become established—much longer than the innate response; however, adaptive immunity is more specific to pathogens and has memory. Adaptive immunity is an immunity that occurs after exposure to an antigen either from a pathogen or a vaccination. This part of the immune system is activated when the innate immune response is insufficient to control an infection. In fact, without information from the innate immune system, the adaptive response could not be mobilized. There are two types of adaptive responses: the cell-mediated immune response, which is carried out by T cells, and the humoral immune response, which is controlled by activated B cells and antibodies. Activated T cells and B cells that are specific to molecular structures on the pathogen proliferate and attack the invading pathogen. Their attack can kill pathogens directly or secrete antibodies that enhance the phagocytosis of pathogens and disrupt the infection. Adaptive immunity also involves a memory to provide the host with long-term protection from reinfection with the same type of pathogen; on re-exposure, this memory will facilitate an efficient and quick response.

Antigen-presenting Cells

Unlike NK cells of the innate immune system, B cells (B lymphocytes) are a type of white blood cell that gives rise to antibodies, whereas T cells (T lymphocytes) are a type of white blood cell that plays an important role in the immune response. T cells are a key component in the cell-mediated response—the specific immune response that utilizes T cells to neutralize cells that have been infected with viruses and certain bacteria. There are three types of T cells: cytotoxic, helper, and suppressor T cells. Cytotoxic T cells destroy virus-infected cells in the cell-mediated immune response, and helper T cells play a part in activating both the antibody and the cell-mediated immune responses. Suppressor T cells deactivate T cells and B cells when needed, and thus prevent the immune response from becoming too intense.

An antigen is a foreign or “non-self” macromolecule that reacts with cells of the immune system. Not all antigens will provoke a response. For instance, individuals produce innumerable “self” antigens and are constantly exposed to harmless foreign antigens, such as food proteins, pollen, or dust components. The suppression of immune responses to harmless macromolecules is highly regulated and typically prevents processes that could be damaging to the host, known as tolerance.

The innate immune system contains cells that detect potentially harmful antigens, and then inform the adaptive immune response about the presence of these antigens. An antigen-presenting cell (APC) is an immune cell that detects, engulfs, and informs the adaptive immune response about an infection. When a pathogen is detected, these APCs will phagocytose the pathogen and digest it to form many different fragments of the antigen. Antigen fragments will then be transported to the surface of the APC, where they will serve as an indicator to other immune cells. Dendritic cells are immune cells that process antigen material; they are present in the skin (Langerhans cells) and the lining of the nose, lungs, stomach, and intestines. Sometimes a dendritic cell presents on the surface of other cells to induce an immune response, thus functioning as an antigen-presenting cell. Macrophages also function as APCs. Before activation and differentiation, B cells can also function as APCs.

After phagocytosis by APCs, the phagocytic vesicle fuses with an intracellular lysosome forming phagolysosome. Within the phagolysosome, the components are broken down into fragments; the fragments are then loaded onto MHC class I or MHC class II molecules and are transported to the cell surface for antigen presentation, as illustrated in Figure 50.2.1. Note that T lymphocytes cannot properly respond to the antigen unless it is processed and embedded in an MHC II molecule. APCs express MHC on their surfaces, and when combined with a foreign antigen, these complexes signal a “non-self” invader. Once the fragment of antigen is embedded in the MHC II molecule, the immune cell can respond. Helper T- cells are one of the main lymphocytes that respond to antigen-presenting cells. Recall that all other nucleated cells of the body expressed MHC I molecules, which signal “healthy” or “normal.”

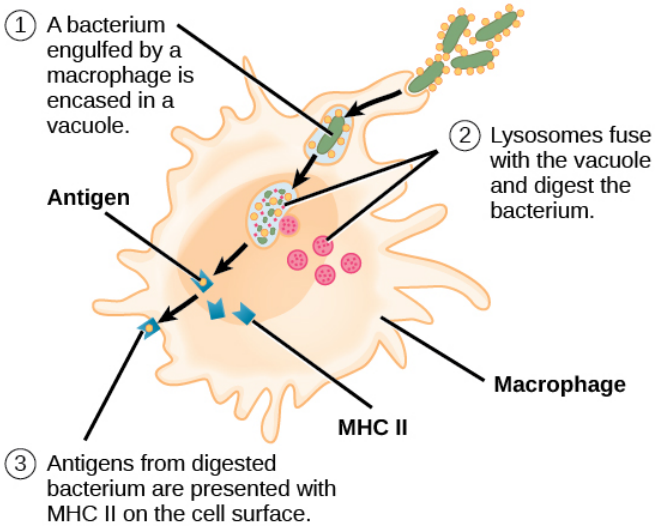


Figure 50.2.1: An APC, such as a macrophage, engulfs and digests a foreign bacterium. An antigen from the bacterium is presented on the cell surface in conjunction with an MHC II molecule Lymphocytes of the adaptive immune response interact with antigen-embedded MHC II molecules to mature into functional immune cells.

T and B Lymphocytes

Lymphocytes in human circulating blood are approximately 80 to 90 percent T cells, shown in Figure 50.2.2, and 10 to 20 percent B cells. Recall that the T cells are involved in the cell-mediated immune response, whereas B cells are part of the humoral immune response.

T cells encompass a heterogeneous population of cells with extremely diverse functions. Some T cells respond to APCs of the innate immune system, and indirectly induce immune responses by releasing cytokines. Other T cells stimulate B cells to prepare their own response. Another population of T cells detects APC signals and directly kills the infected cells. Other T cells are involved in suppressing inappropriate immune reactions to harmless or "self" antigens.

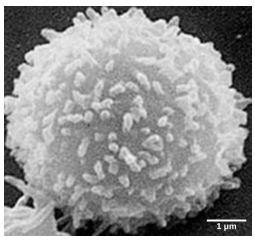


Figure 50.2.2: This scanning electron micrograph shows a T lymphocyte, which is responsible for the cell-mediated immune response. T cells are able to recognize antigens. (credit: modification of work by NCI; scale-bar data from Matt Russell)

T and B cells exhibit a common theme of recognition/binding of specific antigens via a complementary receptor, followed by activation and self-amplification/maturation to specifically bind to the particular antigen of the infecting pathogen. T and B lymphocytes are also similar in that each cell only expresses one type of antigen receptor. Any individual may possess a population of T and B cells that together express a near limitless variety of antigen receptors that are capable of recognizing virtually any infecting pathogen. T and B cells are activated when they recognize small components of antigens, called epitopes, presented by APCs, illustrated in Figure 50.2.3. Note that recognition occurs at a specific epitope rather than on the entire antigen; for this reason, epitopes are known as "antigenic determinants." In the absence of information from APCs, T and B cells remain inactive, or naïve, and are unable to prepare an immune response. The requirement for information from the APCs of innate immunity to trigger B cell or T cell activation illustrates the essential nature of the innate immune response to the functioning of the entire immune system.

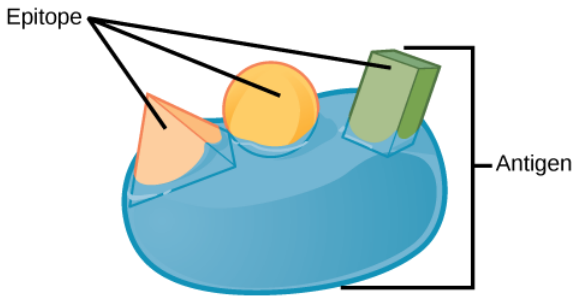


Figure 50.2.3: An antigen is a macromolecule that reacts with components of the immune system. A given antigen may contain several motifs that are recognized by immune cells. Each motif is an epitope. In this figure, the entire structure is an antigen, and the orange, salmon and green components projecting from it represent potential epitopes.

Naïve T cells can express one of two different molecules, CD4 or CD8, on their surface, as shown in Figure 50.2.4, and are accordingly classified as $CD4^+$ or $CD8^+$ cells. These molecules are important because they regulate how a T cell will interact with and respond to an APC. Naïve $CD4^+$ cells bind APCs via their antigen-embedded MHC II molecules and are stimulated to become helper T (T_H) lymphocytes, cells that go on to stimulate B cells (or cytotoxic T cells) directly or secrete cytokines to inform more and various target cells about the pathogenic threat. In contrast, $CD8^+$ cells engage antigen-embedded MHC I molecules on APCs and are stimulated to become cytotoxic T lymphocytes (CTLs), which directly kill infected cells by apoptosis and emit cytokines to amplify the immune response. The two populations of T cells have different mechanisms of immune protection, but both bind MHC molecules via their antigen receptors called T cell receptors (TCRs). The CD4 or CD8 surface molecules differentiate whether the TCR will engage an MHC II or an MHC I molecule. Because they assist in binding specificity, the CD4 and CD8 molecules are described as coreceptors.

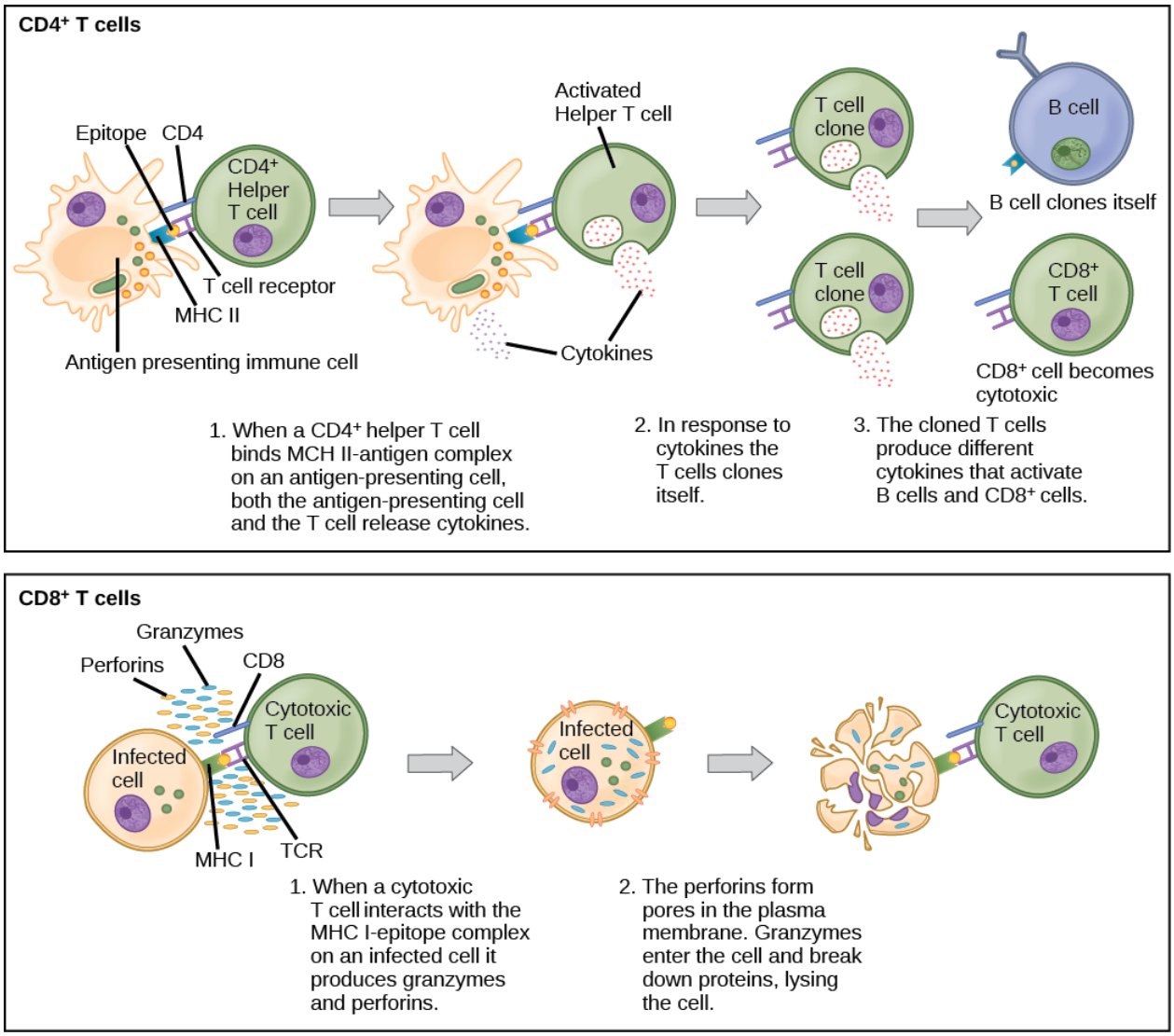


Figure 50.2.4: Naïve $CD4^+$ T cells engage MHC II molecules on antigen-presenting cells (APCs) and become activated. Clones of the activated helper T cell, in turn, activate B cells and $CD8^+$ T cells, which become cytotoxic T cells. Cytotoxic T cells kill infected cells.

Exercise 50.2.1

Which of the following statements about T cells is false?

a. Helper T cells release cytokines while cytotoxic T cells kill the infected cell.
b. Helper T cells are $CD4^+$, while cytotoxic T cells are $CD8^+$.
c. MHC II is a receptor found on most body cells, while MHC I is a receptor found on immune cells only.
d. The T cell receptor is found on both $CD4^+$ and $CD8^+$ T cells.

Answer

C

Consider the innumerable possible antigens that an individual will be exposed to during a lifetime. The mammalian adaptive immune system is adept in responding appropriately to each antigen. Mammals have an enormous diversity of T cell populations, resulting from the diversity of TCRs. Each TCR consists of two polypeptide chains that span the T cell membrane, as illustrated in Figure 50.2.5; the chains are linked by a disulfide bridge. Each polypeptide chain is comprised of a constant domain and a variable domain: a domain, in this sense, is a specific region of a protein that may be regulatory or structural. The intracellular domain is

involved in intracellular signaling. A single T cell will express thousands of identical copies of one specific TCR variant on its cell surface. The specificity of the adaptive immune system occurs because it synthesizes millions of different T cell populations, each expressing a TCR that differs in its variable domain. This TCR diversity is achieved by the mutation and recombination of genes that encode these receptors in stem cell precursors of T cells. The binding between an antigen-displaying MHC molecule and a complementary TCR "match" indicates that the adaptive immune system needs to activate and produce that specific T cell because its structure is appropriate to recognize and destroy the invading pathogen.

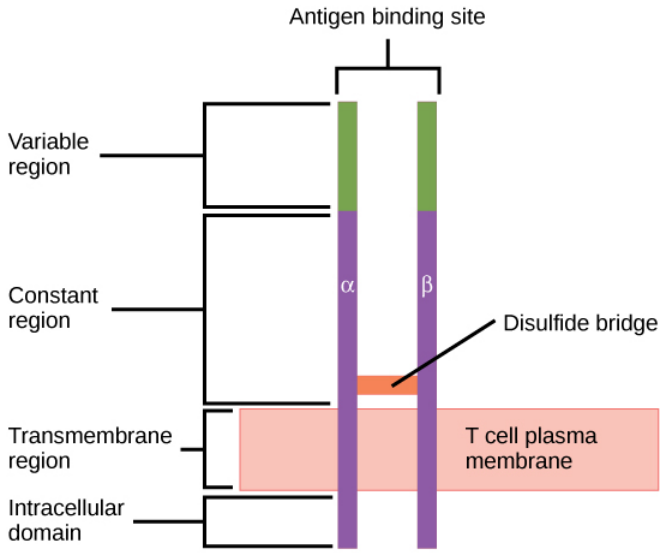


Figure 50.2.5: A T cell receptor spans the membrane and projects variable binding regions into the extracellular space to bind processed antigens via MHC molecules on APCs.

Helper T Lymphocytes

The T_H lymphocytes function indirectly to identify potential pathogens for other cells of the immune system. These cells are important for extracellular infections, such as those caused by certain bacteria, helminths, and protozoa. T_H lymphocytes recognize specific antigens displayed in the MHC II complexes of APCs. There are two major populations of T_H cells: T_H1 and T_H2. T_H1 cells secrete cytokines to enhance the activities of macrophages and other T cells. T_H1 cells activate the action of cyotoxic T cells, as well as macrophages. T_H2 cells stimulate naïve B cells to destroy foreign invaders via antibody secretion. Whether a T_H1 or a T_H2 immune response develops depends on the specific types of cytokines secreted by cells of the innate immune system, which in turn depends on the nature of the invading pathogen.

The T_H1-mediated response involves macrophages and is associated with inflammation. Recall the frontline defenses of macrophages involved in the innate immune response. Some intracellular bacteria, such as *Mycobacterium tuberculosis*, have evolved to multiply in macrophages after they have been engulfed. These pathogens evade attempts by macrophages to destroy and digest the pathogen. When *M. tuberculosis* infection occurs, macrophages can stimulate naïve T cells to become T_H1 cells. These stimulated T cells secrete specific cytokines that send feedback to the macrophage to stimulate its digestive capabilities and allow it to destroy the colonizing *M. tuberculosis*. In the same manner, T_H1-activated macrophages also become better suited to ingest and kill tumor cells. In summary; T_H1 responses are directed toward intracellular invaders while T_H2 responses are aimed at those that are extracellular.

B Lymphocytes

When stimulated by the T_H2 pathway, naïve B cells differentiate into antibody-secreting plasma cells. A plasma cell is an immune cell that secrets antibodies; these cells arise from B cells that were stimulated by antigens. Similar to T cells, naïve B cells initially are coated in thousands of B cell receptors (BCRs), which are membrane-bound forms of Ig (immunoglobulin, or an antibody). The B cell receptor has two heavy chains and two light chains connected by disulfide linkages. Each chain has a constant and a variable region; the latter is involved in antigen binding. Two other membrane proteins, Ig alpha and Ig beta, are involved in signaling. The receptors of any particular B cell, as shown in Figure 50.2.6 are all the same, but the hundreds of millions of different B cells in an individual have distinct recognition domains that contribute to extensive diversity in the types of molecular structures to which they

can bind. In this state, B cells function as APCs. They bind and engulf foreign antigens via their BCRs and then display processed antigens in the context of MHC II molecules to T_H2 cells. When a T_H2 cell detects that a B cell is bound to a relevant antigen, it secretes specific cytokines that induce the B cell to proliferate rapidly, which makes thousands of identical (clonal) copies of it, and then it synthesizes and secretes antibodies with the same antigen recognition pattern as the BCRs. The activation of B cells corresponding to one specific BCR variant and the dramatic proliferation of that variant is known as clonal selection. This phenomenon drastically, but briefly, changes the proportions of BCR variants expressed by the immune system, and shifts the balance toward BCRs specific to the infecting pathogen.

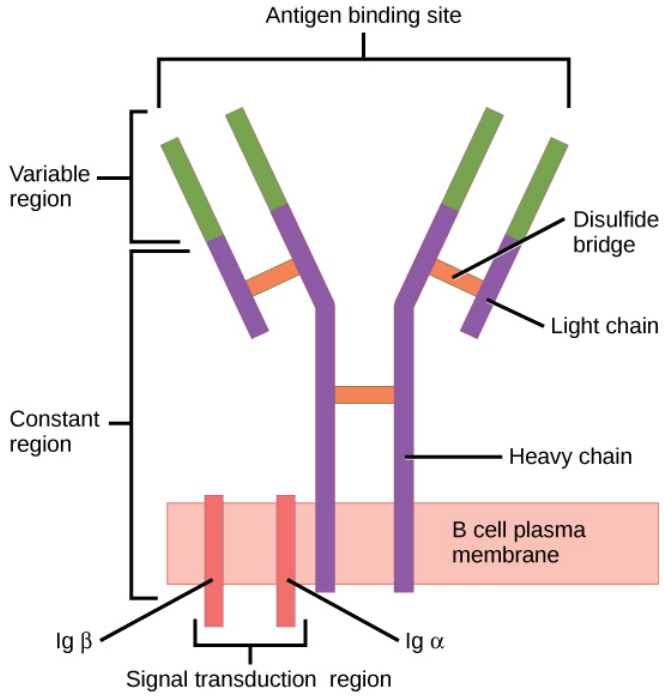


Figure **50.2.6**: B cell receptors are embedded in the membranes of B cells and bind a variety of antigens through their variable regions. The signal transduction region transfers the signal into the cell.

T and B cells differ in one fundamental way: whereas T cells bind antigens that have been digested and embedded in MHC molecules by APCs, B cells function as APCs that bind intact antigens that have not been processed. Although T and B cells both react with molecules that are termed “antigens,” these lymphocytes actually respond to very different types of molecules. B cells must be able to bind intact antigens because they secrete antibodies that must recognize the pathogen directly, rather than digested remnants of the pathogen. Bacterial carbohydrate and lipid molecules can activate B cells independently from the T cells.

Cytotoxic T Lymphocytes

CTLs, a subclass of T cells, function to clear infections directly. The cell-mediated part of the adaptive immune system consists of CTLs that attack and destroy infected cells. CTLs are particularly important in protecting against viral infections; this is because viruses replicate within cells where they are shielded from extracellular contact with circulating antibodies. When APCs phagocytize pathogens and present MHC I-embedded antigens to naïve $CD8^+$ T cells that express complementary TCRs, the $CD8^+$ T cells become activated to proliferate according to clonal selection. These resulting CTLs then identify non-APCs displaying the same MHC I-embedded antigens (for example, viral proteins)—for example, the CTLs identify infected host cells.

Intracellularly, infected cells typically die after the infecting pathogen replicates to a sufficient concentration and lyses the cell, as many viruses do. CTLs attempt to identify and destroy infected cells before the pathogen can replicate and escape, thereby halting the progression of intracellular infections. CTLs also support NK lymphocytes to destroy early cancers. Cytokines secreted by the T_H1 response that stimulates macrophages also stimulate CTLs and enhance their ability to identify and destroy infected cells and tumors.

CTLs sense MHC I-embedded antigens by directly interacting with infected cells via their TCRs. Binding of TCRs with antigens activates CTLs to release perforin and granzyme, degradative enzymes that will induce apoptosis of the infected cell. Recall that

this is a similar destruction mechanism to that used by NK cells. In this process, the CTL does not become infected and is not harmed by the secretion of perforin and granzymes. In fact, the functions of NK cells and CTLs are complementary and maximize the removal of infected cells, as illustrated in Figure 50.2.7. If the NK cell cannot identify the "missing self" pattern of down-regulated MHC I molecules, then the CTL can identify it by the complex of MHC I with foreign antigens, which signals "altered self." Similarly, if the CTL cannot detect antigen-embedded MHC I because the receptors are depleted from the cell surface, NK cells will destroy the cell instead. CTLs also emit cytokines, such as interferons, that alter surface protein expression in other infected cells, such that the infected cells can be easily identified and destroyed. Moreover, these interferons can also prevent virally infected cells from releasing virus particles.

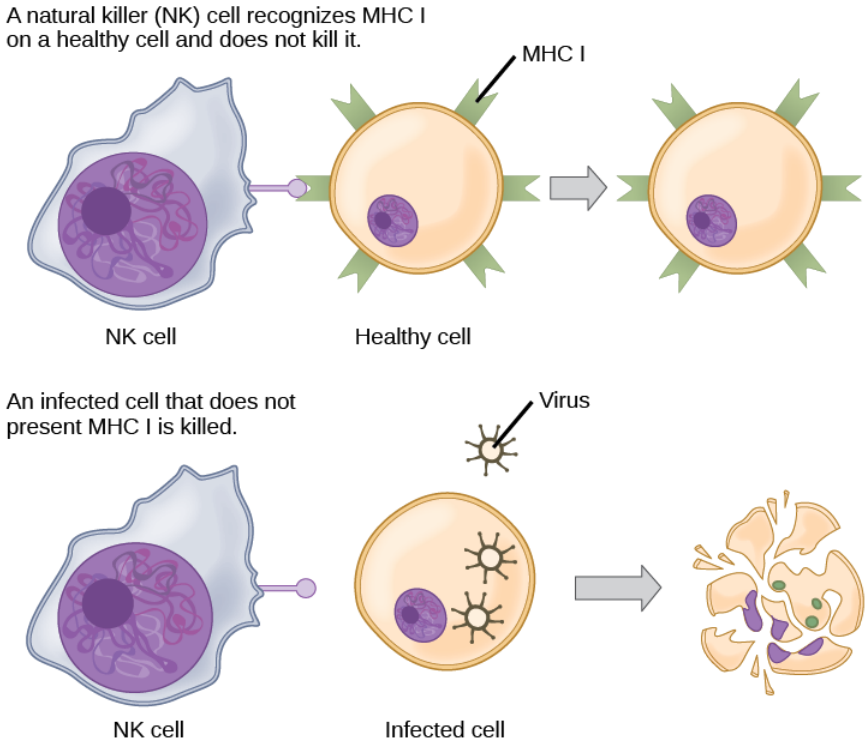


Figure 50.2.7: Natural killer (NK) cells recognize the MHC I receptor on healthy cells. If MHC I is absent, the cell is lysed.

Exercise 50.2.2

Based on what you know about MHC receptors, why do you think an organ transplanted from an incompatible donor to a recipient will be rejected?

Answer

MHC receptors differ from person to person. Thus, MHC receptors on an incompatible donor are considered "non-self" and are rejected by the immune system.

Plasma cells and CTLs are collectively called effector cells: they represent differentiated versions of their naïve counterparts, and they are involved in bringing about the immune defense of killing pathogens and infected host cells.

Mucosal Surfaces and Immune Tolerance

The innate and adaptive immune responses discussed thus far comprise the systemic immune system (affecting the whole body), which is distinct from the mucosal immune system. Mucosal immunity is formed by mucosa-associated lymphoid tissue, which functions independently of the systemic immune system, and which has its own innate and adaptive components. Mucosa-associated lymphoid tissue (MALT), illustrated in Figure 50.2.8, is a collection of lymphatic tissue that combines with epithelial tissue lining the mucosa throughout the body. This tissue functions as the immune barrier and response in areas of the body with direct contact to the external environment. The systemic and mucosal immune systems use many of the same cell types. Foreign

particles that make their way to MALT are taken up by absorptive epithelial cells called M cells and delivered to APCs located directly below the mucosal tissue. M cells function in the transport described, and are located in the Peyer's patch, a lymphoid nodule. APCs of the mucosal immune system are primarily dendritic cells, with B cells and macrophages having minor roles. Processed antigens displayed on APCs are detected by T cells in the MALT and at various mucosal induction sites, such as the tonsils, adenoids, appendix, or the mesenteric lymph nodes of the intestine. Activated T cells then migrate through the lymphatic system and into the circulatory system to mucosal sites of infection.

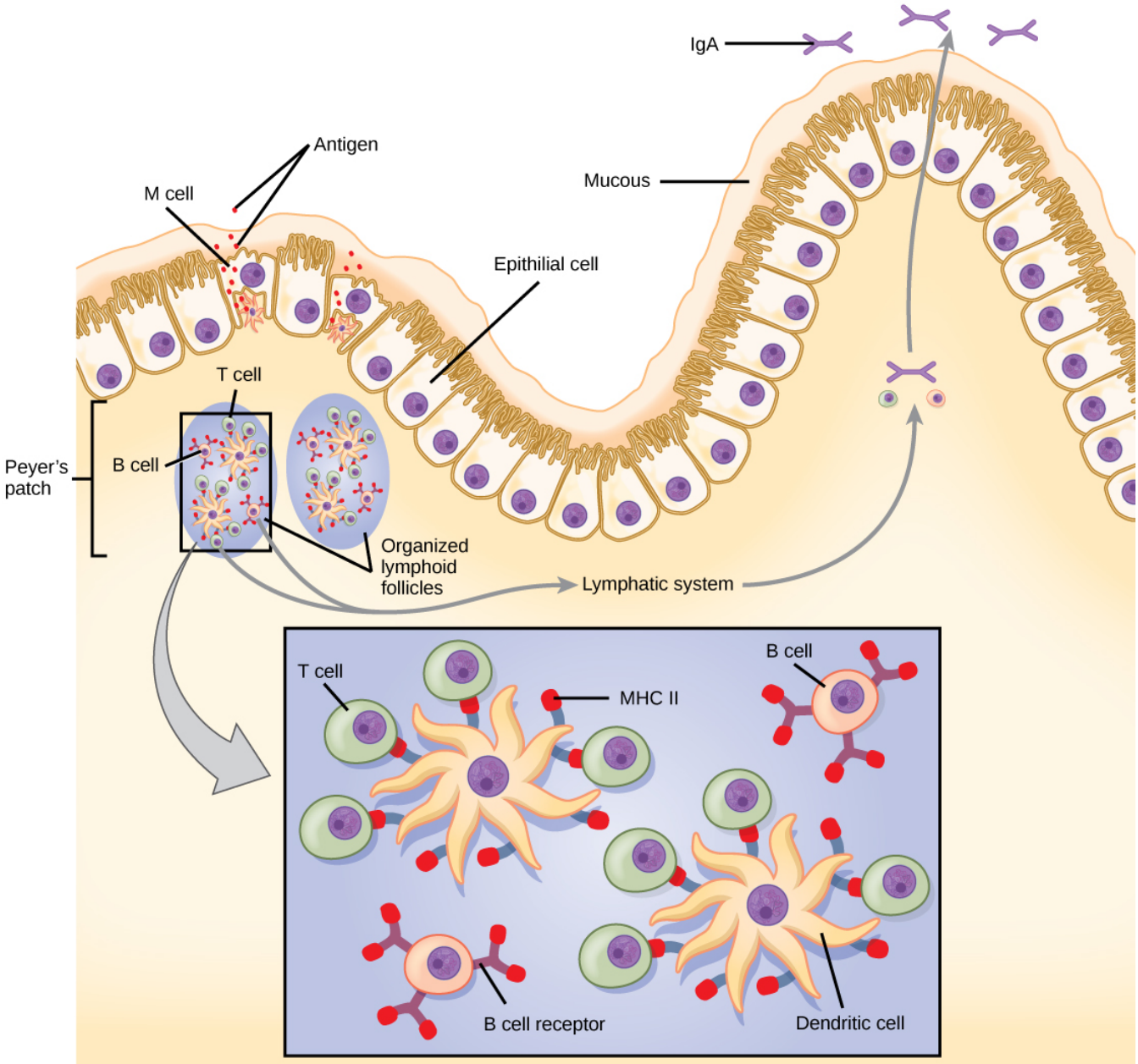


Figure 50.2.8: The topology and function of intestinal MALT is shown. Pathogens are taken up by M cells in the intestinal epithelium and excreted into a pocket formed by the inner surface of the cell. The pocket contains antigen-presenting cells such as dendritic cells, which engulf the antigens, then present them with MHC II molecules on the cell surface. The dendritic cells migrate to an underlying tissue called a Peyer's patch. Antigen-presenting cells, T cells, and B cells aggregate within the Peyer's patch, forming organized lymphoid follicles. There, some T cells and B cells are activated. Other antigen-loaded dendritic cells migrate through the lymphatic system where they activate B cells, T cells, and plasma cells in the lymph nodes. The activated cells then return to MALT tissue effector sites. IgA and other antibodies are secreted into the intestinal lumen.

MALT is a crucial component of a functional immune system because mucosal surfaces, such as the nasal passages, are the first tissues onto which inhaled or ingested pathogens are deposited. The mucosal tissue includes the mouth, pharynx, and esophagus,

and the gastrointestinal, respiratory, and urogenital tracts.

The immune system has to be regulated to prevent wasteful, unnecessary responses to harmless substances, and more importantly so that it does not attack “self.” The acquired ability to prevent an unnecessary or harmful immune response to a detected foreign substance known not to cause disease is described as immune tolerance. Immune tolerance is crucial for maintaining mucosal homeostasis given the tremendous number of foreign substances (such as food proteins) that APCs of the oral cavity, pharynx, and gastrointestinal mucosa encounter. Immune tolerance is brought about by specialized APCs in the liver, lymph nodes, small intestine, and lung that present harmless antigens to an exceptionally diverse population of regulatory T (T_{reg}) cells, specialized lymphocytes that suppress local inflammation and inhibit the secretion of stimulatory immune factors. The combined result of T_{reg} cells is to prevent immunologic activation and inflammation in undesired tissue compartments and to allow the immune system to focus on pathogens instead. In addition to promoting immune tolerance of harmless antigens, other subsets of T_{reg} cells are involved in the prevention of the autoimmune response, which is an inappropriate immune response to host cells or self-antigens. Another T_{reg} class suppresses immune responses to harmful pathogens after the infection has cleared to minimize host cell damage induced by inflammation and cell lysis.

Immunological Memory

The adaptive immune system possesses a memory component that allows for an efficient and dramatic response upon reinvasion of the same pathogen. Memory is handled by the adaptive immune system with little reliance on cues from the innate response. During the adaptive immune response to a pathogen that has not been encountered before, called a primary response, plasma cells secreting antibodies and differentiated T cells increase, then plateau over time. As B and T cells mature into effector cells, a subset of the naïve populations differentiates into B and T memory cells with the same antigen specificities, as illustrated in Figure **50.2.9**.

A memory cell is an antigen-specific B or T lymphocyte that does not differentiate into effector cells during the primary immune response, but that can immediately become effector cells upon re-exposure to the same pathogen. During the primary immune response, memory cells do not respond to antigens and do not contribute to host defenses. As the infection is cleared and pathogenic stimuli subside, the effectors are no longer needed, and they undergo apoptosis. In contrast, the memory cells persist in the circulation.

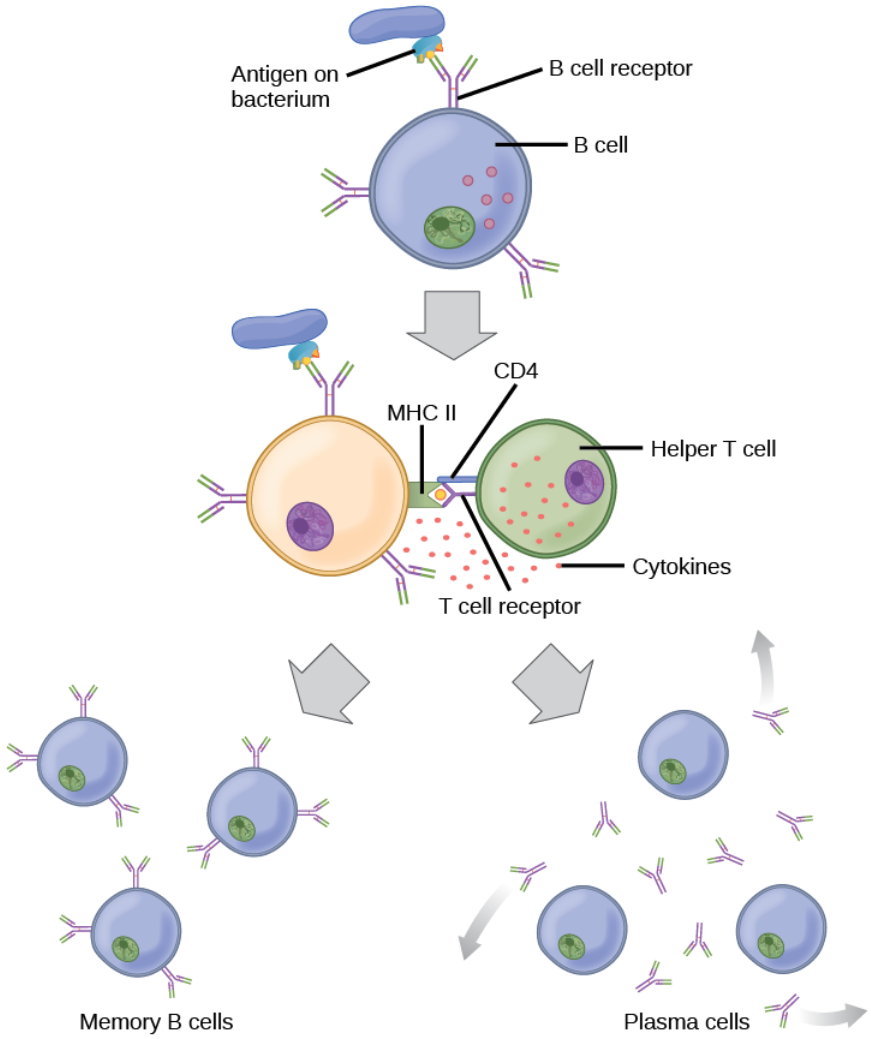


Figure 50.2.9: After initially binding an antigen to the B cell receptor (BCR), a B cell internalizes the antigen and presents it on MHC II. A helper T cell recognizes the MHC II–antigen complex and activates the B cell. As a result, memory B cells and plasma cells are made.

Exercise 50.2.3

The Rh antigen is found on Rh-positive red blood cells. An Rh-negative female can usually carry an Rh-positive fetus to term without difficulty. However, if she has a second Rh-positive fetus, her body may launch an immune attack that causes hemolytic disease of the newborn. Why do you think hemolytic disease is only a problem during the second or subsequent pregnancies?

Answer

If the blood of the mother and fetus mixes, memory cells that recognize the Rh antigen can form late in the first pregnancy. During subsequent pregnancies, these memory cells launch an immune attack on the fetal blood cells. Injection of anti-Rh antibody during the first pregnancy prevents the immune response from occurring.

If the pathogen is never encountered again during the individual's lifetime, B and T memory cells will circulate for a few years or even several decades and will gradually die off, having never functioned as effector cells. However, if the host is re-exposed to the same pathogen type, circulating memory cells will immediately differentiate into plasma cells and CTLs without input from APCs or T_H cells. One reason the adaptive immune response is delayed is because it takes time for naïve B and T cells with the appropriate antigen specificities to be identified and activated. Upon reinfection, this step is skipped, and the result is a more rapid production of immune defenses. Memory B cells that differentiate into plasma cells output tens to hundreds-fold greater antibody

amounts than were secreted during the primary response, as the graph in Figure 50.2.10 illustrates. This rapid and dramatic antibody response may stop the infection before it can even become established, and the individual may not realize they had been exposed.

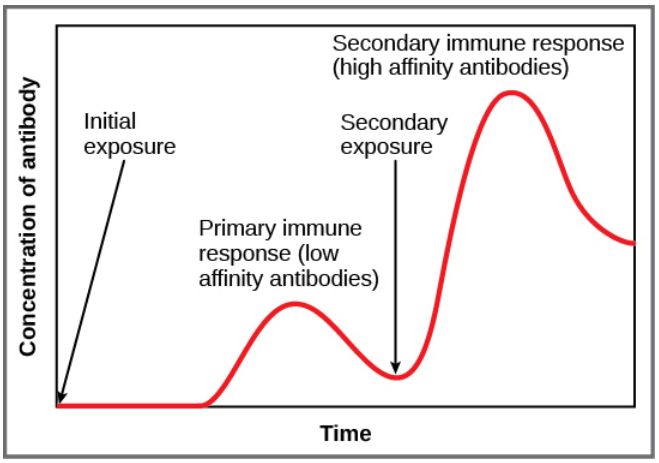


Figure 50.2.10: In the primary response to infection, antibodies are secreted first from plasma cells. Upon re-exposure to the same pathogen, memory cells differentiate into antibody-secreting plasma cells that output a greater amount of antibody for a longer period of time.

Vaccination is based on the knowledge that exposure to noninfectious antigens, derived from known pathogens, generates a mild primary immune response. The immune response to vaccination may not be perceived by the host as illness but still confers immune memory. When exposed to the corresponding pathogen to which an individual was vaccinated, the reaction is similar to a secondary exposure. Because each reinfection generates more memory cells and increased resistance to the pathogen, and because some memory cells die, certain vaccine courses involve one or more booster vaccinations to mimic repeat exposures: for instance, tetanus boosters are necessary every ten years because the memory cells only live that long.

Mucosal Immune Memory

A subset of T and B cells of the mucosal immune system differentiates into memory cells just as in the systemic immune system. Upon reinvasion of the same pathogen type, a pronounced immune response occurs at the mucosal site where the original pathogen deposited, but a collective defense is also organized within interconnected or adjacent mucosal tissue. For instance, the immune memory of an infection in the oral cavity would also elicit a response in the pharynx if the oral cavity was exposed to the same pathogen.

Career Connection: Vaccinologist

Vaccination (or immunization) involves the delivery, usually by injection as shown in Figure 50.2.11, of noninfectious antigen(s) derived from known pathogens. Other components, called adjuvants, are delivered in parallel to help stimulate the immune response. Immunological memory is the reason vaccines work. Ideally, the effect of vaccination is to elicit immunological memory, and thus resistance to specific pathogens without the individual having to experience an infection.



Figure 50.2.11: Vaccines are often delivered by injection into the arm. (credit: U.S. Navy Photographer's Mate Airman Apprentice Christopher D. Blachly)

Vaccinologists are involved in the process of vaccine development from the initial idea to the availability of the completed vaccine. This process can take decades, can cost millions of dollars, and can involve many obstacles along the way. For instance, injected vaccines stimulate the systemic immune system, eliciting humoral and cell-mediated immunity, but have little effect on the mucosal response, which presents a challenge because many pathogens are deposited and replicate in mucosal compartments, and the injection does not provide the most efficient immune memory for these disease agents. For this reason, vaccinologists are actively involved in developing new vaccines that are applied via intranasal, aerosol, oral, or transcutaneous (absorbed through the skin) delivery methods. Importantly, mucosal-administered vaccines elicit both mucosal and systemic immunity and produce the same level of disease resistance as injected vaccines.

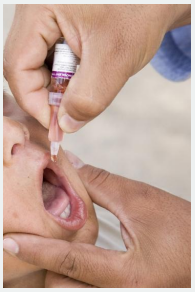


Figure 50.2.12: The polio vaccine can be administered orally. (credit: modification of work by UNICEF Sverige)

Currently, a version of intranasal influenza vaccine is available, and the polio and typhoid vaccines can be administered orally, as shown in Figure 50.2.12. Similarly, the measles and rubella vaccines are being adapted to aerosol delivery using inhalation devices. Eventually, transgenic plants may be engineered to produce vaccine antigens that can be eaten to confer disease resistance. Other vaccines may be adapted to rectal or vaginal application to elicit immune responses in rectal, genitourinary, or reproductive mucosa. Finally, vaccine antigens may be adapted to transdermal application in which the skin is lightly scraped and microneedles are used to pierce the outermost layer. In addition to mobilizing the mucosal immune response, this new generation of vaccines may end the anxiety associated with injections and, in turn, improve patient participation.

Primary Centers of the Immune System

Although the immune system is characterized by circulating cells throughout the body, the regulation, maturation, and intercommunication of immune factors occur at specific sites. The blood circulates immune cells, proteins, and other factors through the body. Approximately 0.1 percent of all cells in the blood are leukocytes, which encompass monocytes (the precursor of macrophages) and lymphocytes. The majority of cells in the blood are erythrocytes (red blood cells). Lymph is a watery fluid that bathes tissues and organs with protective white blood cells and does not contain erythrocytes. Cells of the immune system can travel between the distinct lymphatic and blood circulatory systems, which are separated by interstitial space, by a process called extravasation (passing through to surrounding tissue).

The cells of the immune system originate from hematopoietic stem cells in the bone marrow. Cytokines stimulate these stem cells to differentiate into immune cells. B cell maturation occurs in the bone marrow, whereas naïve T cells transit from the bone marrow to the thymus for maturation. In the thymus, immature T cells that express TCRs complementary to self-antigens are destroyed. This process helps prevent autoimmune responses.

On maturation, T and B lymphocytes circulate to various destinations. Lymph nodes scattered throughout the body, as illustrated in Figure **50.2.13**, house large populations of T and B cells, dendritic cells, and macrophages. Lymph gathers antigens as it drains from tissues. These antigens then are filtered through lymph nodes before the lymph is returned to circulation. APCs in the lymph nodes capture and process antigens and inform nearby lymphocytes about potential pathogens.

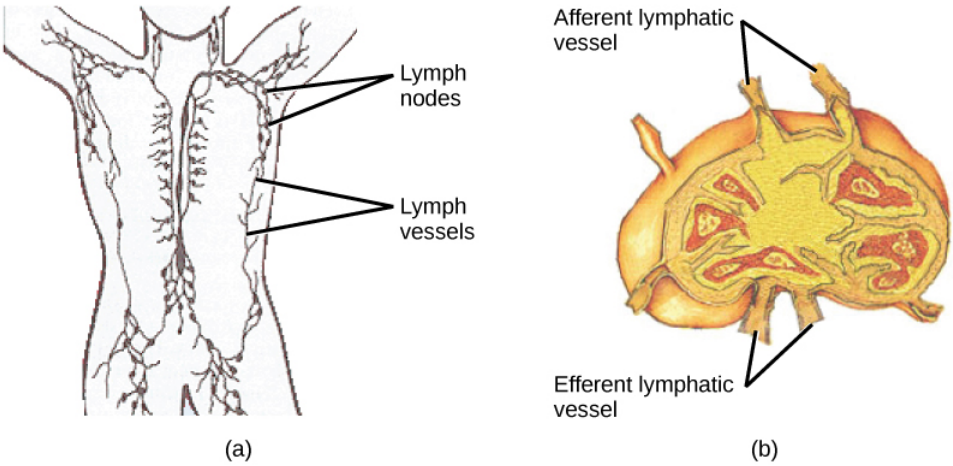


Figure **50.2.13**: (a) Lymphatic vessels carry a clear fluid called lymph throughout the body. The liquid enters (b) lymph nodes through afferent vessels. Lymph nodes are filled with lymphocytes that purge infecting cells. The lymph then exits through efferent vessels. (credit: modification of work by NIH, NCI)

The spleen houses B and T cells, macrophages, dendritic cells, and NK cells. The spleen, shown in Figure **50.2.14**, is the site where APCs that have trapped foreign particles in the blood can communicate with lymphocytes. Antibodies are synthesized and secreted by activated plasma cells in the spleen, and the spleen filters foreign substances and antibody-complexed pathogens from the blood. Functionally, the spleen is to the blood as lymph nodes are to the lymph.

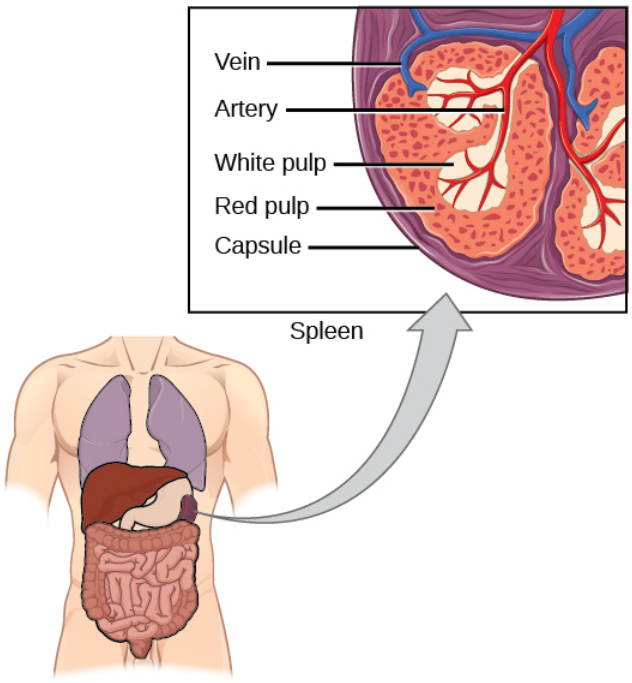


Figure **50.2.14**: The spleen is similar to a lymph node but is much larger and filters blood instead of lymph. Blood enters the spleen through arteries and exits through veins. The spleen contains two types of tissue: red pulp and white pulp. Red pulp consists of cavities that store blood. Within the red pulp, damaged red blood cells are removed and replaced by new ones. White pulp is rich in lymphocytes that remove antigen-coated bacteria from the blood. (credit: modification of work by NCI)

Summary

The adaptive immune response is a slower-acting, longer-lasting, and more specific response than the innate response. However, the adaptive response requires information from the innate immune system to function. APCs display antigens via MHC molecules to complementary naïve T cells. In response, the T cells differentiate and proliferate, becoming T_H cells or CTLs. T_H cells stimulate B cells that have engulfed and presented pathogen-derived antigens. B cells differentiate into plasma cells that secrete antibodies, whereas CTLs induce apoptosis in intracellularly infected or cancerous cells. Memory cells persist after a primary exposure to a pathogen. If re-exposure occurs, memory cells differentiate into effector cells without input from the innate immune system. The mucosal immune system is largely independent from the systemic immune system but functions in a parallel fashion to protect the extensive mucosal surfaces of the body.

Glossary

adaptive immunity
: immunity that has memory and occurs after exposure to an antigen either from a pathogen or a vaccination

antigen
: foreign or “non-self” protein that triggers the immune response

antigen-presenting cell (APC)
: immune cell that detects, engulfs, and informs the adaptive immune response about an infection by presenting the processed antigen on the cell surface

autoimmune response
: inappropriate immune response to host cells or self-antigens

cell-mediated immune response
: adaptive immune response that is carried out by T cells

clonal selection
activation of B cells corresponding to one specific BCR variant and the dramatic proliferation of that variant

cytotoxic T lymphocyte (CTL)
adaptive immune cell that directly kills infected cells via perforin and granzymes, and releases cytokines to enhance the immune response

dendritic cell
immune cell that processes antigen material and presents it on the surface of other cells to induce an immune response

effector cell
lymphocyte that has differentiated, such as a B cell, plasma cell, or cytotoxic T lymphocyte

epitope
small component of an antigen that is specifically recognized by antibodies, B cells, and T cells; the antigenic determinant

helper T lymphocyte (T_H)
cell of the adaptive immune system that binds APCs via MHC II molecules and stimulates B cells or secretes cytokines to initiate the immune response

humoral immune response
adaptive immune response that is controlled by activated B cells and antibodies

immune tolerance
acquired ability to prevent an unnecessary or harmful immune response to a detected foreign body known not to cause disease or to self-antigens

lymph
watery fluid that bathes tissues and organs with protective white blood cells and does not contain erythrocytes

mucosa-associated lymphoid tissue (MALT)
collection of lymphatic tissue that combines with epithelial tissue lining the mucosa throughout the body

memory cell
antigen-specific B or T lymphocyte that does not differentiate into effector cells during the primary immune response but that can immediately become an effector cell upon re-exposure to the same pathogen

plasma cell
immune cell that secrets antibodies; these cells arise from B cells that were stimulated by antigens

regulatory T (T_{reg}) cell
specialized lymphocyte that suppresses local inflammation and inhibits the secretion of cytokines, antibodies, and other stimulatory immune factors; involved in immune tolerance

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50.3: Cell-Mediated Immunity

Skills to Develop

- Explain adaptive immunity
- Compare and contrast adaptive and innate immunity
- Describe cell-mediated immune response and humoral immune response
- Describe immune tolerance

The adaptive, or acquired, immune response takes days or even weeks to become established—much longer than the innate response; however, adaptive immunity is more specific to pathogens and has memory. Adaptive immunity is an immunity that occurs after exposure to an antigen either from a pathogen or a vaccination. This part of the immune system is activated when the innate immune response is insufficient to control an infection. In fact, without information from the innate immune system, the adaptive response could not be mobilized. There are two types of adaptive responses: the cell-mediated immune response, which is carried out by T cells, and the humoral immune response, which is controlled by activated B cells and antibodies. Activated T cells and B cells that are specific to molecular structures on the pathogen proliferate and attack the invading pathogen. Their attack can kill pathogens directly or secrete antibodies that enhance the phagocytosis of pathogens and disrupt the infection. Adaptive immunity also involves a memory to provide the host with long-term protection from reinfection with the same type of pathogen; on re-exposure, this memory will facilitate an efficient and quick response.

Antigen-presenting Cells

Unlike NK cells of the innate immune system, B cells (B lymphocytes) are a type of white blood cell that gives rise to antibodies, whereas T cells (T lymphocytes) are a type of white blood cell that plays an important role in the immune response. T cells are a key component in the cell-mediated response—the specific immune response that utilizes T cells to neutralize cells that have been infected with viruses and certain bacteria. There are three types of T cells: cytotoxic, helper, and suppressor T cells. Cytotoxic T cells destroy virus-infected cells in the cell-mediated immune response, and helper T cells play a part in activating both the antibody and the cell-mediated immune responses. Suppressor T cells deactivate T cells and B cells when needed, and thus prevent the immune response from becoming too intense.

An antigen is a foreign or “non-self” macromolecule that reacts with cells of the immune system. Not all antigens will provoke a response. For instance, individuals produce innumerable “self” antigens and are constantly exposed to harmless foreign antigens, such as food proteins, pollen, or dust components. The suppression of immune responses to harmless macromolecules is highly regulated and typically prevents processes that could be damaging to the host, known as tolerance.

The innate immune system contains cells that detect potentially harmful antigens, and then inform the adaptive immune response about the presence of these antigens. An antigen-presenting cell (APC) is an immune cell that detects, engulfs, and informs the adaptive immune response about an infection. When a pathogen is detected, these APCs will phagocytose the pathogen and digest it to form many different fragments of the antigen. Antigen fragments will then be transported to the surface of the APC, where they will serve as an indicator to other immune cells. Dendritic cells are immune cells that process antigen material; they are present in the skin (Langerhans cells) and the lining of the nose, lungs, stomach, and intestines. Sometimes a dendritic cell presents on the surface of other cells to induce an immune response, thus functioning as an antigen-presenting cell. Macrophages also function as APCs. Before activation and differentiation, B cells can also function as APCs.

After phagocytosis by APCs, the phagocytic vesicle fuses with an intracellular lysosome forming phagolysosome. Within the phagolysosome, the components are broken down into fragments; the fragments are then loaded onto MHC class I or MHC class II molecules and are transported to the cell surface for antigen presentation, as illustrated in Figure 50.3.1. Note that T lymphocytes cannot properly respond to the antigen unless it is processed and embedded in an MHC II molecule. APCs express MHC on their surfaces, and when combined with a foreign antigen, these complexes signal a “non-self” invader. Once the fragment of antigen is embedded in the MHC II molecule, the immune cell can respond. Helper T- cells are one of the main lymphocytes that respond to antigen-presenting cells. Recall that all other nucleated cells of the body expressed MHC I molecules, which signal “healthy” or “normal.”

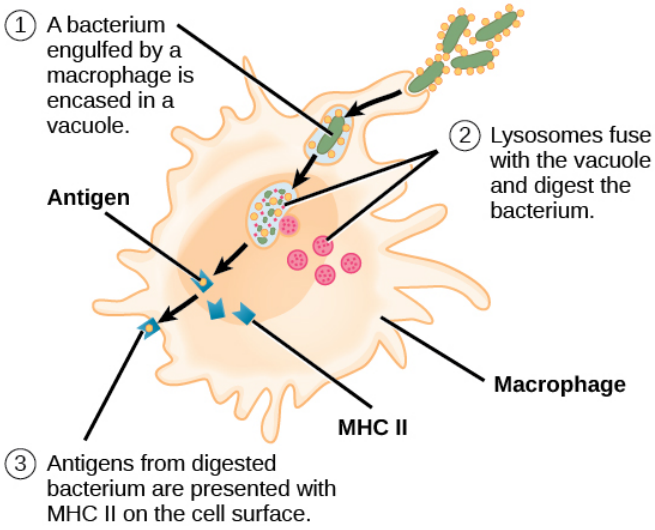


Figure 50.3.1: An APC, such as a macrophage, engulfs and digests a foreign bacterium. An antigen from the bacterium is presented on the cell surface in conjunction with an MHC II molecule Lymphocytes of the adaptive immune response interact with antigen-embedded MHC II molecules to mature into functional immune cells.

T and B Lymphocytes

Lymphocytes in human circulating blood are approximately 80 to 90 percent T cells, shown in Figure 50.3.2, and 10 to 20 percent B cells. Recall that the T cells are involved in the cell-mediated immune response, whereas B cells are part of the humoral immune response.

T cells encompass a heterogeneous population of cells with extremely diverse functions. Some T cells respond to APCs of the innate immune system, and indirectly induce immune responses by releasing cytokines. Other T cells stimulate B cells to prepare their own response. Another population of T cells detects APC signals and directly kills the infected cells. Other T cells are involved in suppressing inappropriate immune reactions to harmless or "self" antigens.

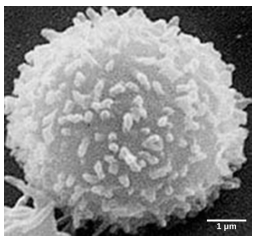


Figure 50.3.2: This scanning electron micrograph shows a T lymphocyte, which is responsible for the cell-mediated immune response. T cells are able to recognize antigens. (credit: modification of work by NCI; scale-bar data from Matt Russell)

T and B cells exhibit a common theme of recognition/binding of specific antigens via a complementary receptor, followed by activation and self-amplification/maturation to specifically bind to the particular antigen of the infecting pathogen. T and B lymphocytes are also similar in that each cell only expresses one type of antigen receptor. Any individual may possess a population of T and B cells that together express a near limitless variety of antigen receptors that are capable of recognizing virtually any infecting pathogen. T and B cells are activated when they recognize small components of antigens, called epitopes, presented by APCs, illustrated in Figure 50.3.3. Note that recognition occurs at a specific epitope rather than on the entire antigen; for this reason, epitopes are known as "antigenic determinants." In the absence of information from APCs, T and B cells remain inactive, or naïve, and are unable to prepare an immune response. The requirement for information from the APCs of innate immunity to trigger B cell or T cell activation illustrates the essential nature of the innate immune response to the functioning of the entire immune system.

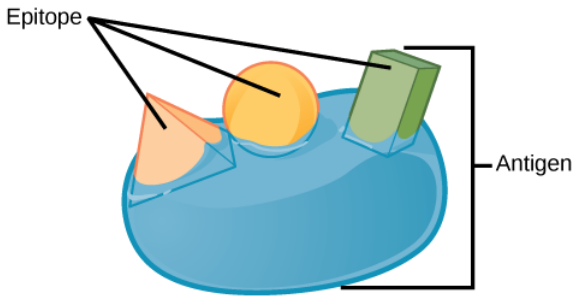


Figure 50.3.3: An antigen is a macromolecule that reacts with components of the immune system. A given antigen may contain several motifs that are recognized by immune cells. Each motif is an epitope. In this figure, the entire structure is an antigen, and the orange, salmon and green components projecting from it represent potential epitopes.

Naïve T cells can express one of two different molecules, CD4 or CD8, on their surface, as shown in Figure 50.3.4, and are accordingly classified as $CD4^+$ or $CD8^+$ cells. These molecules are important because they regulate how a T cell will interact with and respond to an APC. Naïve $CD4^+$ cells bind APCs via their antigen-embedded MHC II molecules and are stimulated to become helper T (T_H) lymphocytes, cells that go on to stimulate B cells (or cytotoxic T cells) directly or secrete cytokines to inform more and various target cells about the pathogenic threat. In contrast, $CD8^+$ cells engage antigen-embedded MHC I molecules on APCs and are stimulated to become cytotoxic T lymphocytes (CTLs), which directly kill infected cells by apoptosis and emit cytokines to amplify the immune response. The two populations of T cells have different mechanisms of immune protection, but both bind MHC molecules via their antigen receptors called T cell receptors (TCRs). The CD4 or CD8 surface molecules differentiate whether the TCR will engage an MHC II or an MHC I molecule. Because they assist in binding specificity, the CD4 and CD8 molecules are described as coreceptors.

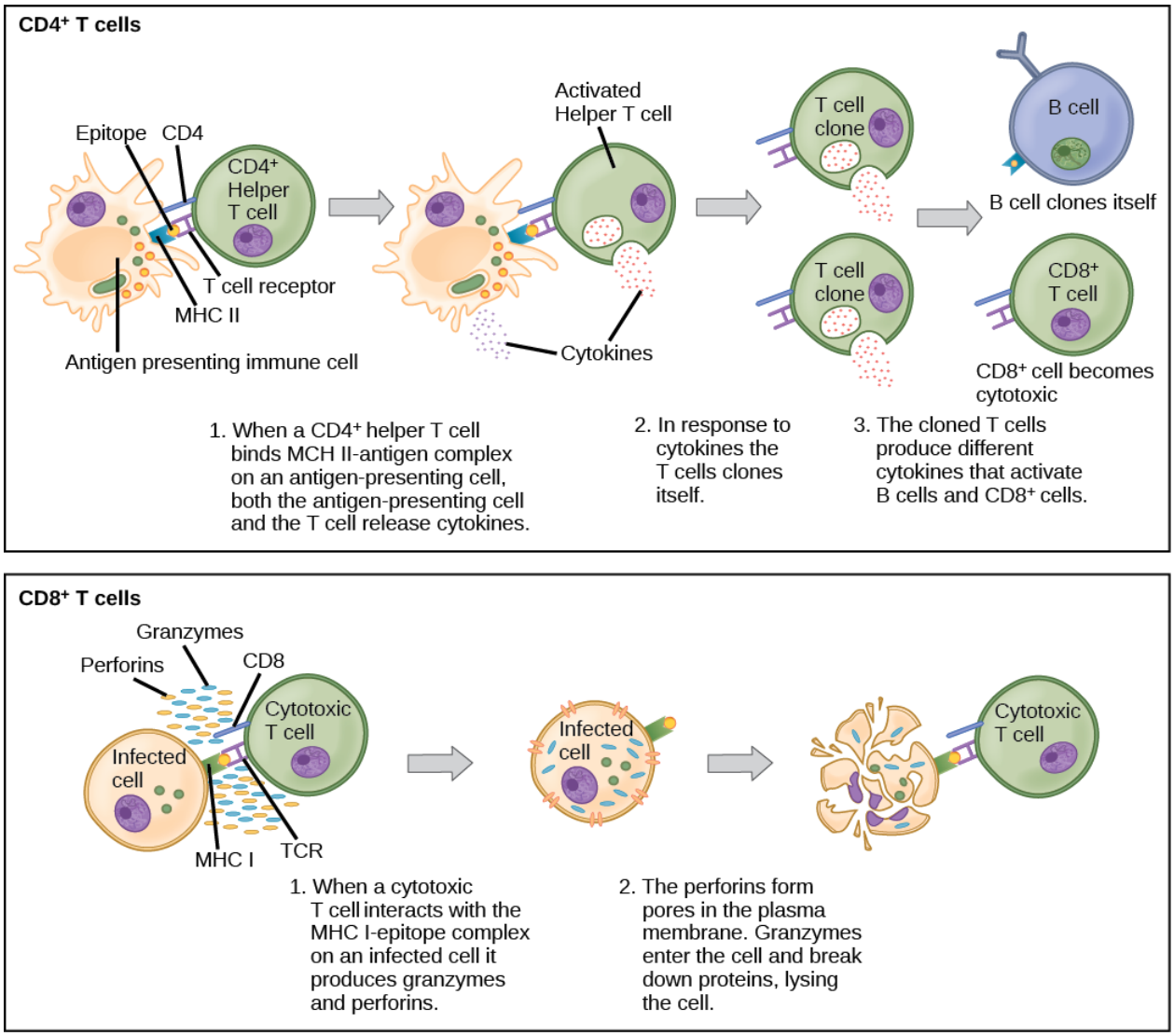


Figure **50.3.4**: Naïve $CD4^+$ T cells engage MHC II molecules on antigen-presenting cells (APCs) and become activated. Clones of the activated helper T cell, in turn, activate B cells and $CD8^+$ T cells, which become cytotoxic T cells. Cytotoxic T cells kill infected cells.

Exercise 50.3.1

Which of the following statements about T cells is false?

a. Helper T cells release cytokines while cytotoxic T cells kill the infected cell.
b. Helper T cells are $CD4^+$, while cytotoxic T cells are $CD8^+$.
c. MHC II is a receptor found on most body cells, while MHC I is a receptor found on immune cells only.
d. The T cell receptor is found on both $CD4^+$ and $CD8^+$ T cells.

Answer

C

Consider the innumerable possible antigens that an individual will be exposed to during a lifetime. The mammalian adaptive immune system is adept in responding appropriately to each antigen. Mammals have an enormous diversity of T cell populations, resulting from the diversity of TCRs. Each TCR consists of two polypeptide chains that span the T cell membrane, as illustrated in Figure **50.3.5**; the chains are linked by a disulfide bridge. Each polypeptide chain is comprised of a constant domain and a variable domain: a domain, in this sense, is a specific region of a protein that may be regulatory or structural. The intracellular domain is

involved in intracellular signaling. A single T cell will express thousands of identical copies of one specific TCR variant on its cell surface. The specificity of the adaptive immune system occurs because it synthesizes millions of different T cell populations, each expressing a TCR that differs in its variable domain. This TCR diversity is achieved by the mutation and recombination of genes that encode these receptors in stem cell precursors of T cells. The binding between an antigen-displaying MHC molecule and a complementary TCR "match" indicates that the adaptive immune system needs to activate and produce that specific T cell because its structure is appropriate to recognize and destroy the invading pathogen.

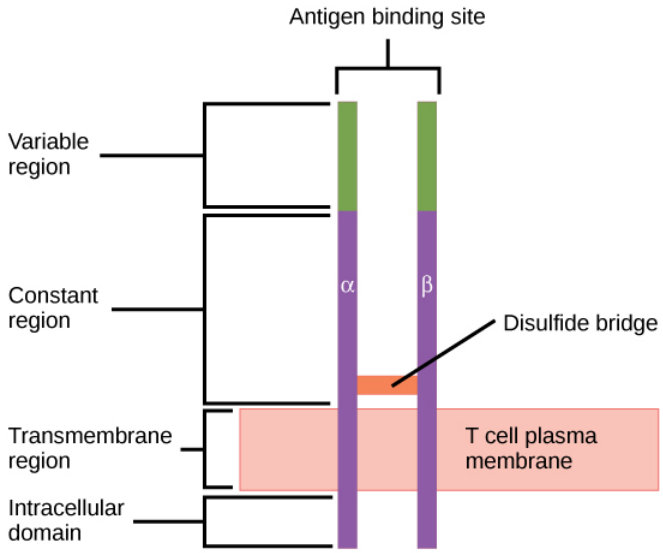


Figure **50.3.5**: A T cell receptor spans the membrane and projects variable binding regions into the extracellular space to bind processed antigens via MHC molecules on APCs.

Helper T Lymphocytes

The T_H lymphocytes function indirectly to identify potential pathogens for other cells of the immune system. These cells are important for extracellular infections, such as those caused by certain bacteria, helminths, and protozoa. T_H lymphocytes recognize specific antigens displayed in the MHC II complexes of APCs. There are two major populations of T_H cells: T_H1 and T_H2. T_H1 cells secrete cytokines to enhance the activities of macrophages and other T cells. T_H1 cells activate the action of cyotoxic T cells, as well as macrophages. T_H2 cells stimulate naïve B cells to destroy foreign invaders via antibody secretion. Whether a T_H1 or a T_H2 immune response develops depends on the specific types of cytokines secreted by cells of the innate immune system, which in turn depends on the nature of the invading pathogen.

The T_H1-mediated response involves macrophages and is associated with inflammation. Recall the frontline defenses of macrophages involved in the innate immune response. Some intracellular bacteria, such as *Mycobacterium tuberculosis*, have evolved to multiply in macrophages after they have been engulfed. These pathogens evade attempts by macrophages to destroy and digest the pathogen. When *M. tuberculosis* infection occurs, macrophages can stimulate naïve T cells to become T_H1 cells. These stimulated T cells secrete specific cytokines that send feedback to the macrophage to stimulate its digestive capabilities and allow it to destroy the colonizing *M. tuberculosis*. In the same manner, T_H1-activated macrophages also become better suited to ingest and kill tumor cells. In summary; T_H1 responses are directed toward intracellular invaders while T_H2 responses are aimed at those that are extracellular.

B Lymphocytes

When stimulated by the T_H2 pathway, naïve B cells differentiate into antibody-secreting plasma cells. A plasma cell is an immune cell that secrets antibodies; these cells arise from B cells that were stimulated by antigens. Similar to T cells, naïve B cells initially are coated in thousands of B cell receptors (BCRs), which are membrane-bound forms of Ig (immunoglobulin, or an antibody). The B cell receptor has two heavy chains and two light chains connected by disulfide linkages. Each chain has a constant and a variable region; the latter is involved in antigen binding. Two other membrane proteins, Ig alpha and Ig beta, are involved in signaling. The receptors of any particular B cell, as shown in Figure **50.3.6** are all the same, but the hundreds of millions of different B cells in an individual have distinct recognition domains that contribute to extensive diversity in the types of molecular structures to which they

can bind. In this state, B cells function as APCs. They bind and engulf foreign antigens via their BCRs and then display processed antigens in the context of MHC II molecules to T_H2 cells. When a T_H2 cell detects that a B cell is bound to a relevant antigen, it secretes specific cytokines that induce the B cell to proliferate rapidly, which makes thousands of identical (clonal) copies of it, and then it synthesizes and secretes antibodies with the same antigen recognition pattern as the BCRs. The activation of B cells corresponding to one specific BCR variant and the dramatic proliferation of that variant is known as clonal selection. This phenomenon drastically, but briefly, changes the proportions of BCR variants expressed by the immune system, and shifts the balance toward BCRs specific to the infecting pathogen.

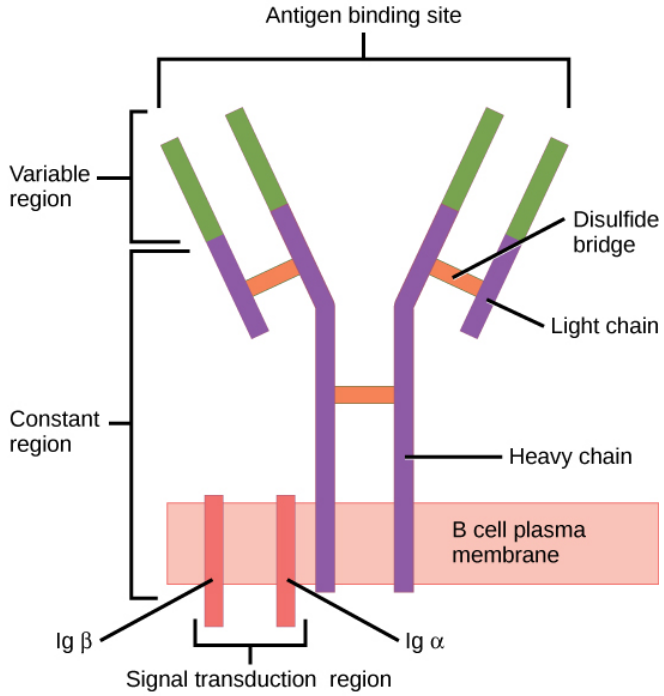


Figure **50.3.6**: B cell receptors are embedded in the membranes of B cells and bind a variety of antigens through their variable regions. The signal transduction region transfers the signal into the cell.

T and B cells differ in one fundamental way: whereas T cells bind antigens that have been digested and embedded in MHC molecules by APCs, B cells function as APCs that bind intact antigens that have not been processed. Although T and B cells both react with molecules that are termed “antigens,” these lymphocytes actually respond to very different types of molecules. B cells must be able to bind intact antigens because they secrete antibodies that must recognize the pathogen directly, rather than digested remnants of the pathogen. Bacterial carbohydrate and lipid molecules can activate B cells independently from the T cells.

Cytotoxic T Lymphocytes

CTLs, a subclass of T cells, function to clear infections directly. The cell-mediated part of the adaptive immune system consists of CTLs that attack and destroy infected cells. CTLs are particularly important in protecting against viral infections; this is because viruses replicate within cells where they are shielded from extracellular contact with circulating antibodies. When APCs phagocytize pathogens and present MHC I-embedded antigens to naïve $CD8^+$ T cells that express complementary TCRs, the $CD8^+$ T cells become activated to proliferate according to clonal selection. These resulting CTLs then identify non-APCs displaying the same MHC I-embedded antigens (for example, viral proteins)—for example, the CTLs identify infected host cells.

Intracellularly, infected cells typically die after the infecting pathogen replicates to a sufficient concentration and lyses the cell, as many viruses do. CTLs attempt to identify and destroy infected cells before the pathogen can replicate and escape, thereby halting the progression of intracellular infections. CTLs also support NK lymphocytes to destroy early cancers. Cytokines secreted by the T_H1 response that stimulates macrophages also stimulate CTLs and enhance their ability to identify and destroy infected cells and tumors.

CTLs sense MHC I-embedded antigens by directly interacting with infected cells via their TCRs. Binding of TCRs with antigens activates CTLs to release perforin and granzyme, degradative enzymes that will induce apoptosis of the infected cell. Recall that

this is a similar destruction mechanism to that used by NK cells. In this process, the CTL does not become infected and is not harmed by the secretion of perforin and granzymes. In fact, the functions of NK cells and CTLs are complementary and maximize the removal of infected cells, as illustrated in Figure 50.3.7. If the NK cell cannot identify the "missing self" pattern of down-regulated MHC I molecules, then the CTL can identify it by the complex of MHC I with foreign antigens, which signals "altered self." Similarly, if the CTL cannot detect antigen-embedded MHC I because the receptors are depleted from the cell surface, NK cells will destroy the cell instead. CTLs also emit cytokines, such as interferons, that alter surface protein expression in other infected cells, such that the infected cells can be easily identified and destroyed. Moreover, these interferons can also prevent virally infected cells from releasing virus particles.

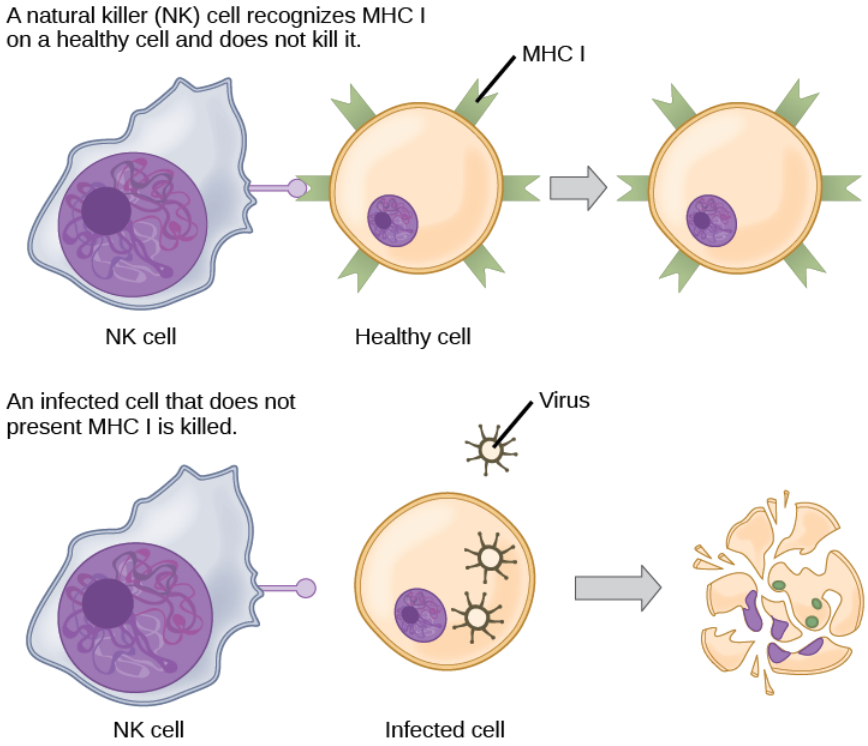


Figure 50.3.7: Natural killer (NK) cells recognize the MHC I receptor on healthy cells. If MHC I is absent, the cell is lysed.

Exercise 50.3.2

Based on what you know about MHC receptors, why do you think an organ transplanted from an incompatible donor to a recipient will be rejected?

Answer

MHC receptors differ from person to person. Thus, MHC receptors on an incompatible donor are considered "non-self" and are rejected by the immune system.

Plasma cells and CTLs are collectively called effector cells: they represent differentiated versions of their naïve counterparts, and they are involved in bringing about the immune defense of killing pathogens and infected host cells.

Mucosal Surfaces and Immune Tolerance

The innate and adaptive immune responses discussed thus far comprise the systemic immune system (affecting the whole body), which is distinct from the mucosal immune system. Mucosal immunity is formed by mucosa-associated lymphoid tissue, which functions independently of the systemic immune system, and which has its own innate and adaptive components. Mucosa-associated lymphoid tissue (MALT), illustrated in Figure 50.3.8, is a collection of lymphatic tissue that combines with epithelial tissue lining the mucosa throughout the body. This tissue functions as the immune barrier and response in areas of the body with direct contact to the external environment. The systemic and mucosal immune systems use many of the same cell types. Foreign

particles that make their way to MALT are taken up by absorptive epithelial cells called M cells and delivered to APCs located directly below the mucosal tissue. M cells function in the transport described, and are located in the Peyer's patch, a lymphoid nodule. APCs of the mucosal immune system are primarily dendritic cells, with B cells and macrophages having minor roles. Processed antigens displayed on APCs are detected by T cells in the MALT and at various mucosal induction sites, such as the tonsils, adenoids, appendix, or the mesenteric lymph nodes of the intestine. Activated T cells then migrate through the lymphatic system and into the circulatory system to mucosal sites of infection.

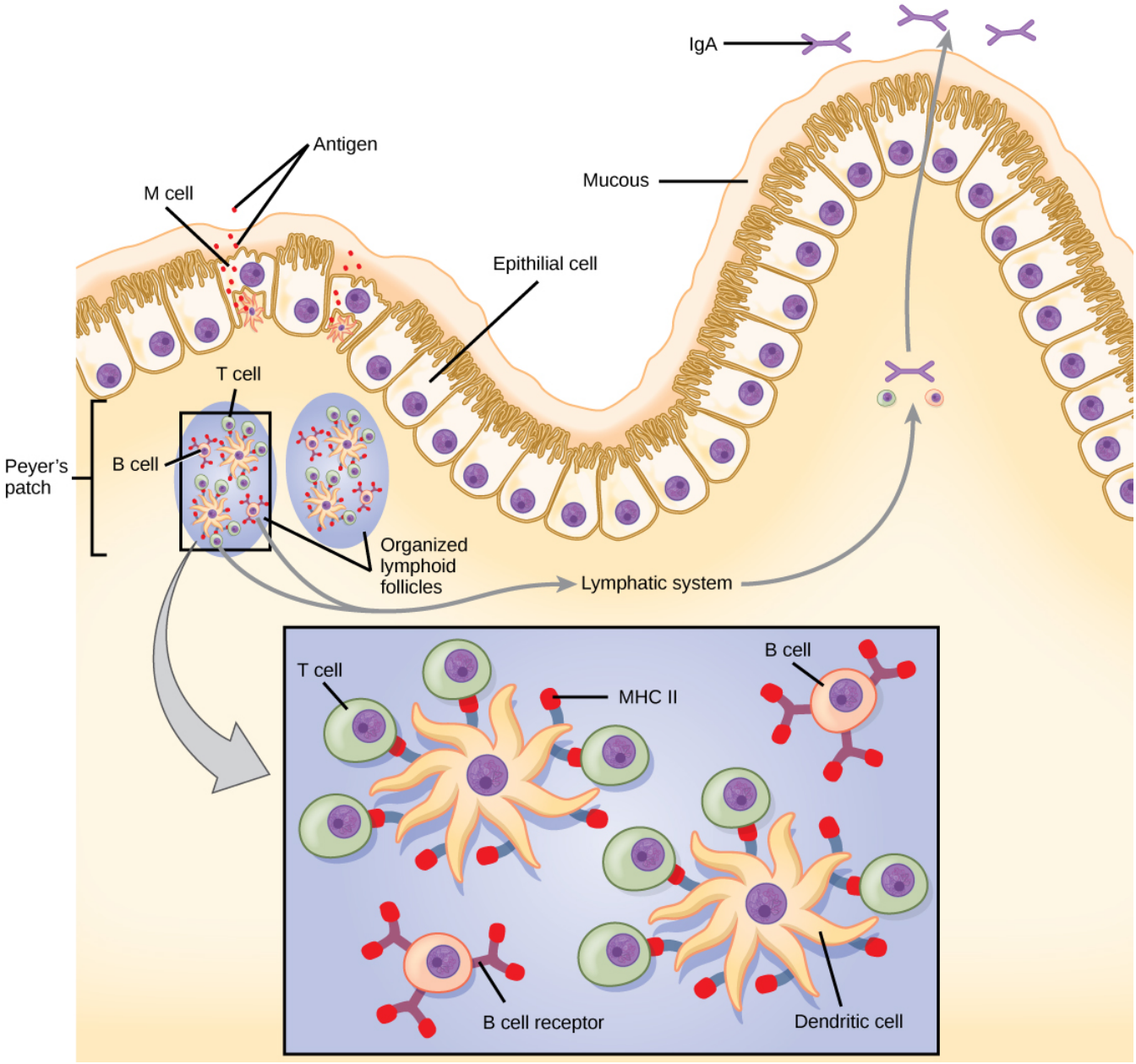


Figure 50.3.8: The topology and function of intestinal MALT is shown. Pathogens are taken up by M cells in the intestinal epithelium and excreted into a pocket formed by the inner surface of the cell. The pocket contains antigen-presenting cells such as dendritic cells, which engulf the antigens, then present them with MHC II molecules on the cell surface. The dendritic cells migrate to an underlying tissue called a Peyer's patch. Antigen-presenting cells, T cells, and B cells aggregate within the Peyer's patch, forming organized lymphoid follicles. There, some T cells and B cells are activated. Other antigen-loaded dendritic cells migrate through the lymphatic system where they activate B cells, T cells, and plasma cells in the lymph nodes. The activated cells then return to MALT tissue effector sites. IgA and other antibodies are secreted into the intestinal lumen.

MALT is a crucial component of a functional immune system because mucosal surfaces, such as the nasal passages, are the first tissues onto which inhaled or ingested pathogens are deposited. The mucosal tissue includes the mouth, pharynx, and esophagus,

and the gastrointestinal, respiratory, and urogenital tracts.

The immune system has to be regulated to prevent wasteful, unnecessary responses to harmless substances, and more importantly so that it does not attack “self.” The acquired ability to prevent an unnecessary or harmful immune response to a detected foreign substance known not to cause disease is described as immune tolerance. Immune tolerance is crucial for maintaining mucosal homeostasis given the tremendous number of foreign substances (such as food proteins) that APCs of the oral cavity, pharynx, and gastrointestinal mucosa encounter. Immune tolerance is brought about by specialized APCs in the liver, lymph nodes, small intestine, and lung that present harmless antigens to an exceptionally diverse population of regulatory T (T_{reg}) cells, specialized lymphocytes that suppress local inflammation and inhibit the secretion of stimulatory immune factors. The combined result of T_{reg} cells is to prevent immunologic activation and inflammation in undesired tissue compartments and to allow the immune system to focus on pathogens instead. In addition to promoting immune tolerance of harmless antigens, other subsets of T_{reg} cells are involved in the prevention of the autoimmune response, which is an inappropriate immune response to host cells or self-antigens. Another T_{reg} class suppresses immune responses to harmful pathogens after the infection has cleared to minimize host cell damage induced by inflammation and cell lysis.

Immunological Memory

The adaptive immune system possesses a memory component that allows for an efficient and dramatic response upon reinvasion of the same pathogen. Memory is handled by the adaptive immune system with little reliance on cues from the innate response. During the adaptive immune response to a pathogen that has not been encountered before, called a primary response, plasma cells secreting antibodies and differentiated T cells increase, then plateau over time. As B and T cells mature into effector cells, a subset of the naïve populations differentiates into B and T memory cells with the same antigen specificities, as illustrated in Figure **50.3.9**.

A memory cell is an antigen-specific B or T lymphocyte that does not differentiate into effector cells during the primary immune response, but that can immediately become effector cells upon re-exposure to the same pathogen. During the primary immune response, memory cells do not respond to antigens and do not contribute to host defenses. As the infection is cleared and pathogenic stimuli subside, the effectors are no longer needed, and they undergo apoptosis. In contrast, the memory cells persist in the circulation.

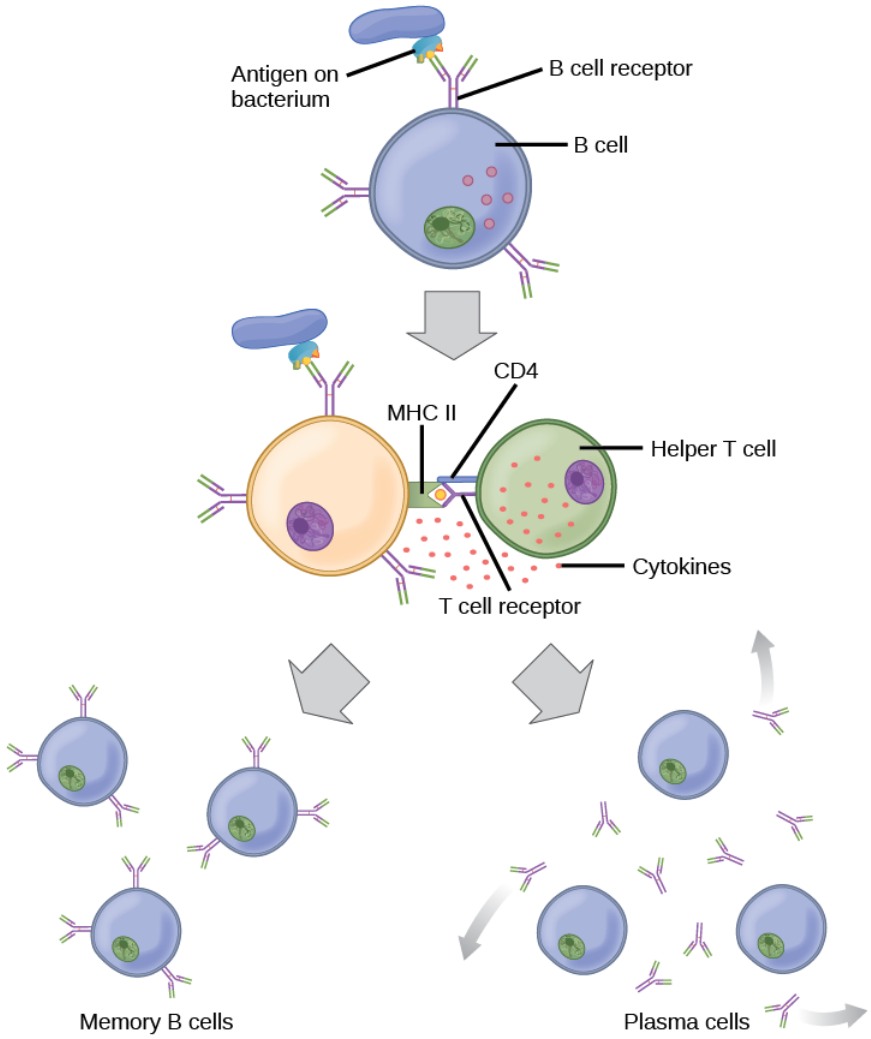


Figure 50.3.9: After initially binding an antigen to the B cell receptor (BCR), a B cell internalizes the antigen and presents it on MHC II. A helper T cell recognizes the MHC II–antigen complex and activates the B cell. As a result, memory B cells and plasma cells are made.

Exercise 50.3.3

The Rh antigen is found on Rh-positive red blood cells. An Rh-negative female can usually carry an Rh-positive fetus to term without difficulty. However, if she has a second Rh-positive fetus, her body may launch an immune attack that causes hemolytic disease of the newborn. Why do you think hemolytic disease is only a problem during the second or subsequent pregnancies?

Answer

If the blood of the mother and fetus mixes, memory cells that recognize the Rh antigen can form late in the first pregnancy. During subsequent pregnancies, these memory cells launch an immune attack on the fetal blood cells. Injection of anti-Rh antibody during the first pregnancy prevents the immune response from occurring.

If the pathogen is never encountered again during the individual's lifetime, B and T memory cells will circulate for a few years or even several decades and will gradually die off, having never functioned as effector cells. However, if the host is re-exposed to the same pathogen type, circulating memory cells will immediately differentiate into plasma cells and CTLs without input from APCs or T_H cells. One reason the adaptive immune response is delayed is because it takes time for naïve B and T cells with the appropriate antigen specificities to be identified and activated. Upon reinfection, this step is skipped, and the result is a more rapid production of immune defenses. Memory B cells that differentiate into plasma cells output tens to hundreds-fold greater antibody

amounts than were secreted during the primary response, as the graph in Figure 50.3.10 illustrates. This rapid and dramatic antibody response may stop the infection before it can even become established, and the individual may not realize they had been exposed.

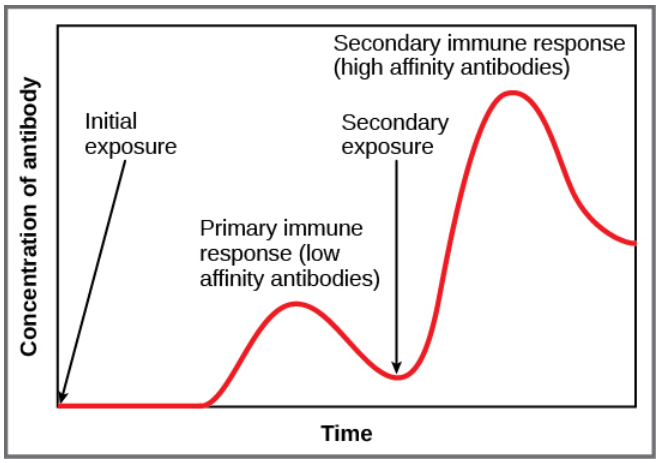


Figure 50.3.10: In the primary response to infection, antibodies are secreted first from plasma cells. Upon re-exposure to the same pathogen, memory cells differentiate into antibody-secreting plasma cells that output a greater amount of antibody for a longer period of time.

Vaccination is based on the knowledge that exposure to noninfectious antigens, derived from known pathogens, generates a mild primary immune response. The immune response to vaccination may not be perceived by the host as illness but still confers immune memory. When exposed to the corresponding pathogen to which an individual was vaccinated, the reaction is similar to a secondary exposure. Because each reinfection generates more memory cells and increased resistance to the pathogen, and because some memory cells die, certain vaccine courses involve one or more booster vaccinations to mimic repeat exposures: for instance, tetanus boosters are necessary every ten years because the memory cells only live that long.

Mucosal Immune Memory

A subset of T and B cells of the mucosal immune system differentiates into memory cells just as in the systemic immune system. Upon reinvasion of the same pathogen type, a pronounced immune response occurs at the mucosal site where the original pathogen deposited, but a collective defense is also organized within interconnected or adjacent mucosal tissue. For instance, the immune memory of an infection in the oral cavity would also elicit a response in the pharynx if the oral cavity was exposed to the same pathogen.

Career Connection: Vaccinologist

Vaccination (or immunization) involves the delivery, usually by injection as shown in Figure 50.3.11, of noninfectious antigen(s) derived from known pathogens. Other components, called adjuvants, are delivered in parallel to help stimulate the immune response. Immunological memory is the reason vaccines work. Ideally, the effect of vaccination is to elicit immunological memory, and thus resistance to specific pathogens without the individual having to experience an infection.



Figure 50.3.11: Vaccines are often delivered by injection into the arm. (credit: U.S. Navy Photographer's Mate Airman Apprentice Christopher D. Blachly)

Vaccinologists are involved in the process of vaccine development from the initial idea to the availability of the completed vaccine. This process can take decades, can cost millions of dollars, and can involve many obstacles along the way. For instance, injected vaccines stimulate the systemic immune system, eliciting humoral and cell-mediated immunity, but have little effect on the mucosal response, which presents a challenge because many pathogens are deposited and replicate in mucosal compartments, and the injection does not provide the most efficient immune memory for these disease agents. For this reason, vaccinologists are actively involved in developing new vaccines that are applied via intranasal, aerosol, oral, or transcutaneous (absorbed through the skin) delivery methods. Importantly, mucosal-administered vaccines elicit both mucosal and systemic immunity and produce the same level of disease resistance as injected vaccines.

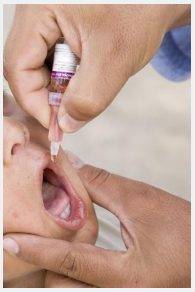


Figure 50.3.12: The polio vaccine can be administered orally. (credit: modification of work by UNICEF Sverige)

Currently, a version of intranasal influenza vaccine is available, and the polio and typhoid vaccines can be administered orally, as shown in Figure 50.3.12. Similarly, the measles and rubella vaccines are being adapted to aerosol delivery using inhalation devices. Eventually, transgenic plants may be engineered to produce vaccine antigens that can be eaten to confer disease resistance. Other vaccines may be adapted to rectal or vaginal application to elicit immune responses in rectal, genitourinary, or reproductive mucosa. Finally, vaccine antigens may be adapted to transdermal application in which the skin is lightly scraped and microneedles are used to pierce the outermost layer. In addition to mobilizing the mucosal immune response, this new generation of vaccines may end the anxiety associated with injections and, in turn, improve patient participation.

Primary Centers of the Immune System

Although the immune system is characterized by circulating cells throughout the body, the regulation, maturation, and intercommunication of immune factors occur at specific sites. The blood circulates immune cells, proteins, and other factors through the body. Approximately 0.1 percent of all cells in the blood are leukocytes, which encompass monocytes (the precursor of macrophages) and lymphocytes. The majority of cells in the blood are erythrocytes (red blood cells). Lymph is a watery fluid that bathes tissues and organs with protective white blood cells and does not contain erythrocytes. Cells of the immune system can travel between the distinct lymphatic and blood circulatory systems, which are separated by interstitial space, by a process called extravasation (passing through to surrounding tissue).

The cells of the immune system originate from hematopoietic stem cells in the bone marrow. Cytokines stimulate these stem cells to differentiate into immune cells. B cell maturation occurs in the bone marrow, whereas naïve T cells transit from the bone marrow to the thymus for maturation. In the thymus, immature T cells that express TCRs complementary to self-antigens are destroyed. This process helps prevent autoimmune responses.

On maturation, T and B lymphocytes circulate to various destinations. Lymph nodes scattered throughout the body, as illustrated in Figure **50.3.13**, house large populations of T and B cells, dendritic cells, and macrophages. Lymph gathers antigens as it drains from tissues. These antigens then are filtered through lymph nodes before the lymph is returned to circulation. APCs in the lymph nodes capture and process antigens and inform nearby lymphocytes about potential pathogens.

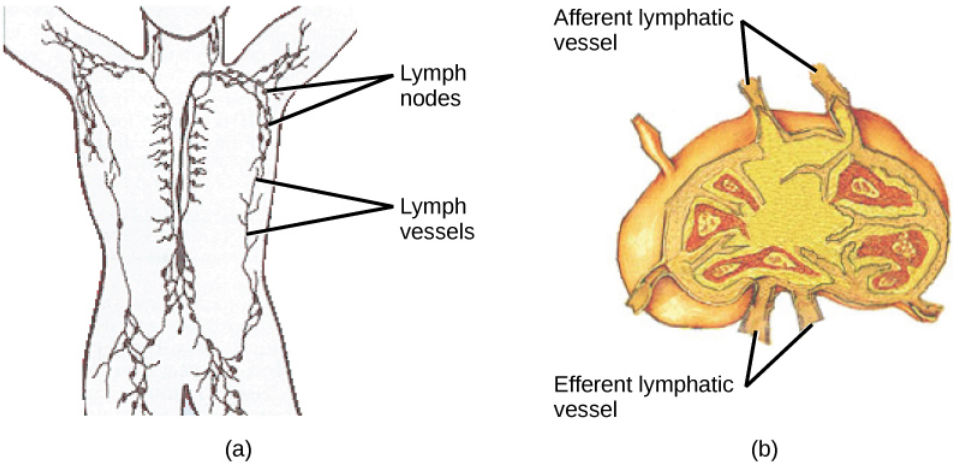


Figure **50.3.13**: (a) Lymphatic vessels carry a clear fluid called lymph throughout the body. The liquid enters (b) lymph nodes through afferent vessels. Lymph nodes are filled with lymphocytes that purge infecting cells. The lymph then exits through efferent vessels. (credit: modification of work by NIH, NCI)

The spleen houses B and T cells, macrophages, dendritic cells, and NK cells. The spleen, shown in Figure **50.3.14**, is the site where APCs that have trapped foreign particles in the blood can communicate with lymphocytes. Antibodies are synthesized and secreted by activated plasma cells in the spleen, and the spleen filters foreign substances and antibody-complexed pathogens from the blood. Functionally, the spleen is to the blood as lymph nodes are to the lymph.

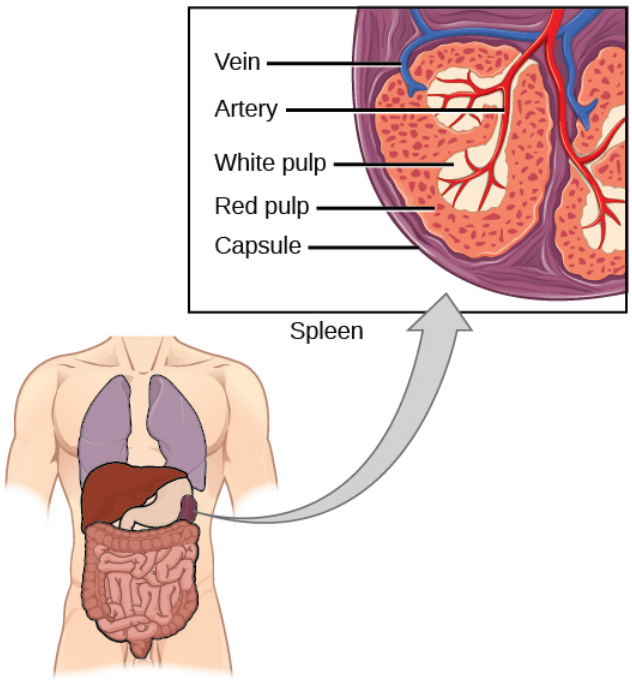


Figure **50.3.14**: The spleen is similar to a lymph node but is much larger and filters blood instead of lymph. Blood enters the spleen through arteries and exits through veins. The spleen contains two types of tissue: red pulp and white pulp. Red pulp consists of cavities that store blood. Within the red pulp, damaged red blood cells are removed and replaced by new ones. White pulp is rich in lymphocytes that remove antigen-coated bacteria from the blood. (credit: modification of work by NCI)

Summary

The adaptive immune response is a slower-acting, longer-lasting, and more specific response than the innate response. However, the adaptive response requires information from the innate immune system to function. APCs display antigens via MHC molecules to complementary naïve T cells. In response, the T cells differentiate and proliferate, becoming T_H cells or CTLs. T_H cells stimulate B cells that have engulfed and presented pathogen-derived antigens. B cells differentiate into plasma cells that secrete antibodies, whereas CTLs induce apoptosis in intracellularly infected or cancerous cells. Memory cells persist after a primary exposure to a pathogen. If re-exposure occurs, memory cells differentiate into effector cells without input from the innate immune system. The mucosal immune system is largely independent from the systemic immune system but functions in a parallel fashion to protect the extensive mucosal surfaces of the body.

Glossary

adaptive immunity
: immunity that has memory and occurs after exposure to an antigen either from a pathogen or a vaccination

antigen
: foreign or “non-self” protein that triggers the immune response

antigen-presenting cell (APC)
: immune cell that detects, engulfs, and informs the adaptive immune response about an infection by presenting the processed antigen on the cell surface

autoimmune response
: inappropriate immune response to host cells or self-antigens

cell-mediated immune response
: adaptive immune response that is carried out by T cells

clonal selection
activation of B cells corresponding to one specific BCR variant and the dramatic proliferation of that variant

cytotoxic T lymphocyte (CTL)
adaptive immune cell that directly kills infected cells via perforin and granzymes, and releases cytokines to enhance the immune response

dendritic cell
immune cell that processes antigen material and presents it on the surface of other cells to induce an immune response

effector cell
lymphocyte that has differentiated, such as a B cell, plasma cell, or cytotoxic T lymphocyte

epitope
small component of an antigen that is specifically recognized by antibodies, B cells, and T cells; the antigenic determinant

helper T lymphocyte (T_H)
cell of the adaptive immune system that binds APCs via MHC II molecules and stimulates B cells or secretes cytokines to initiate the immune response

humoral immune response
adaptive immune response that is controlled by activated B cells and antibodies

immune tolerance
acquired ability to prevent an unnecessary or harmful immune response to a detected foreign body known not to cause disease or to self-antigens

lymph
watery fluid that bathes tissues and organs with protective white blood cells and does not contain erythrocytes

mucosa-associated lymphoid tissue (MALT)
collection of lymphatic tissue that combines with epithelial tissue lining the mucosa throughout the body

memory cell
antigen-specific B or T lymphocyte that does not differentiate into effector cells during the primary immune response but that can immediately become an effector cell upon re-exposure to the same pathogen

plasma cell
immune cell that secrets antibodies; these cells arise from B cells that were stimulated by antigens

regulatory T (T_{reg}) cell
specialized lymphocyte that suppresses local inflammation and inhibits the secretion of cytokines, antibodies, and other stimulatory immune factors; involved in immune tolerance

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50.4: Humoral Immunity and Antibody Production

Skills to Develop

- Explain cross-reactivity
- Describe the structure and function of antibodies
- Discuss antibody production

An antibody, also known as an immunoglobulin (Ig), is a protein that is produced by plasma cells after stimulation by an antigen. Antibodies are the functional basis of humoral immunity. Antibodies occur in the blood, in gastric and mucus secretions, and in breast milk. Antibodies in these bodily fluids can bind pathogens and mark them for destruction by phagocytes before they can infect cells.

Antibody Structure

An antibody molecule is comprised of four polypeptides: two identical heavy chains (large peptide units) that are partially bound to each other in a "Y" formation, which are flanked by two identical light chains (small peptide units), as illustrated in Figure **50.4.1**. Bonds between the cysteine amino acids in the antibody molecule attach the polypeptides to each other. The areas where the antigen is recognized on the antibody are variable domains and the antibody base is composed of constant domains.

In germ-line B cells, the variable region of the light chain gene has 40 variable (V) and five joining (J) segments. An enzyme called DNA recombinase randomly excises most of these segments out of the gene, and splices one V segment to one J segment. During RNA processing, all but one V and J segment are spliced out. Recombination and splicing may result in over 10^6 possible VJ combinations. As a result, each differentiated B cell in the human body typically has a unique variable chain. The constant domain, which does not bind antibody, is the same for all antibodies.

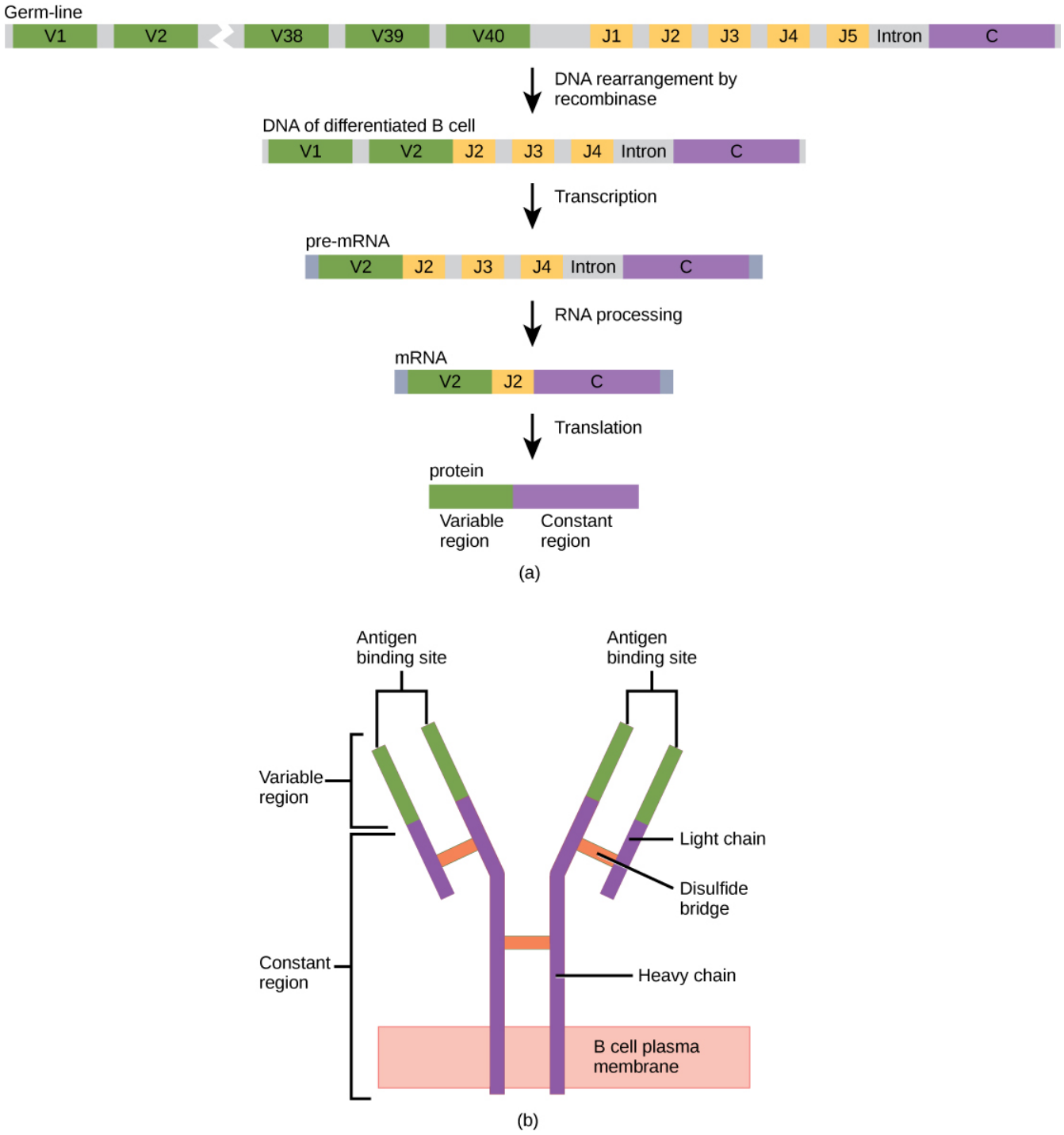


Figure 50.4.1: (a) As a germ-line B cell matures, an enzyme called DNA recombinase randomly excises V and J segments from the light chain gene. Splicing at the mRNA level results in further gene rearrangement. As a result, (b) each antibody has a unique variable region capable of binding a different antigen.

Similar to TCRs and BCRs, antibody diversity is produced by the mutation and recombination of approximately 300 different gene segments encoding the light and heavy chain variable domains in precursor cells that are destined to become B cells. The variable domains from the heavy and light chains interact to form the binding site through which an antibody can bind a specific epitope on an antigen. The numbers of repeated constant domains in Ig classes are the same for all antibodies corresponding to a specific class. Antibodies are structurally similar to the extracellular component of the BCRs, and B cell maturation to plasma cells can be visualized in simple terms as the cell acquires the ability to secrete the extracellular portion of its BCR in large quantities.

Antibody Classes

Antibodies can be divided into five classes—IgM, IgG, IgA, IgD, IgE—based on their physiochemical, structural, and immunological properties. IgGs, which make up about 80 percent of all antibodies, have heavy chains that consist of one variable domain and three identical constant domains. IgA and IgD also have three constant domains per heavy chain, whereas IgM and IgE each have four constant domains per heavy chain. The variable domain determines binding specificity and the constant domain of the heavy chain determines the immunological mechanism of action of the corresponding antibody class. It is possible for two antibodies to have the same binding specificities but be in different classes and, therefore, to be involved in different functions.

After an adaptive defense is produced against a pathogen, typically plasma cells first secrete IgM into the blood. BCRs on naïve B cells are of the IgM class and occasionally IgD class. IgM molecules make up approximately ten percent of all antibodies. Prior to antibody secretion, plasma cells assemble IgM molecules into pentamers (five individual antibodies) linked by a joining (J) chain, as shown in Figure 50.4.1. The pentamer arrangement means that these macromolecules can bind ten identical antigens. However, IgM molecules released early in the adaptive immune response do not bind to antigens as stably as IgGs, which are one of the possible types of antibodies secreted in large quantities upon re-exposure to the same pathogen. Figure 50.4.2 summarizes the properties of immunoglobulins and illustrates their basic structures.

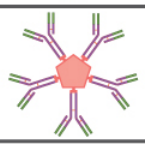
Name	Properties	Structure
IgA	Found in mucous, saliva, tears, and breast milk. Protects against pathogens.	
IgD	Part of the B cell receptor. Activates basophils and mast cells.	
IgE	Protects against parasitic worms. Responsible for allergic reactions.	
IgG	Secreted by plasma cells in the blood. Able to cross the placenta into the fetus.	
IgM	May be attached to the surface of a B cell or secreted into the blood. Responsible for early stages of immunity.	

Figure 50.4.2: Immunoglobulins have different functions, but all are composed of light and heavy chains that form a Y-shaped structure.

IgAs populate the saliva, tears, breast milk, and mucus secretions of the gastrointestinal, respiratory, and genitourinary tracts. Collectively, these bodily fluids coat and protect the extensive mucosa (4000 square feet in humans). The total number of IgA molecules in these bodily secretions is greater than the number of IgG molecules in the blood serum. A small amount of IgA is also secreted into the serum in monomeric form. Conversely, some IgM is secreted into bodily fluids of the mucosa. Similar to IgM, IgA molecules are secreted as polymeric structures linked with a J chain. However, IgAs are secreted mostly as dimeric molecules, not pentamers.

IgE is present in the serum in small quantities and is best characterized in its role as an allergy mediator. IgD is also present in small quantities. Similar to IgM, BCRs of the IgD class are found on the surface of naïve B cells. This class supports antigen recognition and maturation of B cells to plasma cells.

Antibody Functions

Differentiated plasma cells are crucial players in the humoral response, and the antibodies they secrete are particularly significant against extracellular pathogens and toxins. Antibodies circulate freely and act independently of plasma cells. Antibodies can be transferred from one individual to another to temporarily protect against infectious disease. For instance, a person who has recently produced a successful immune response against a particular disease agent can donate blood to a nonimmune recipient and confer temporary immunity through antibodies in the donor's blood serum. This phenomenon is called passive immunity; it also occurs naturally during breastfeeding, which makes breastfed infants highly resistant to infections during the first few months of life.

Antibodies coat extracellular pathogens and neutralize them, as illustrated in Figure **50.4.3**, by blocking key sites on the pathogen that enhance their infectivity (such as receptors that "dock" pathogens on host cells). Antibody neutralization can prevent pathogens from entering and infecting host cells, as opposed to the CTL-mediated approach of killing cells that are already infected to prevent progression of an established infection. The neutralized antibody-coated pathogens can then be filtered by the spleen and eliminated in urine or feces.

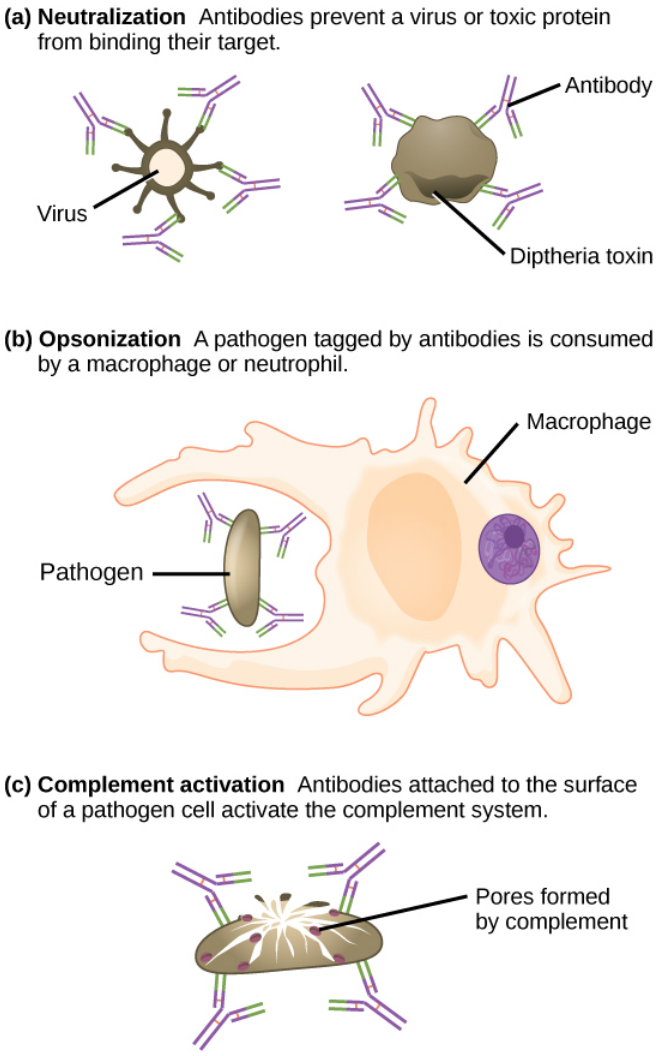


Figure **50.4.3**: Antibodies may inhibit infection by (a) preventing the antigen from binding its target, (b) tagging a pathogen for destruction by macrophages or neutrophils, or (c) activating the complement cascade.

Antibodies also mark pathogens for destruction by phagocytic cells, such as macrophages or neutrophils, because phagocytic cells are highly attracted to macromolecules complexed with antibodies. Phagocytic enhancement by antibodies is called opsonization. In a process called complement fixation, IgM and IgG in serum bind to antigens and provide docking sites onto which sequential complement proteins can bind. The combination of antibodies and complement enhances opsonization even further and promotes rapid clearing of pathogens.

Affinity, Avidity, and Cross Reactivity

Not all antibodies bind with the same strength, specificity, and stability. In fact, antibodies exhibit different affinities (attraction) depending on the molecular complementarity between antigen and antibody molecules, as illustrated in Figure 50.4.4. An antibody with a higher affinity for a particular antigen would bind more strongly and stably, and thus would be expected to present a more challenging defense against the pathogen corresponding to the specific antigen.

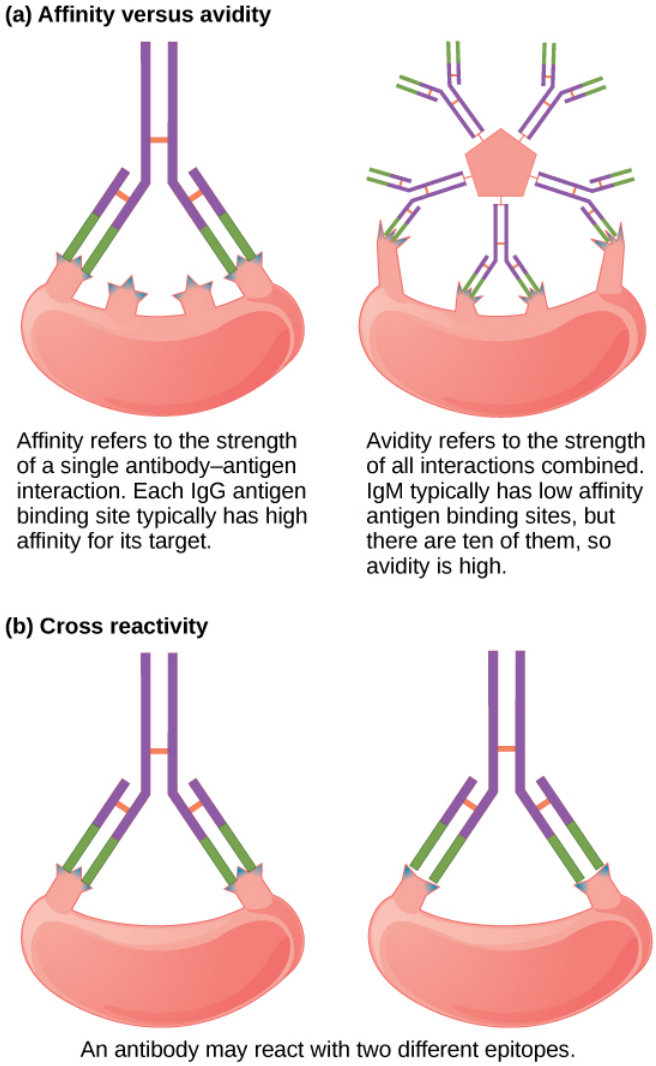


Figure 50.4.4: (a) Affinity refers to the strength of single interaction between antigen and antibody, while avidity refers to the strength of all interactions combined. (b) An antibody may cross react with different epitopes.

The term avidity describes binding by antibody classes that are secreted as joined, multivalent structures (such as IgM and IgA). Although avidity measures the strength of binding, just as affinity does, the avidity is not simply the sum of the affinities of the antibodies in a multimeric structure. The avidity depends on the number of identical binding sites on the antigen being detected, as well as other physical and chemical factors. Typically, multimeric antibodies, such as pentameric IgM, are classified as having lower affinity than monomeric antibodies, but high avidity. Essentially, the fact that multimeric antibodies can bind many antigens simultaneously balances their slightly lower binding strength for each antibody/antigen interaction.

Antibodies secreted after binding to one epitope on an antigen may exhibit cross reactivity for the same or similar epitopes on different antigens. Because an epitope corresponds to such a small region (the surface area of about four to six amino acids), it is possible for different macromolecules to exhibit the same molecular identities and orientations over short regions. Cross reactivity describes when an antibody binds not to the antigen that elicited its synthesis and secretion, but to a different antigen.

Cross reactivity can be beneficial if an individual develops immunity to several related pathogens despite having only been exposed to or vaccinated against one of them. For instance, antibody cross reactivity may occur against the similar surface structures of various Gram-negative bacteria. Conversely, antibodies raised against pathogenic molecular components that resemble self molecules may incorrectly mark host cells for destruction and cause autoimmune damage. Patients who develop systemic lupus erythematosus (SLE) commonly exhibit antibodies that react with their own DNA. These antibodies may have been initially raised against the nucleic acid of microorganisms but later cross-reacted with self-antigens. This phenomenon is also called molecular mimicry.

Antibodies of the Mucosal Immune System

Antibodies synthesized by the mucosal immune system include IgA and IgM. Activated B cells differentiate into mucosal plasma cells that synthesize and secrete dimeric IgA, and to a lesser extent, pentameric IgM. Secreted IgA is abundant in tears, saliva, breast milk, and in secretions of the gastrointestinal and respiratory tracts. Antibody secretion results in a local humoral response at epithelial surfaces and prevents infection of the mucosa by binding and neutralizing pathogens.

Summary

Antibodies (immunoglobulins) are the molecules secreted from plasma cells that mediate the humoral immune response. There are five antibody classes; an antibody's class determines its mechanism of action and production site but does not control its binding specificity. Antibodies bind antigens via variable domains and can either neutralize pathogens or mark them for phagocytosis or activate the complement cascade.

Glossary

affinity
: attraction of molecular complementarity between antigen and antibody molecules

antibody
: protein that is produced by plasma cells after stimulation by an antigen; also known as an immunoglobulin

avidity
: total binding strength of a multivalent antibody with antigen

cross reactivity
: binding of an antibody to an epitope corresponding to an antigen that is different from the one the antibody was raised against

passive immunity
: transfer of antibodies from one individual to another to provide temporary protection against pathogens

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50.5: Autoimmunity and Hypersensitivity

Skills to Develop

- Describe hypersensitivity
- Define autoimmunity

A functioning immune system is essential for survival, but even the sophisticated cellular and molecular defenses of the mammalian immune response can be defeated by pathogens at virtually every step. In the competition between immune protection and pathogen evasion, pathogens have the advantage of more rapid evolution because of their shorter generation time and other characteristics. For instance, *Streptococcus pneumoniae* (bacterium that cause pneumonia and meningitis) surrounds itself with a capsule that inhibits phagocytes from engulfing it and displaying antigens to the adaptive immune system. *Staphylococcus aureus* (bacterium that can cause skin infections, abscesses, and meningitis) synthesizes a toxin called leukocidin that kills phagocytes after they engulf the bacterium. Other pathogens can also hinder the adaptive immune system. HIV infects T_H cells via their CD4 surface molecules, gradually depleting the number of T_H cells in the body; this inhibits the adaptive immune system's capacity to generate sufficient responses to infection or tumors. As a result, HIV-infected individuals often suffer from infections that would not cause illness in people with healthy immune systems but which can cause devastating illness to immune-compromised individuals. Maladaptive responses of immune cells and molecules themselves can also disrupt the proper functioning of the entire system, leading to host cell damage that could become fatal.

Immunodeficiency

Failures, insufficiencies, or delays at any level of the immune response can allow pathogens or tumor cells to gain a foothold and replicate or proliferate to high enough levels that the immune system becomes overwhelmed. Immunodeficiency is the failure, insufficiency, or delay in the response of the immune system, which may be acquired or inherited. Immunodeficiency can be acquired as a result of infection with certain pathogens (such as HIV), chemical exposure (including certain medical treatments), malnutrition, or possibly by extreme stress. For instance, radiation exposure can destroy populations of lymphocytes and elevate an individual's susceptibility to infections and cancer. Dozens of genetic disorders result in immunodeficiencies, including Severe Combined Immunodeficiency (SCID), Bare lymphocyte syndrome, and MHC II deficiencies. Rarely, primary immunodeficiencies that are present from birth may occur. Neutropenia is one form in which the immune system produces a below-average number of neutrophils, the body's most abundant phagocytes. As a result, bacterial infections may go unrestricted in the blood, causing serious complications.

Hypersensitivities

Maladaptive immune responses toward harmless foreign substances or self antigens that occur after tissue sensitization are termed hypersensitivities. The types of hypersensitivities include immediate, delayed, and autoimmunity. A large proportion of the population is affected by one or more types of hypersensitivity.

Allergies

The immune reaction that results from immediate hypersensitivities in which an antibody-mediated immune response occurs within minutes of exposure to a harmless antigen is called an allergy. In the United States, 20 percent of the population exhibits symptoms of allergy or asthma, whereas 55 percent test positive against one or more allergens. Upon initial exposure to a potential allergen, an allergic individual synthesizes antibodies of the IgE class via the typical process of APCs presenting processed antigen to T_H cells that stimulate B cells to produce IgE. This class of antibodies also mediates the immune response to parasitic worms. The constant domain of the IgE molecules interact with mast cells embedded in connective tissues. This process primes, or sensitizes, the tissue. Upon subsequent exposure to the same allergen, IgE molecules on mast cells bind the antigen via their variable domains and stimulate the mast cell to release the modified amino acids histamine and serotonin; these chemical mediators then recruit eosinophils which mediate allergic responses. Figure 50.5.1 shows an example of an allergic response to ragweed pollen. The effects of an allergic reaction range from mild symptoms like sneezing and itchy, watery eyes to more severe or even life-threatening reactions involving intensely itchy welts or hives, airway contraction with severe respiratory distress, and plummeting

blood pressure. This extreme reaction is known as anaphylactic shock. If not treated with epinephrine to counter the blood pressure and breathing effects, this condition can be fatal.

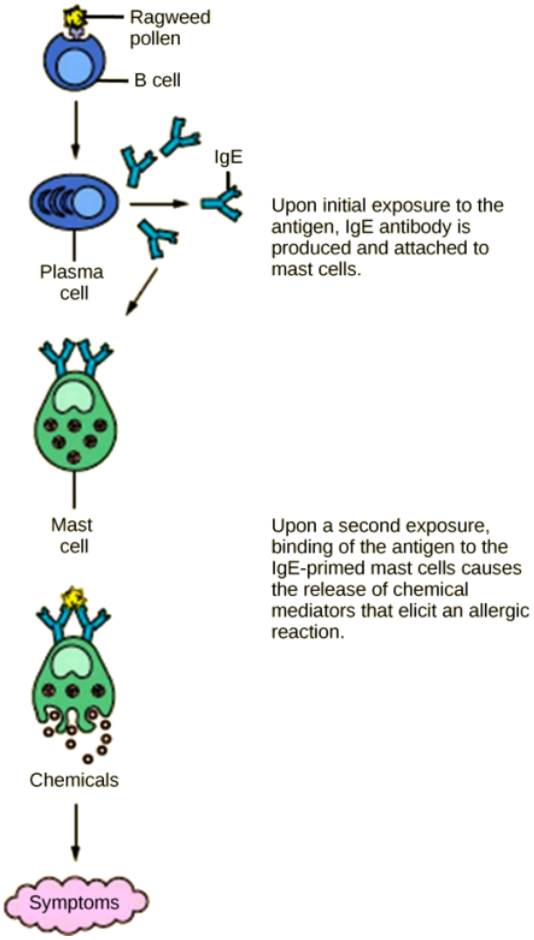


Figure **50.5.1**: On first exposure to an allergen, an IgE antibody is synthesized by plasma cells in response to a harmless antigen. The IgE molecules bind to mast cells, and on secondary exposure, the mast cells release histamines and other modulators that affect the symptoms of allergy. (credit: modification of work by NIH)

Delayed hypersensitivity is a cell-mediated immune response that takes approximately one to two days after secondary exposure for a maximal reaction to be observed. This type of hypersensitivity involves the T_H1 cytokine-mediated inflammatory response and may manifest as local tissue lesions or contact dermatitis (rash or skin irritation). Delayed hypersensitivity occurs in some individuals in response to contact with certain types of jewelry or cosmetics. Delayed hypersensitivity facilitates the immune response to poison ivy and is also the reason why the skin test for tuberculosis results in a small region of inflammation on individuals who were previously exposed to *Mycobacterium tuberculosis*. That is also why cortisone is used to treat such responses: it will inhibit cytokine production.

Autoimmunity

Autoimmunity is a type of hypersensitivity to self antigens that affects approximately five percent of the population. Most types of autoimmunity involve the humoral immune response. Antibodies that inappropriately mark self components as foreign are termed autoantibodies. In patients with the autoimmune disease myasthenia gravis, muscle cell receptors that induce contraction in response to acetylcholine are targeted by antibodies. The result is muscle weakness that may include marked difficultly with fine and/or gross motor functions. In systemic lupus erythematosus, a diffuse autoantibody response to the individual's own DNA and proteins results in various systemic diseases. As illustrated in Figure **50.5.2**, systemic lupus erythematosus may affect the heart, joints, lungs, skin, kidneys, central nervous system, or other tissues, causing tissue damage via antibody binding, complement recruitment, lysis, and inflammation.

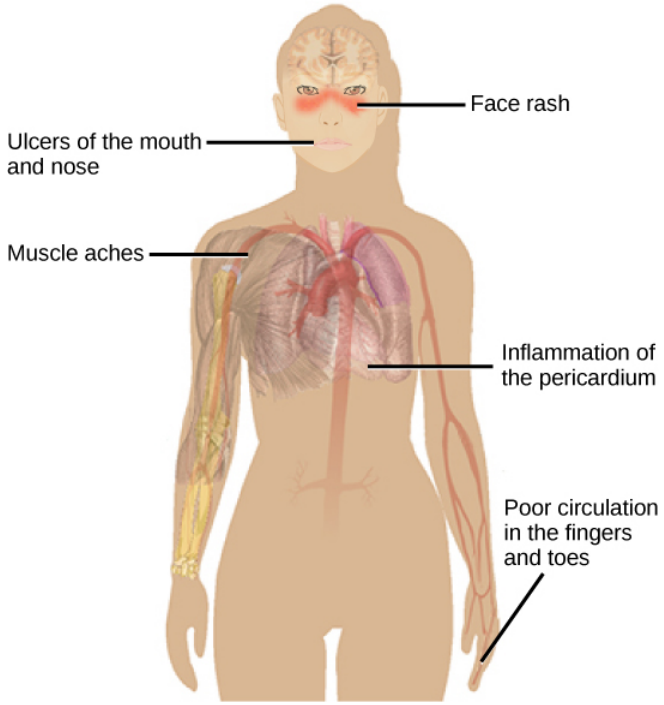


Figure **50.5.2**: Systemic lupus erythematosus is characterized by autoimmunity to the individual's own DNA and/or proteins, which leads to varied dysfunction of the organs. (credit: modification of work by Mikael Häggström)

Autoimmunity can develop with time, and its causes may be rooted in molecular mimicry. Antibodies and TCRs may bind self antigens that are structurally similar to pathogen antigens, which the immune receptors first raised. As an example, infection with *Streptococcus pyogenes* (bacterium that causes strep throat) may generate antibodies or T cells that react with heart muscle, which has a similar structure to the surface of *S. pyogenes*. These antibodies can damage heart muscle with autoimmune attacks, leading to rheumatic fever. Insulin-dependent (Type 1) diabetes mellitus arises from a destructive inflammatory T_H1 response against insulin-producing cells of the pancreas. Patients with this autoimmunity must be injected with insulin that originates from other sources.

Summary

Immune disruptions may involve insufficient immune responses or inappropriate immune targets. Immunodeficiency increases an individual's susceptibility to infections and cancers. Hypersensitivities are misdirected responses either to harmless foreign particles, as in the case of allergies, or to host factors, as in the case of autoimmunity. Reactions to self components may be the result of molecular mimicry.

Glossary

allergy
: immune reaction that results from immediate hypersensitivities in which an antibody-mediated immune response occurs within minutes of exposure to a harmless antigen

autoantibody
: antibody that incorrectly marks "self" components as foreign and stimulates the immune response

autoimmunity
: type of hypersensitivity to self antigens

hypersensitivities
: spectrum of maladaptive immune responses toward harmless foreign particles or self antigens; occurs after tissue sensitization and includes immediate-type (allergy), delayed-type, and autoimmunity

immunodeficiency

failure, insufficiency, or delay at any level of the immune system, which may be acquired or inherited

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CHAPTER OVERVIEW

50.6: Antibodies in Medical Treatment and Diagnosis

Many laboratory tests are designed to confirm a presumptive diagnosis by detecting antibodies specific to a suspected pathogen. Unfortunately, many such tests are time-consuming and expensive. That is now changing, however, with the development of new, miniaturized technologies that are fast and inexpensive. For example, researchers at Columbia University are developing a "lab-on-a-chip" technology that will test a single drop of blood for 15 different infectious diseases, including HIV and syphilis, in a matter of minutes.[1] The blood is pulled through tiny capillaries into reaction chambers where the patient's antibodies mix with reagents. A chip reader that attaches to a cell phone analyzes the results and sends them to the patient's healthcare provider. Currently the device is being field tested in Rwanda to check pregnant women for chronic diseases. Researchers estimate that the chip readers will sell for about $100 and individual chips for $1.[2]

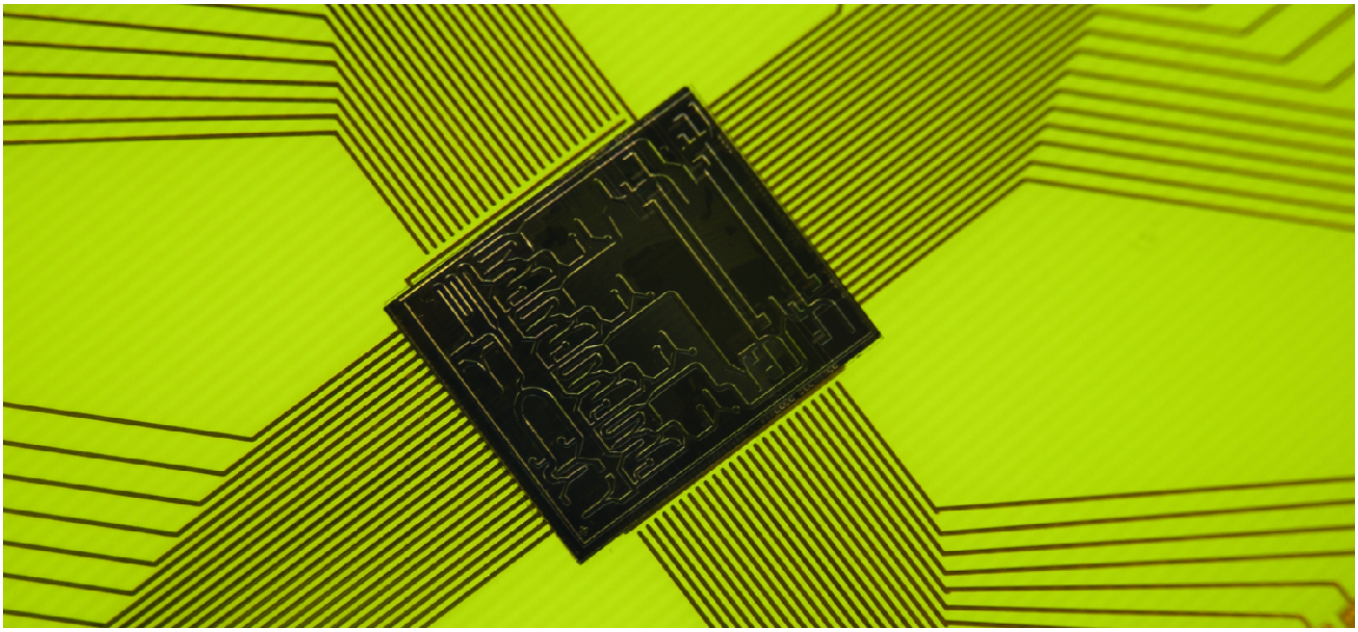


Figure **50.6.1**: Lab-on-a-chip technology allows immunological assays to be miniaturized so tests can be done rapidly with minimum quantities of expensive reagents. The chips contain tiny flow tubes to allow movement of fluids by capillary action, reactions sites with embedded reagents, and data output through electronic sensors. (credit: modification of work by Maggie Bartlett, NHGRI)

50.6.1: Practical Applications of Monoclonal and Polyclonal Antibodies

50.6.2: Detecting Antigen-Antibody Complexes in vitro

50.6.3: Agglutination Assays

50.6.4: Fluorescent Auto-Antibody Techniques

Footnotes

1. 1 Chin, Curtis D. et al., "Mobile Device for Disease Diagnosis and Data Tracking in Resource-Limited Settings," *Clinical Chemistry* 59, no. 4 (2013): 629-40.
2. 2 Evarts, H., "Fast, Low-Cost Device Uses the Cloud to Speed Up Testing for HIV and More," January 24, 2013. Accessed July 14, 2016. http://engineering.columbia.edu/fast...g-hiv-and-more.

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50.6.1: Practical Applications of Monoclonal and Polyclonal Antibodies

Learning Objectives

- Compare the method of development, use, and characteristics of monoclonal and polyclonal antibodies
- Explain the nature of antibody cross-reactivity and why this is less of a problem with monoclonal antibodies

Clinical Focus: Part 1

In an unfortunate incident, a healthcare worker struggling with addiction was caught stealing syringes of painkillers and replacing them with syringes filled with unknown substances. The hospital immediately fired the employee and had him arrested; however, two patients that he had worked with later tested positive for HIV.

While there was no proof that the infections originated from the tainted syringes, the hospital's public health physician took immediate steps to determine whether any other patients had been put at risk. Although the worker had only been employed for a short time, it was determined that he had come into contact with more than 1300 patients. The hospital decided to contact all of these patients and have them tested for HIV.

Exercise 50.6.1.1

1. Why does the hospital feel it is necessary to test every patient for HIV?
2. What types of tests can be used to determine if a patient has HIV?

In addition to being crucial for our normal immune response, antibodies provide powerful tools for research and diagnostic purposes. The high specificity of antibodies makes them an excellent tool for detecting and quantifying a broad array of targets, from drugs to serum proteins to microorganisms. With *in vitro* assays, antibodies can be used to precipitate soluble antigens, agglutinate (clump) cells, opsonize and kill bacteria with the assistance of complement, and neutralize drugs, toxins, and viruses.

An antibody's specificity results from the antigen-binding site formed within the variable regions—regions of the antibody that have unique patterns of amino acids that can only bind to target antigens with a molecular sequence that provides complementary charges and noncovalent bonds. There are limitations to antibody specificity, however. Some antigens are so chemically similar that cross-reactivity occurs; in other words, antibodies raised against one antigen bind to a chemically similar but different antigen. Consider an antigen that consists of a single protein with multiple epitopes (Figure 50.6.1.1). This single protein may stimulate the production of many different antibodies, some of which may bind to chemically identical epitopes on other proteins.

Cross-reactivity is more likely to occur between antibodies and antigens that have low affinity or avidity. Affinity, which can be determined experimentally, is a measure of the binding strength between an antibody's binding site and an epitope, whereas avidity is the total strength of all the interactions in an antibody-antigen complex (which may have more than one bonding site). Avidity is influenced by affinity as well as the structural arrangements of the epitope and the variable regions of the antibody. If an antibody has a high affinity/avidity for a specific antigen, it is less likely to cross-react with an antigen for which it has a lower affinity/avidity.

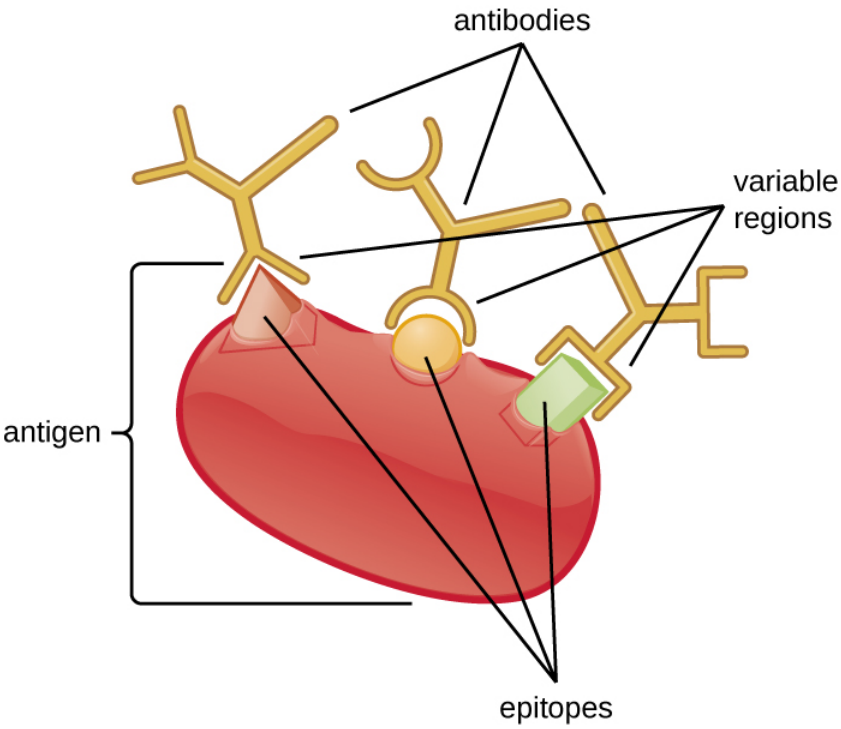


Figure **50.6.1.1**: An antibody binds to a specific region on an antigen called an epitope. A single antigen can have multiple epitopes for different, specific antibodies.

? Exercise 50.6.1.2

1. What property makes antibodies useful for research and clinical diagnosis?
2. What is cross-reactivity and why does it occur?

Producing Polyclonal Antibodies

Antibodies used for research and diagnostic purposes are often obtained by injecting a lab animal such as a rabbit or a goat with a specific antigen. Within a few weeks, the animal's immune system will produce high levels of antibodies specific for the antigen. These antibodies can be harvested in an antiserum, which is whole serum collected from an animal following exposure to an antigen. Because most antigens are complex structures with multiple epitopes, they result in the production of multiple antibodies in the lab animal. This so-called polyclonal antibody response is also typical of the response to infection by the human immune system. Antiserum drawn from an animal will thus contain antibodies from multiple clones of B cells, with each B cell responding to a specific epitope on the antigen (Figure **50.6.1.2**).

Lab animals are usually injected at least twice with antigen when being used to produce antiserum. The second injection will activate memory cells that make class IgG antibodies against the antigen. The memory cells also undergo affinity maturation, resulting in a pool of antibodies with higher average affinity. Affinity maturation occurs because of mutations in the immunoglobulin gene variable regions, resulting in B cells with slightly altered antigen-binding sites. On re-exposure to the antigen, those B cells capable of producing antibody with higher affinity antigen-binding sites will be stimulated to proliferate and produce more antibody than their lower-affinity peers. An adjuvant, which is a chemical that provokes a generalized activation of the immune system that stimulates greater antibody production, is often mixed with the antigen prior to injection.

Antiserum obtained from animals will not only contain antibodies against the antigen artificially introduced in the laboratory, but it will also contain antibodies to any other antigens to which the animal has been exposed during its lifetime. For this reason, antisera must first be "purified" to remove other antibodies before using the antibodies for research or diagnostic assays.

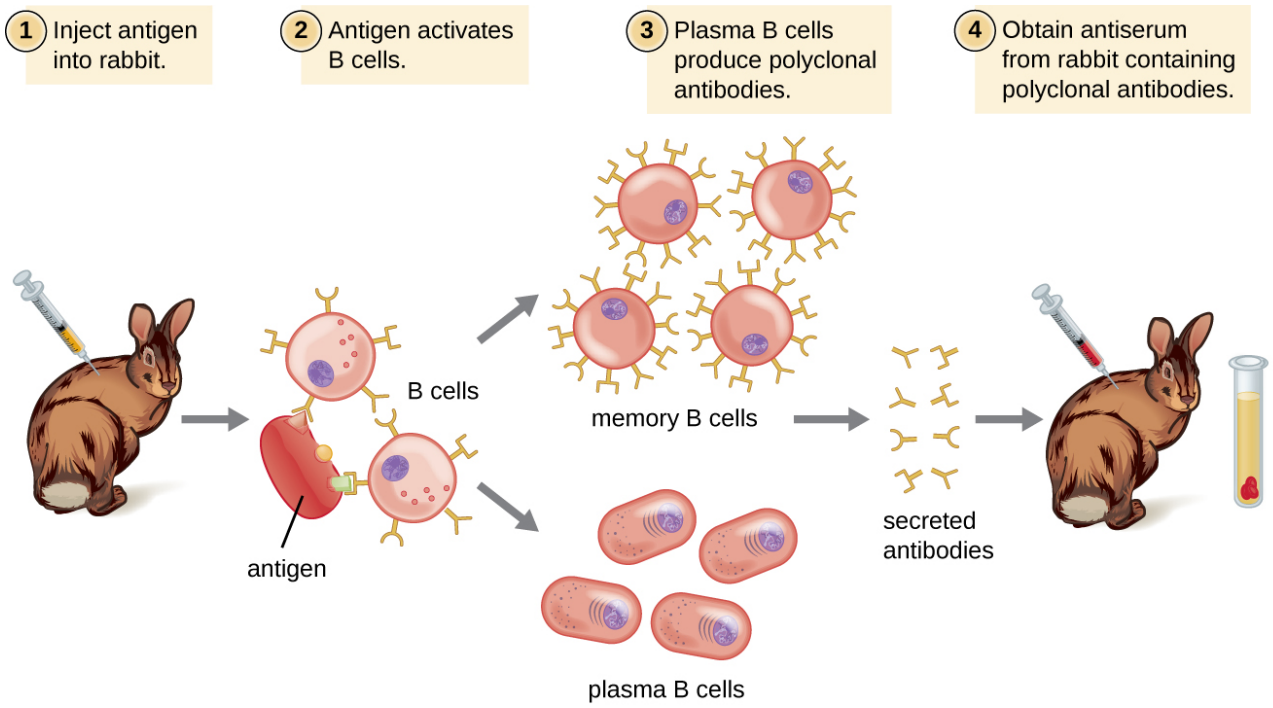


Figure **50.6.1.2**: This diagram illustrates the process for harvesting polyclonal antibodies produced in response to an antigen.

Clinical Uses of Polyclonal Antisera

Polyclonal antisera are used in many clinical tests that are designed to determine whether a patient is producing antibodies in response to a particular pathogen. While these tests are certainly powerful diagnostic tools, they have their limitations, because they are an indirect means of determining whether a particular pathogen is present. Tests based on a polyclonal response can sometimes lead to a false-positive result—in other words, a test that confirms the presence of an antigen that is, in fact, not present. Antibody-based tests can also result in a false-negative result, which occurs when the test fails to detect an antibody that is, in fact, present.

The accuracy of antibody tests can be described in terms of test sensitivity and test specificity. Test sensitivity is the probability of getting a positive test result when the patient is indeed infected. If a test has high sensitivity, the probability of a false negative is low. Test specificity, on the other hand, is the probability of getting a negative test result when the patient is not infected. If a test has high specificity, the probability of a false positive is low.

False positives often occur due to cross-reactivity, which can occur when epitopes from a different pathogen are similar to those found on the pathogen being tested for. For this reason, antibody-based tests are often used only as screening tests; if the results are positive, other confirmatory tests are used to make sure that the results were not a false positive.

For example, a blood sample from a patient suspected of having hepatitis C can be screened for the virus using antibodies that bind to antigens on hepatitis C virus. If the patient is indeed infected with hepatitis C virus, the antibodies will bind to the antigens, yielding a positive test result. If the patient is not infected with hepatitic C virus, the antibodies will generally not bind to anything and the test should be negative; however, a false positive may occur if the patient has been previously infected by any of a variety of pathogens that elicit antibodies that cross-react with the hepatitis C virus antigens. Antibody tests for hepatitis C have high sensitivity (a low probability of a false negative) but low specificity (a high probability of a false positive). Thus, patients who test positive must have a second, confirmatory test to rule out the possibility of a false positive. The confirmatory test is a more expensive and time-consuming test that directly tests for the presence of hepatitis C viral RNA in the blood. Only after the confirmatory test comes back positive can the patient be definitively diagnosed with a hepatitis C infection. Antibody-based tests can result in a false negative if, for any reason, the patient's immune system has not produced detectable levels of antibodies. For some diseases, it may take several weeks following infection before the immune system produces enough antibodies to cross the detection threshold of the assay. In immunocompromised patients, the immune system may not be capable of producing a detectable level of antibodies.

Another limitation of using antibody production as an indicator of disease is that antibodies in the blood will persist long after the infection has been cleared. Depending on the type of infection, antibodies will be present for many months; sometimes, they may be present for the remainder of the patient's life. Thus, a positive antibody-based test only means that the patient was infected at some point in time; it does not prove that the infection is active.

In addition to their role in diagnosis, polyclonal antisera can activate complement, detect the presence of bacteria in clinical and food industry settings, and perform a wide array of precipitation reactions that can detect and quantify serum proteins, viruses, or other antigens. However, with the many specificities of antibody present in a polyclonal antiserum, there is a significant likelihood that the antiserum will cross-react with antigens to which the individual was never exposed. Therefore, we must always account for the possibility of false-positive results when working with a polyclonal antiserum.

? Exercise 50.6.1.3

1. What is a false positive and what are some reasons that false positives occur?
2. What is a false negative and what are some reasons that false positives occur?
3. If a patient tests negative on a highly sensitive test, what is the likelihood that the person is infected with the pathogen?

Producing Monoclonal Antibodies

Some types of assays require better antibody specificity and affinity than can be obtained using a polyclonal antiserum. To attain this high specificity, all of the antibodies must bind with high affinity to a single epitope. This high specificity can be provided by monoclonal antibodies (mAbs). Table **50.6.1.1** compares some of the important characteristics of monoclonal and polyclonal antibodies.

Unlike polyclonal antibodies, which are produced in live animals, monoclonal antibodies are produced *in vitro* using tissue-culture techniques. mAbs are produced by immunizing an animal, often a mouse, multiple times with a specific antigen. B cells from the spleen of the immunized animal are then removed. Since normal B cells are unable to proliferate forever, they are fused with immortal, cancerous B cells called myeloma cells, to yield hybridoma cells. All of the cells are then placed in a selective medium that allows only the hybridomas to grow; unfused myeloma cells cannot grow, and any unfused B cells die off. The hybridomas, which are capable of growing continuously in culture while producing antibodies, are then screened for the desired mAb. Those producing the desired mAb are grown in tissue culture; the culture medium is harvested periodically and mAbs are purified from the medium. This is a very expensive and time-consuming process. It may take weeks of culturing and many liters of media to provide enough mAbs for an experiment or to treat a single patient. mAbs are expensive (Figure **50.6.1.3**).

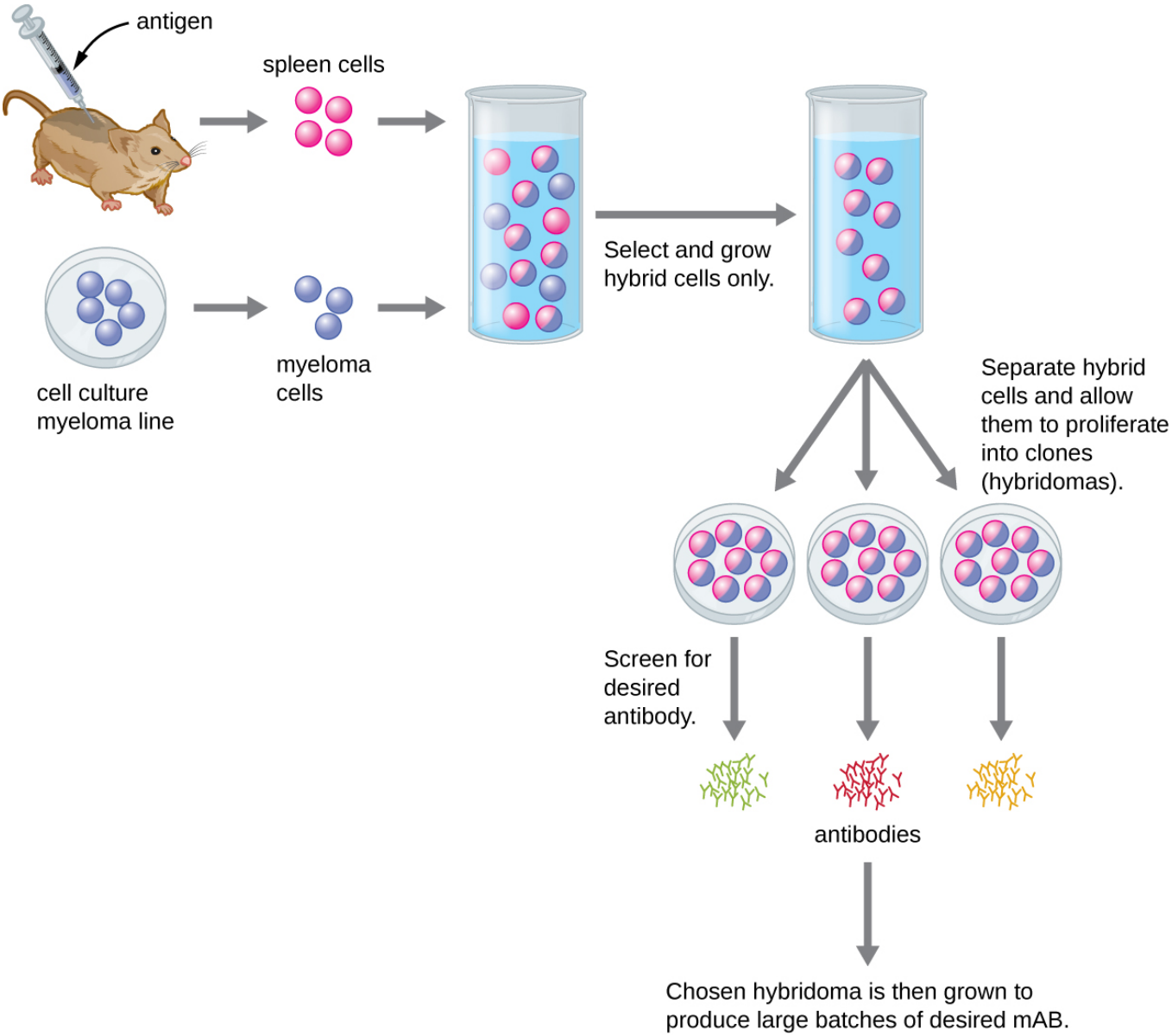


Figure **50.6.1.3**: Monoclonal antibodies (mAbs) are produced by introducing an antigen to a mouse and then fusing polyclonal B cells from the mouse's spleen to myeloma cells. The resulting hybridoma cells are cultured and continue to produce antibodies to the antigen. Hybridomas producing the desired mAb are then grown in large numbers on a selective medium that is periodically harvested to obtain the desired mAbs.

Table **50.6.1.1**: Characteristics of Polyclonal and Monoclonal Antibodies

Monoclonal Antibodies	Polyclonal Antibodies
Expensive production	Inexpensive production
Long production time	Rapid production
Large quantities of specific antibodies	Large quantities of nonspecific antibodies
Recognize a single epitope on an antigen	Recognize multiple epitopes on an antigen
Production is continuous and uniform once the hybridoma is made	Different batches vary in composition

Clinical Uses of Monoclonal Antibodies

Since the most common methods for producing monoclonal antibodies use mouse cells, it is necessary to create humanized monoclonal antibodies for human clinical use. Mouse antibodies cannot be injected repeatedly into humans, because the immune system will recognize them as being foreign and will respond to them with neutralizing antibodies. This problem can be minimized by genetically engineering the antibody in the mouse B cell. The variable regions of the mouse light and heavy chain genes are ligated to human constant regions, and the chimeric gene is then transferred into a host cell. This allows production of a mAb that is mostly "human" with only the antigen-binding site being of mouse origin.

Humanized mAbs have been successfully used to treat cancer with minimal side effects. For example, the humanized monoclonal antibody drug Herceptin has been helpful for the treatment of some types of breast cancer. There have also been a few preliminary trials of humanized mAb for the treatment of infectious diseases, but none of these treatments are currently in use. In some cases, mAbs have proven too specific to treat infectious diseases, because they recognize some serovars of a pathogen but not others. Using a cocktail of multiple mAbs that target different strains of the pathogen can address this problem. However, the great cost associated with mAb production is another challenge that has prevented mAbs from becoming practical for use in treating microbial infections.[1]

One promising technology for inexpensive mAbs is the use of genetically engineered plants to produce antibodies (or plantibodies). This technology transforms plant cells into antibody factories rather than relying on tissue culture cells, which are expensive and technically demanding. In some cases, it may even be possible to deliver these antibodies by having patients eat the plants rather than by extracting and injecting the antibodies. For example, in 2013, a research group cloned antibody genes into plants that had the ability to neutralize an important toxin from bacteria that can cause severe gastrointestinal disease.[2] Eating the plants could potentially deliver the antibodies directly to the toxin.

? Exercise 50.6.1.4

1. How are humanized monoclonal antibodies produced?
2. What does the "monoclonal" of monoclonal antibodies mean?

Using Monoclonal Antibodies to Combat Ebola

During the 2014–2015 Ebola outbreak in West Africa, a few Ebola-infected patients were treated with ZMapp, a drug that had been shown to be effective in trials done in rhesus macaques only a few months before.[3] ZMapp is a combination of three mAbs produced by incorporating the antibody genes into tobacco plants using a viral vector. By using three mAbs, the drug is effective across multiple strains of the virus. Unfortunately, there was only enough ZMapp to treat a tiny number of patients.

While the current technology is not adequate for producing large quantities of ZMapp, it does show that plantibodies—plant-produced mAbs—are feasible for clinical use, potentially cost effective, and worth further development. The last several years have seen an explosion in the number of new mAb-based drugs for the treatment of cancer and infectious diseases; however, the widespread use of such drugs is currently inhibited by their exorbitant cost, especially in underdeveloped parts of the world, where a single dose might cost more than the patient's lifetime income. Developing methods for cloning antibody genes into plants could reduce costs dramatically.

Key Concepts and Summary

- Antibodies bind with high **specificity** to antigens used to challenge the immune system, but they may also show **cross-reactivity** by binding to other antigens that share chemical properties with the original antigen.
- Injection of an antigen into an animal will result in a **polyclonal antibody** response in which different antibodies are produced that react with the various epitopes on the antigen.
- **Polyclonal antisera** are useful for some types of laboratory assays, but other assays require more specificity. Diagnostic tests that use polyclonal antisera are typically only used for screening because of the possibility of **false-positive** and **false-negative** results.
- **Monoclonal antibodies** provide higher specificity than polyclonal antisera because they bind to a single epitope and usually have high **affinity**.

- Monoclonal antibodies are typically produced by culturing antibody-secreting **hybridomas** derived from mice. mAbs are currently used to treat cancer, but their exorbitant cost has prevented them from being used more widely to treat infectious diseases. Still, their potential for laboratory and clinical use is driving the development of new, cost-effective solutions such as **plantibodies**.

Footnotes

1. 1 Saylor, Carolyn, Ekaterina Dadachova and Arturo Casadevall, “Monoclonal Antibody-Based Therapies for Microbial Diseases,” *Vaccine* 27 (2009): G38-G46.
2. 2 Nakanishi, Katsuhiro et al., “Production of Hybrid-IgG/IgA Plantibodies with Neutralizing Activity against Shiga Toxin 1,” *PloS One* 8, no. 11 (2013): e80712.
3. 3 Qiu, Xiangguo et al., “Reversion of Advanced Ebola Virus Disease in Nonhuman Primates with ZMapp,” *Nature* 514 (2014): 47–53.

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50.6.3: Agglutination Assays

Learning Objectives

- Compare direct and indirect agglutination
- Identify various uses of hemagglutination in the diagnosis of disease
- Explain how blood types are determined
- Explain the steps used to cross-match blood to be used in a transfusion

In addition to causing precipitation of soluble molecules and flocculation of molecules in suspension, antibodies can also clump together cells or particles (e.g., antigen-coated latex beads) in a process called agglutination (Figure 18.1.8). Agglutination can be used as an indicator of the presence of antibodies against bacteria or red blood cells. Agglutination assays are usually quick and easy to perform on a glass slide or microtiter plate (Figure **50.6.3.1**). Microtiter plates have an array of wells to hold small volumes of reagents and to observe reactions (e.g., agglutination) either visually or using a specially designed spectrophotometer. The wells come in many different sizes for assays involving different volumes of reagents.

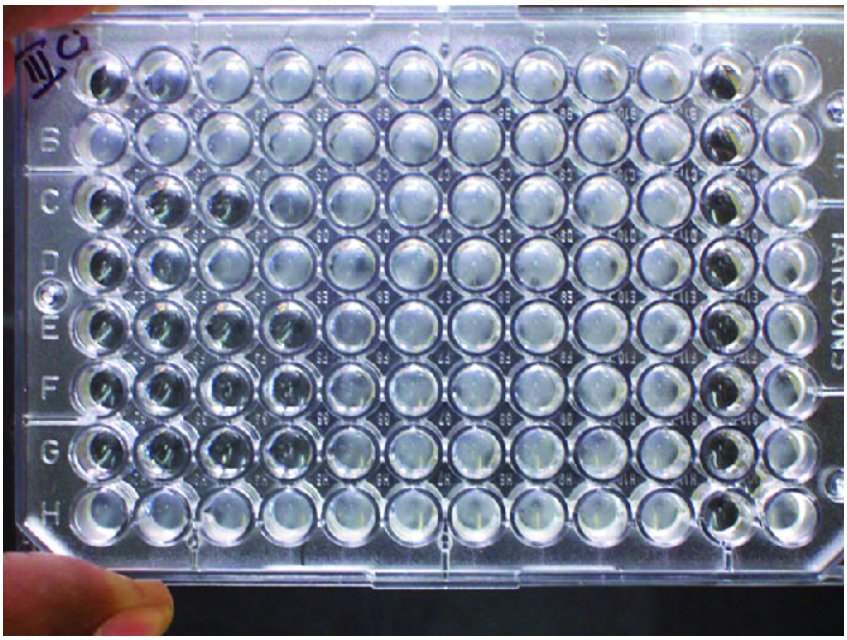


Figure **50.6.3.1**: Microtiter plates are used for conducting numerous reactions simultaneously in an array of wells. (credit: modification of work by “Microrao”/Wikimedia)

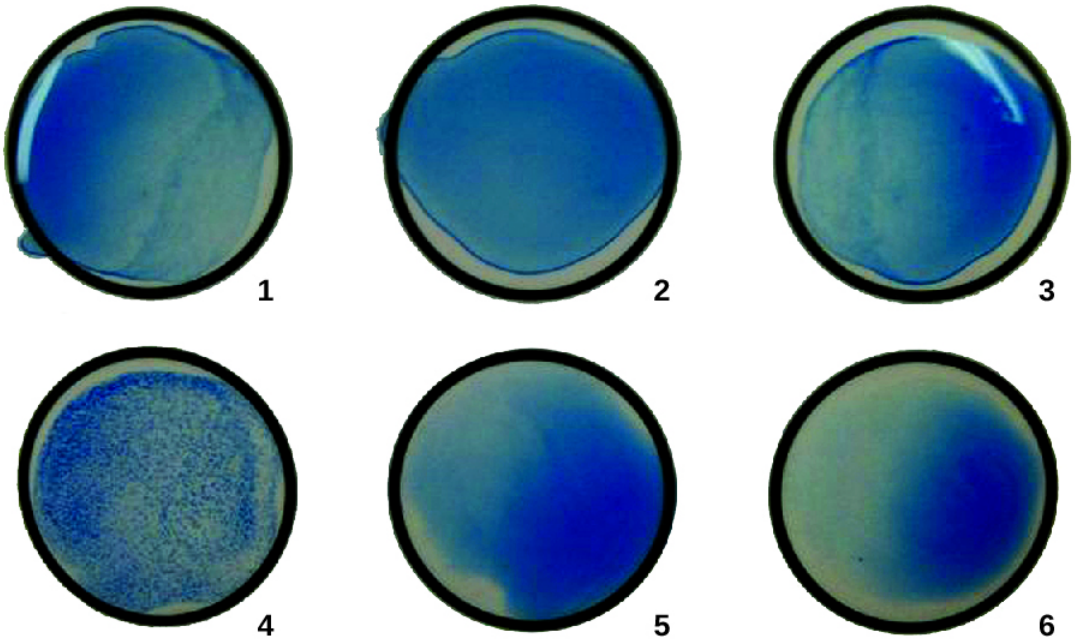
Agglutination of Bacteria and Viruses

The use of agglutination tests to identify streptococcal bacteria was developed in the 1920s by Rebecca Lancefieldworking with her colleagues A.R. Dochez and Oswald Avery.[1] She used antibodies to identify M protein, a virulence factor on streptococci that is necessary for the bacteria’s ability to cause strep throat. Production of antibodies against M protein is crucial in mounting a protective response against the bacteria.

Lancefield used antisera to show that different strains of the same species of streptococci express different versions of M protein, which explains why children can come down with strep throat repeatedly. Lancefield classified beta-hemolytic streptococci into many groups based on antigenic differences in group-specific polysaccharides located in the bacterial cell wall. The strains are called serovars because they are differentiated using antisera. Identifying the serovars present in a disease outbreak is important because some serovars may cause more severe disease than others.

The method developed by Lancefield is a direct agglutination assay, since the bacterial cells themselves agglutinate. A similar strategy is more commonly used today when identifying serovars of bacteria and viruses; however, to improve visualization of the agglutination, the antibodies may be attached to inert latex beads. This technique is called an indirect agglutination assay (or latex

fixation assay), because the agglutination of the beads is a marker for antibody binding to some other antigen (Figure 50.6.3.2). Indirect assays can be used to detect the presence of either antibodies or specific antigens.



ASM MicrobeLibrary © Hare Figure 50.6.3.2: Antibodies against six different serovars of Group A strep were attached to latex beads. Each of the six antibody preparations was mixed with bacteria isolated from a patient. The tiny clumps seen in well 4 are indicative of agglutination, which is absent from all other wells. This indicates that the serovar associated with well 4 is present in the patient sample. (credit: modification of work by American Society for Microbiology)

To identify antibodies in a patient's serum, the antigen of interest is attached to latex beads. When mixed with patient serum, the antibodies will bind the antigen, cross-linking the latex beads and causing the beads to agglutinate indirectly; this indicates the presence of the antibody (Figure 50.6.3.3). This technique is most often used when looking for IgM antibodies, because their structure provides maximum cross-linking. One widely used example of this assay is a test for rheumatoid factor (RF) to confirm a diagnosis of rheumatoid arthritis. RF is, in fact, the presence of IgM antibodies that bind to the patient's own IgG. RF will agglutinate IgG-coated latex beads.

In the reverse test, soluble antigens can be detected in a patient's serum by attaching specific antibodies (commonly mAbs) to the latex beads and mixing this complex with the serum (Figure 50.6.3.3).

Agglutination tests are widely used in underdeveloped countries that may lack appropriate facilities for culturing bacteria. For example, the Widal test, used for the diagnosis of typhoid fever, looks for agglutination of *Salmonella enterica* subspecies *typhi* in patient sera. The Widal test is rapid, inexpensive, and useful for monitoring the extent of an outbreak; however, it is not as accurate as tests that involve culturing of the bacteria. The Widal test frequently produces false positives in patients with previous infections with other subspecies of *Salmonella*, as well as false negatives in patients with hyperproteinemia or immune deficiencies.

In addition, agglutination tests are limited by the fact that patients generally do not produce detectable levels of antibody during the first week (or longer) of an infection. A patient is said to have undergone seroconversion when antibody levels reach the threshold for detection. Typically, seroconversion coincides with the onset of signs and symptoms of disease. However, in an HIV infection, for example, it generally takes 3 weeks for seroconversion to take place, and in some instances, it may take much longer.

Similar to techniques for the precipitin ring test and plaque assays, it is routine to prepare serial two-fold dilutions of the patient's serum and determine the titer of agglutinating antibody present. Since antibody levels change over time in both primary and secondary immune responses, by checking samples over time, changes in antibody titer can be detected. For example, a comparison of the titer during the acute phase of an infection versus the titer from the convalescent phase will distinguish whether an infection

is current or has occurred in the past. It is also possible to monitor how well the patient's immune system is responding to the pathogen.

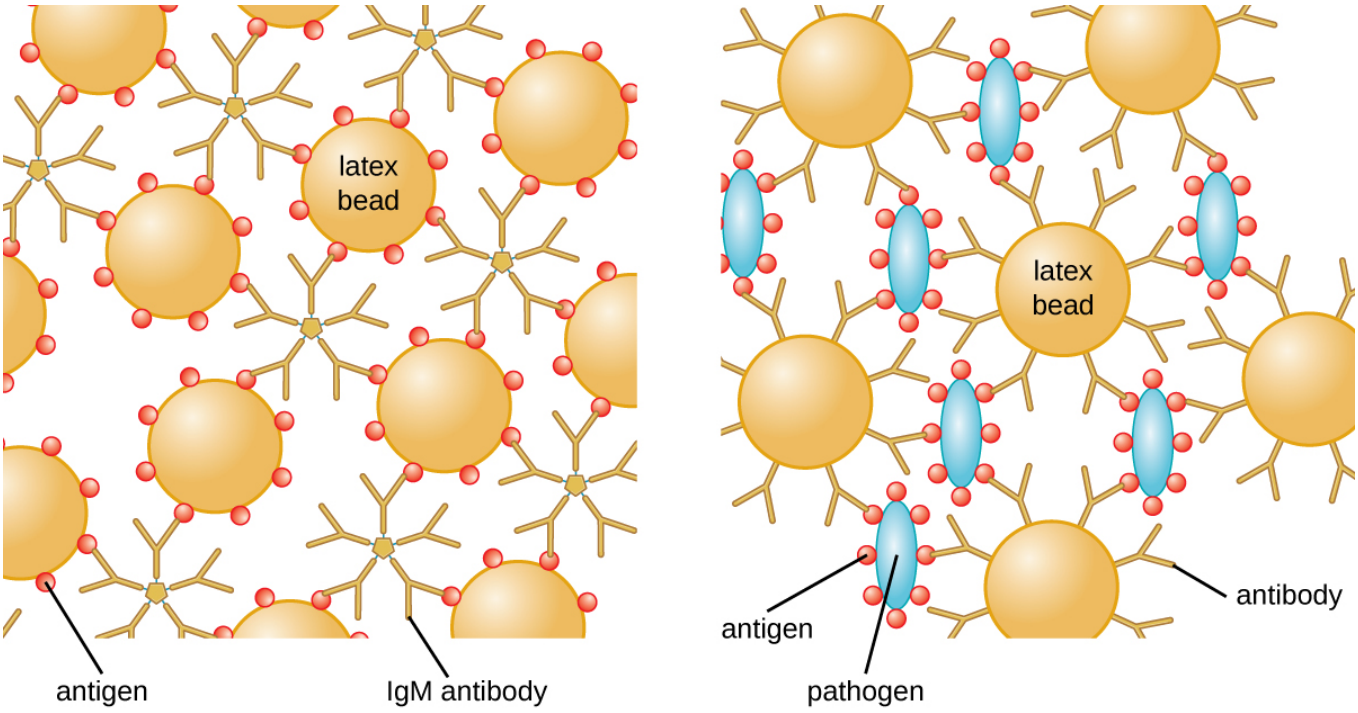


Figure 50.6.3.3: (a) Latex beads coated with an antigen will agglutinate when mixed with patient serum if the serum contains IgM antibodies against the antigen. (b) Latex beads coated with antibodies will agglutinate when mixed with patient serum if the serum contains antigens specific to the antibodies.

Link to Learning

Watch this video that demonstrates agglutination reactions with latex beads.

Exercise 50.6.3.1

1. How is agglutination used to distinguish serovars from each other?
2. In a latex bead assay to test for antibodies in a patient's serum, with what are the beads coated?
3. What has happened when a patient has undergone seroconversion?

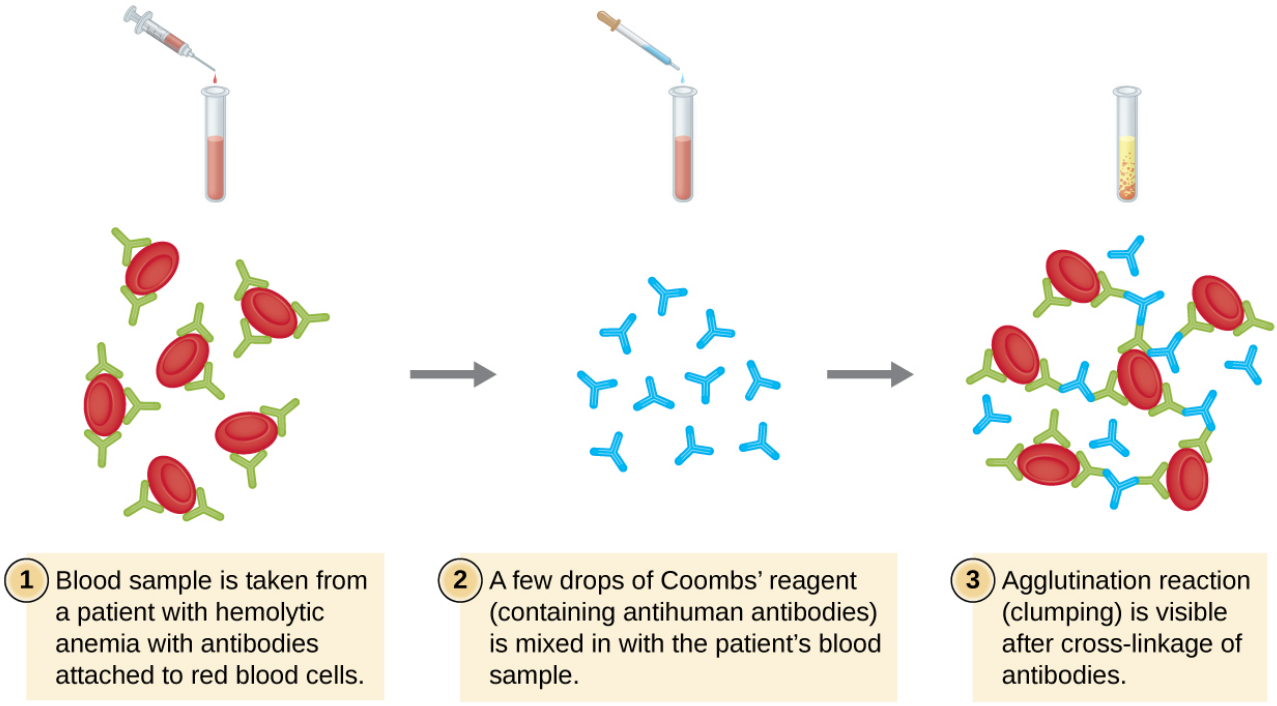
Hemagglutination

Agglutination of red blood cells is called hemagglutination. One common assay that uses hemagglutination is the direct Coombs' test, also called the direct antihuman globulin test (DAT), which generally looks for nonagglutinating antibodies. The test can also detect complement attached to red blood cells.

The Coombs' test is often employed when a newborn has jaundice, yellowing of the skin caused by high blood concentrations of bilirubin, a product of the breakdown of hemoglobin in the blood. The Coombs' test is used to determine whether the child's red blood cells have been bound by the mother's antibodies. These antibodies would activate complement, leading to red blood cell lysis and the subsequent jaundice. Other conditions that can cause positive direct Coombs' tests include hemolytic transfusion reactions, autoimmune hemolytic anemia, infectious mononucleosis (caused by Epstein-Barr virus), syphilis, and *Mycoplasma* pneumonia. A positive direct Coombs' test may also be seen in some cancers and as an allergic reaction to some drugs (e.g., penicillin).

The antibodies bound to red blood cells in these conditions are most often IgG, and because of the orientation of the antigen-binding sites on IgG and the comparatively large size of a red blood cell, it is unlikely that any visible agglutination will occur. However, the presence of IgG bound to red blood cells can be detected by adding Coombs' reagent, an antiserum containing antihuman IgG antibodies (that may be combined with anti-complement) (Figure **50.6.3.4**). The Coombs' reagent links the IgG attached to neighboring red blood cells and thus promotes agglutination.

There is also an indirect Coombs' test known as the indirect antiglobulin test (IAT). This screens an individual for antibodies against red blood cell antigens (other than the A and B antigens) that are unbound in a patient's serum (Figure **50.6.3.4**). IAT can be used to screen pregnant women for antibodies that may cause hemolytic disease of the newborn. It can also be used prior to giving blood transfusions. More detail on how the IAT is performed is discussed below.



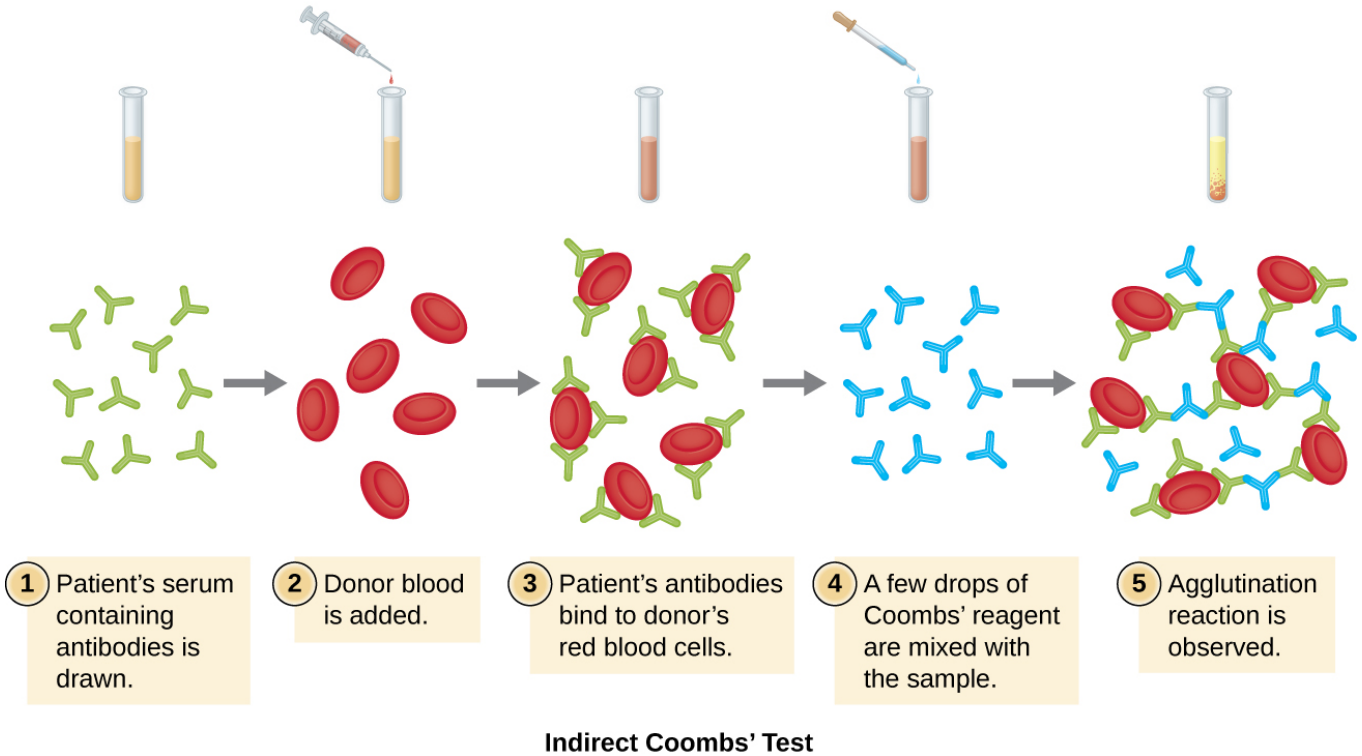


Figure 50.6.3.4: The steps in direct and indirect Coombs' tests are shown in the illustration.

Antibodies that bind to red blood cells are not the only cause of hemagglutination. Some viruses also bind to red blood cells, and this binding can cause agglutination when the viruses cross-link the red blood cells. For example, influenza viruses have two different types of viral spikes called neuraminidase (N) and hemagglutinin (H), the latter named for its ability to agglutinate red blood cells (see Viruses). Thus, we can use red blood cells to detect the presence of influenza virus by direct hemagglutination

assays (HA), in which the virus causes visible agglutination of red blood cells. The mumps and rubella viruses can also be detected using HA.

Most frequently, a serial dilution viral agglutination assay is used to measure the titer or estimate the amount of virus produced in cell culture or for vaccine production. A viral titer can be determined using a direct HA by making a serial dilution of the sample containing the virus, starting with a high concentration of sample that is then diluted in a series of wells. The highest dilution producing visible agglutination is the titer. The assay is carried out in a microtiter plate with V- or round-bottomed wells. In the presence of agglutinating viruses, the red blood cells and virus clump together and produce a diffuse mat over the bottom of the well. In the absence of virus, the red blood cells roll or sediment to the bottom of the well and form a dense pellet, which is why flat-bottomed wells cannot be used (Figure **50.6.3.5**).

A modification of the HA assay can be used to determine the titer of antiviral antibodies. The presence of these antibodies in a patient's serum or in a lab-produced antiserum will neutralize the virus and block it from agglutinating the red cells, making this a viral hemagglutination inhibition assay (HIA). In this assay, patient serum is mixed with a standardized amount of virus. After a short incubation, a standardized amount of red blood cells is added and hemagglutination is observed. The titer of the patient's serum is the highest dilution that blocks agglutination (Figure **50.6.3.6**).

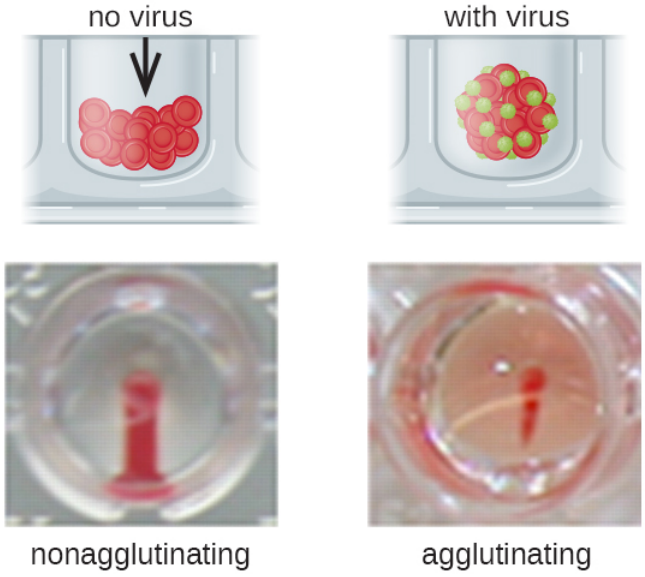
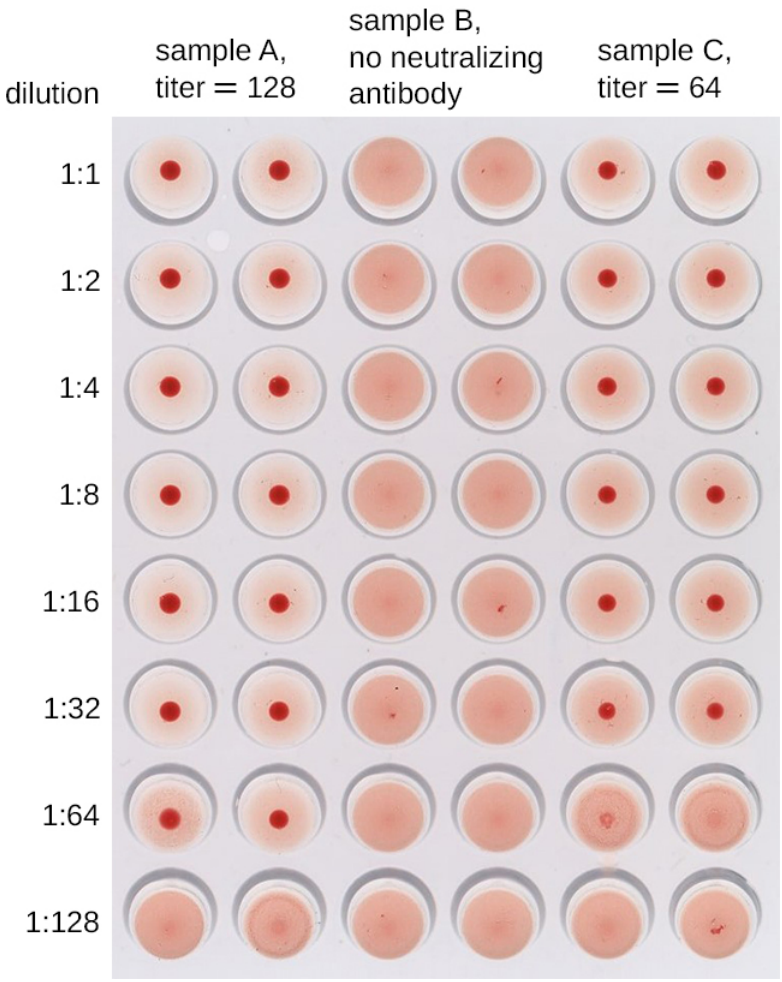


Figure **50.6.3.5**: A viral suspension is mixed with a standardized amount of red blood cells. No agglutination of red blood cells is visible when the virus is absent, and the cells form a compact pellet at the bottom of the well. In the presence of virus, a diffuse pink precipitate forms in the well. (credit bottom: modification of



work by American Society for Microbiology) Figure **50.6.3.6**: In this HIA, serum containing antibodies to influenzavirus underwent serial two-fold dilutions in a microtiter plate. Red blood cells were then added to the wells. Agglutination only occurred in those wells where the antibodies were too dilute to neutralize the virus. The highest concentration at which agglutination occurs is the titer of the antibodies in the patient's serum. In the case of this test, Sample A shows a titer of 128, and Sample C shows a titer of 64. (credit: modification of work by Evan Burkala)

? Exercise 50.6.3.2

1. What is the mechanism by which viruses are detected in a hemagglutination assay?
2. Which hemagglutination result tells us the titer of virus in a sample?

Animals in the Laboratory

Much of what we know today about the human immune system has been learned through research conducted using animals—primarily, mammals—as models. Besides research, mammals are also used for the production of most of the antibodies and other immune system components needed for immunodiagnostics. Vaccines, diagnostics, therapies, and translational medicine in general have all been developed through research with animal models.

Consider some of the common uses of laboratory animals for producing immune system components. Guinea pigs are used as a source of complement, and mice are the primary source of cells for making mAbs. These mAbs can be used in research and for therapeutic purposes. Antisera are raised in a variety of species, including horses, sheep, goats, and rabbits. When producing an antiserum, the animal will usually be injected at least twice, and adjuvants may be used to boost the antibody response. The larger animals used for making antisera will have blood harvested repeatedly over long periods of time, with little harm to the animals, but that is not usually the case for rabbits. Although we can obtain a few milliliters of blood from the ear veins of rabbits, we usually need larger volumes, which results in the deaths of the animals.

We also use animals for the study of disease. The only way to grow *Treponema pallidum* for the study of syphilis is in living animals. Many viruses can be grown in cell culture, but growth in cell culture tells us very little about how the immune system will respond to the virus. When working on a newly discovered disease, we still employ Koch's postulates, which require causing disease in lab animals using pathogens from pure culture as a crucial step in proving that a particular microorganism is the cause of a disease. Studying the proliferation of bacteria and viruses in animal hosts, and how the host immune system responds, has been central to microbiological research for well over 100 years.

While the practice of using laboratory animals is essential to scientific research and medical diagnostics, many people strongly object to the exploitation of animals for human benefit. This ethical argument is not a new one—indeed, one of Charles Darwin's daughters was an active antivivisectionist (vivisection is the practice of cutting or dissecting a live animal to study it). Most scientists acknowledge that there should be limits on the extent to which animals can be exploited for research purposes. Ethical considerations have led the National Institutes of Health (NIH) to develop strict regulations on the types of research that may be performed. These regulations also include guidelines for the humane treatment of lab animals, setting standards for their housing, care, and euthanization. The NIH document "Guide for the Care and Use of Laboratory Animals" makes it clear that the use of animals in research is a privilege granted by society to researchers.

The NIH guidelines are based on the principle of the three R's: replace, refine, and reduce. Researchers should strive to *replace* animal models with nonliving models, *replace* vertebrates with invertebrates whenever possible, or use computer-models when applicable. They should *refine* husbandry and experimental procedures to reduce pain and suffering, and use experimental designs and procedures that *reduce* the number of animals needed to obtain the desired information. To obtain funding, researchers must satisfy NIH reviewers that the research justifies the use of animals and that their use is in accordance with the guidelines.

At the local level, any facility that uses animals and receives federal funding must have an Institutional Animal Care and Use Committee (IACUC) that ensures that the NIH guidelines are being followed. The IACUC must include researchers, administrators, a veterinarian, and at least one person with no ties to the institution, that is, a concerned citizen. This committee also performs inspections of laboratories and protocols. For research involving human subjects, an Institutional Review Board (IRB) ensures that proper guidelines are followed.

Link to Learning

Visit this site to view the NIH Guide for the Care and Use of Laboratory Animals.

Blood Typing and Cross-Matching

In addition to antibodies against bacteria and viruses to which they have previously been exposed, most individuals also carry antibodies against blood types other than their own. There are presently 33 immunologically important blood-type systems, many of which are restricted within various ethnic groups or rarely result in the production of antibodies. The most important and perhaps best known are the ABO and Rh blood groups (see Figure 19.1.3).

When units of blood are being considered for transfusion, pretransfusion blood testing must be performed. For the blood unit, commercially prepared antibodies against the A, B, and Rh antigens are mixed with red blood cells from the units to initially confirm that the blood type on the unit is accurate. Once a unit of blood has been requested for transfusion, it is vitally important to make sure the donor (unit of blood) and recipient (patient) are compatible for these crucial antigens. In addition to confirming the blood type of the unit, the patient's blood type is also confirmed using the same commercially prepared antibodies to A, B, and Rh. For example, as shown in Figure **50.6.3.7**, if the donor blood is A-positive, it will agglutinate with the anti-A antiserum and with the anti-Rh antiserum. If no agglutination is observed with any of the sera, then the blood type would be O-negative.

Following determination of the blood type, immediately prior to releasing the blood for transfusion, a cross-match is performed in which a small aliquot of the donor red blood cells are mixed with serum from the patient awaiting transfusion. If the patient does have antibodies against the donor red blood cells, hemagglutination will occur. To confirm any negative test results and check for sensitized red blood cells, Coombs' reagent may be added to the mix to facilitate visualization of the antibody-red blood cell interaction.

Under some circumstances, a minor cross-match may be performed as well. In this assay, a small aliquot of donor serum is mixed with patient red blood cells. This allows the detection of agglutinizing antibodies in the donor serum. This test is rarely necessary because transfusions generally use packed red blood cells with most of the plasma removed by centrifugation.

Red blood cells have many other antigens in addition to ABO and Rh. While most people are unlikely to have antibodies against these antigens, women who have had multiple pregnancies or patients who have had multiple transfusions may have them because of repeated exposure. For this reason, an antibody screen test is used to determine if such antibodies are present. Patient serum is checked against commercially prepared, pooled, type O red blood cells that express these antigens. If agglutination occurs, the antigen to which the patient is responding must be identified and determined not to be present in the donor unit.

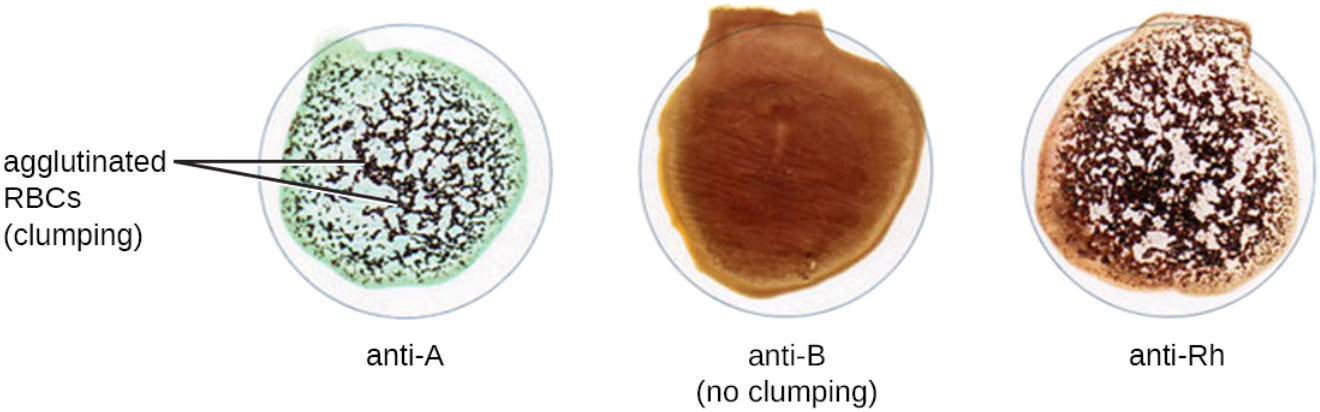


Figure **50.6.3.7**: This sample of a commercially produced “bedside” card enables quick typing of both a recipient’s and donor’s blood before transfusion. The card contains three reaction sites or wells. One is coated with an anti-A antibody, one with an anti-B antibody, and one with an anti-Rh antibody. Agglutination of red blood cells in a given site indicates a positive identification of the blood antigens: in this case, A and Rh antigens for blood type A-positive.

? Exercise 50.6.3.3

1. If a patient's blood agglutinates with anti-B serum, what is the patient’s blood type?
2. What is a cross-match assay, and why is it performed?

Table **50.6.3.1** summarizes the various kinds of agglutination assays discussed in this section.

Table **50.6.3.1**: Mechanisms of Select Antibody-Antigen Assays

Type of Assay	Mechanism	Example
Agglutination	Direct: Antibody is used to clump bacterial cells or other large structures	Serotyping bacteria
	Indirect: Latex beads are coupled with antigen or antibody to look for antibody or antigen, respectively, in patient serum	Confirming the presence of rheumatoid factor (IgM-binding Ig) in patient serum
Hemagglutination	Direct: Some bacteria and viruses cross-link red blood cells and clump them together	Diagnosing influenza, mumps, and measles
	Direct Coombs' test (DAT): Detects nonagglutinating antibodies or complement proteins on red blood cells *in vivo*	Checking for maternal antibodies binding to neonatal red blood cells
	Indirect Coombs' test (IAT): Screens an individual for antibodies against red blood cell antigens (other than the A and B antigens) that are unbound in a patient's serum *in vitro*	Performing pretransfusion blood testing
	Viral hemagglutination inhibition: Uses antibodies from a patient to inhibit viral agglutination	Diagnosing various viral diseases by the presence of patient antibodies against the virus
	Blood typing and cross-matching: Detects ABO, Rh, and minor antigens in the blood	Matches donor blood to recipient immune requirements

Key Concepts and Summary

- Antibodies can agglutinate cells or large particles into a visible matrix. **Agglutination** tests are often done on cards or in **microtiter plates** that allow multiple reactions to take place side by side using small volumes of reagents.
- Using antisera against certain proteins allows identification of **serovars** within species of bacteria.
- Detecting antibodies against a pathogen can be a powerful tool for diagnosing disease, but there is a period of time before patients go through **seroconversion** and the level of antibodies becomes detectable.
- Agglutination of latex beads in **indirect agglutination assays** can be used to detect the presence of specific antigens or specific antibodies in patient serum.
- The presence of some antibacterial and antiviral antibodies can be confirmed by the use of the direct **Coombs' test**, which uses Coombs' reagent to cross-link antibodies bound to red blood cells and facilitate **hemagglutination**.
- Some viruses and bacteria will bind and agglutinate red blood cells; this interaction is the basis of the **direct hemagglutination assay**, most often used to determine the titer of virus in solution.
- **Neutralization assays** quantify the level of virus-specific antibody by measuring the decrease in hemagglutination observed after mixing patient serum with a standardized amount of virus.
- Hemagglutination assays are also used to screen and **cross-match** donor and recipient blood to ensure that the transfusion recipient does not have antibodies to antigens in the donated blood.

Footnotes

1. 1 Lancefield, Rebecca C., "The Antigenic Complex of *Streptococcus haemoliticus*. I. Demonstration of a Type-Specific Substance in Extracts of *Streptococcus haemolyticus*," *The Journal of Experimental Medicine* 47, no. 1 (1928): 91-103.

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50.6.4: Fluorescent Auto-Antibody Techniques

Learning Objectives

- Describe the benefits of immunofluorescent antibody assays in comparison to nonfluorescent assays
- Compare direct and indirect fluorescent antibody assays
- Explain how a flow cytometer can be used to quantify specific subsets of cells present in a complex mixture of cell types
- Explain how a fluorescence-activated cell sorter can be used to separate unique types of cells

Rapid visualization of bacteria from a clinical sample such as a throat swab or sputum can be achieved through fluorescent antibody (FA) techniques that attach a fluorescent marker (fluorogen) to the constant region of an antibody, resulting in a reporter molecule that is quick to use, easy to see or measure, and able to bind to target markers with high specificity. We can also label cells, allowing us to precisely quantify particular subsets of cells or even purify these subsets for further research.

As with the enzyme assays, FA methods may be direct, in which a labeled mAb binds an antigen, or indirect, in which secondary polyclonal antibodies bind patient antibodies that react to a prepared antigen. Applications of these two methods were demonstrated in Figure 2.3.8. FA methods are also used in automated cell counting and sorting systems to enumerate or segregate labeled subpopulations of cells in a sample.

Direct Fluorescent Antibody Techniques

Direct fluorescent antibody (DFA) tests use a fluorescently labeled mAb to bind and illuminate a target antigen. DFA tests are particularly useful for the rapid diagnosis of bacterial diseases. For example, fluorescence-labeled antibodies against *Streptococcus pyogenes* (group A strep) can be used to obtain a diagnosis of strep throat from a throat swab. The diagnosis is ready in a matter of minutes, and the patient can be started on antibiotics before even leaving the clinic. DFA techniques may also be used to diagnose pneumonia caused by *Mycoplasma pneumoniae* or *Legionella pneumophila* from sputum samples (Figure **50.6.4.1**). The fluorescent antibodies bind to the bacteria on a microscope slide, allowing ready detection of the bacteria using a fluorescence microscope. Thus, the DFA technique is valuable for visualizing certain bacteria that are difficult to isolate or culture from patient samples.

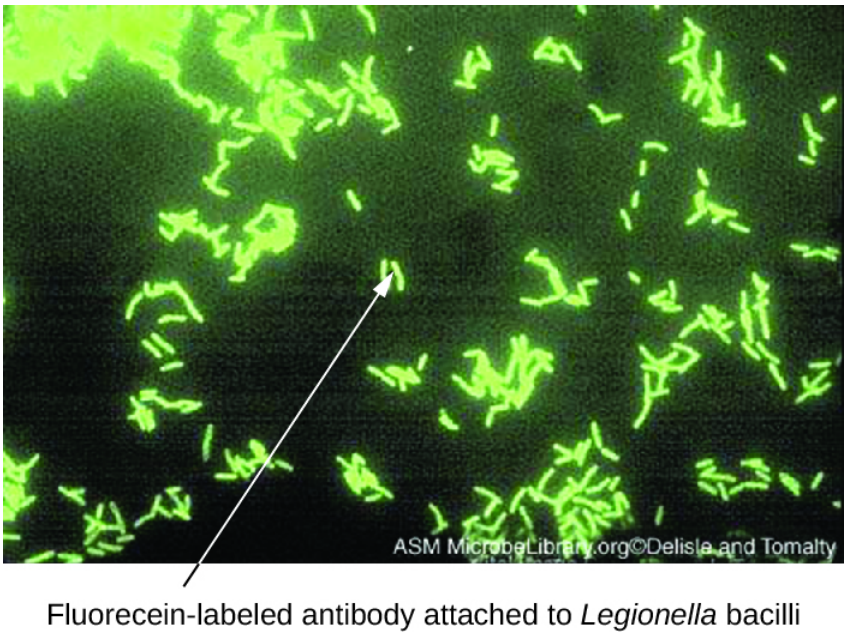


Figure **50.6.4.1**: A green fluorescent mAb against *L. pneumophila* is used here to visualize and identify bacteria from a smear of a sample from the respiratory tract of a pneumonia patient. (credit: modification of work by American Society for Microbiology)

? Exercise 50.6.4.1

In a direct fluorescent antibody test, what does the fluorescent antibody bind to?

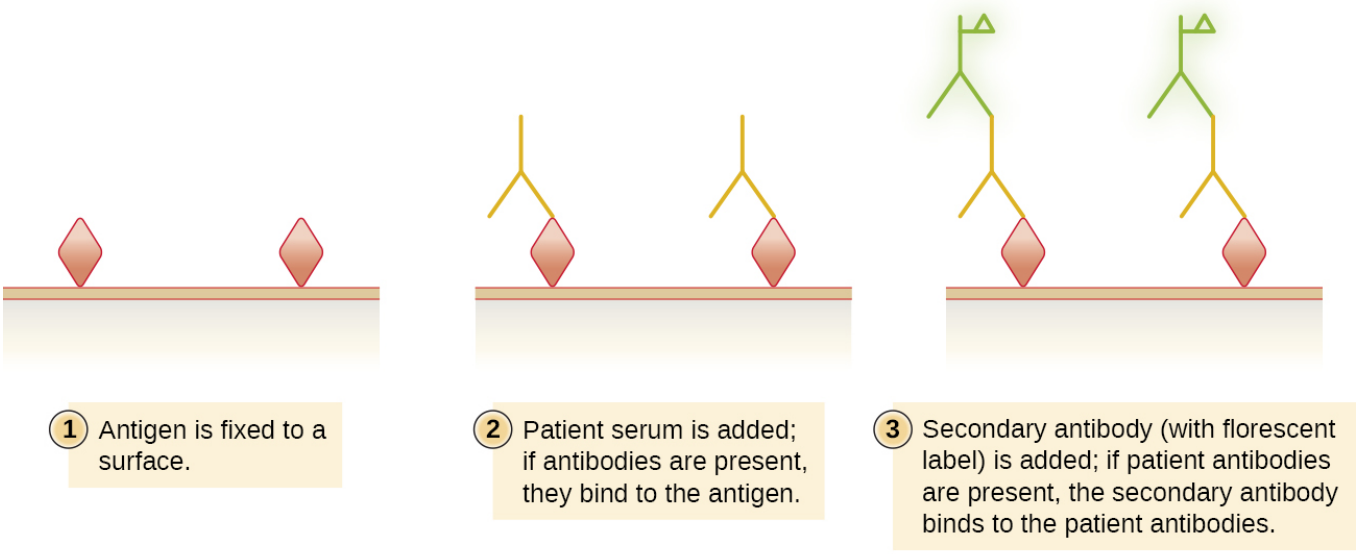
Indirect Fluorescent Antibody Techniques

Indirect fluorescent antibody (IFA) tests (Figure **50.6.4.2**) are used to look for antibodies in patient serum. For example, an IFA test for the diagnosis of syphilis uses *T. pallidum* cells isolated from a lab animal (the bacteria cannot be grown on lab media) and a smear prepared on a glass slide. Patient serum is spread over the smear and anti-treponemal antibodies, if present, are allowed to bind. The serum is washed off and a secondary antibody added. The secondary antibody is an antihuman immunoglobulin conjugated to a fluorogen. On examination, the *T. pallidum* bacteria will only be visible if they have been bound by the antibodies from the patient's serum.

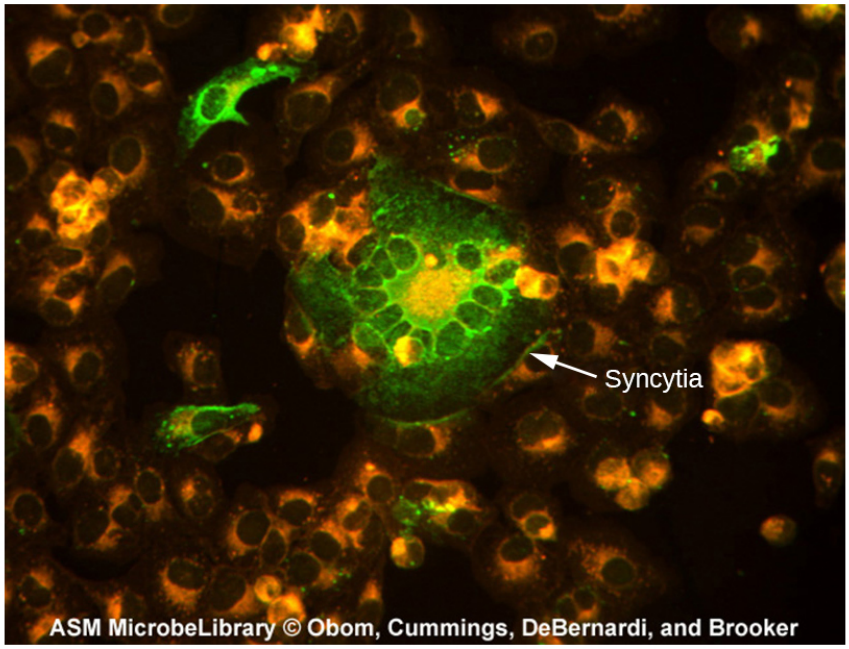
The IFA test for syphilis provides an important complement to the VDRL test discussed in Detecting Antigen-Antibody Complexes. The VDRL is more likely to generate false-positive reactions than the IFA test; however, the VDRL is a better test for determining whether an infection is currently active.

IFA tests are also useful for the diagnosis of autoimmune diseases. For example, systemic lupus erythematosus (SLE) (see Autoimmune Disorders) is characterized by elevated expression levels of antinuclear antibodies (ANA). These autoantibodies can be expressed against a variety of DNA-binding proteins and even against DNA itself. Because autoimmunity is often difficult to diagnose, especially early in disease progression, testing for ANA can be a valuable clue in making a diagnosis and starting appropriate treatment.

The IFA for ANA begins by fixing cells grown in culture to a glass slide and making them permeable to antibody. The slides are then incubated with serial dilutions of serum from the patient. After incubation, the slide is washed to remove unbound proteins, and the fluorescent antibody (antihuman IgG conjugated to a fluorogen) added. After an incubation and wash, the cells can be examined for fluorescence evident around the nucleus (Figure **50.6.4.3**). The titer of ANA in the serum is determined by the highest dilution showing fluorescence. Because many healthy people express ANA, the American College of Rheumatology recommends that the titer must be at least 1:40 in the presence of symptoms involving two or more organ systems to be considered indicative of SLE.[1]

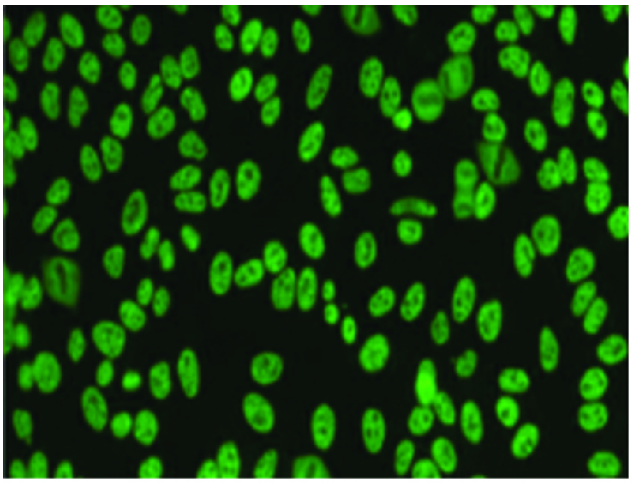


(a)

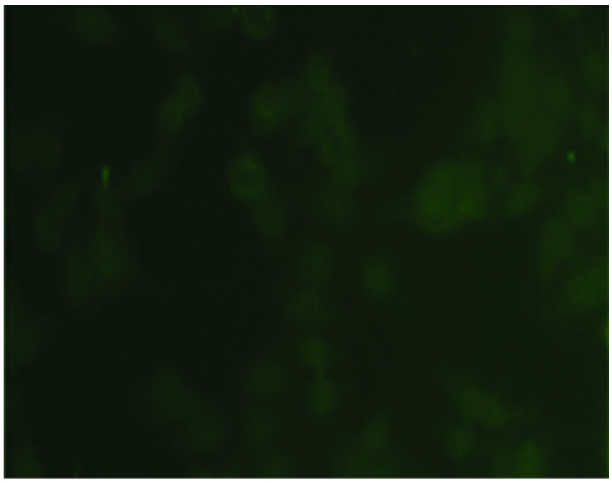


(b)

Figure 50.6.4.2: (a) The IFA test is used to detect antigen-specific antibodies by allowing them to bind to antigen fixed to a surface and then illuminating these complexes with a secondary antibody-fluorogen conjugate. (b) In this example of a micrograph of an indirect fluorescent antibody test, a patient's antibodies to the measles virus bind to viral antigens present on inactivated measles-infected cells affixed to a slide. Secondary antibodies bind the patient's antibodies and carry a fluorescent molecule. (credit b: modification of work by American Society for Microbiology)



diseased



healthy control

Figure 50.6.4.3: In this test for antinuclear antibodies (ANA), cells are exposed to serum from a patient suspected of making ANA and then to a fluorescent mAb specific for human immunoglobulin. As a control, serum from a healthy patient is also used. Visible fluorescence around the nucleus demonstrates the presence of ANA in the patient's serum. In the healthy control where lower levels of ANA are produced, very faint green is detected. (credit left, right: modification of work by Al-Hussaini AA, Alzahrani MD, Alenizi AS, Suliman NM, Khan MA, Alharbi SA, Chentoufi AA)

? Exercise 50.6.4.2

1. In an indirect fluorescent antibody test, what does the fluorescent antibody bind to?
2. What is the ANA test looking for?

Flow Cytometry

Fluorescently labeled antibodies can be used to quantify cells of a specific type in a complex mixture using flow cytometry (Figure 50.6.4.4), an automated, cell-counting system that detects fluorescing cells as they pass through a narrow tube one cell at a time. For example, in HIV infections, it is important to know the level of CD4 T cells in the patient's blood; if the numbers fall below 500 per µL of blood, the patient becomes more likely to acquire opportunistic infections; below 200 per µL, the patient can no longer mount a useful adaptive immune response at all. The analysis begins by incubating a mixed-cell population (e.g., white blood cells from a donor) with a fluorescently labeled mAb specific for a subpopulation of cells (e.g., anti-CD4). Some experiments look at two cell markers simultaneously by adding a different fluorogen to the appropriate mAb. The cells are then introduced to the flow cytometer through a narrow capillary that forces the cells to pass in single file. A laser is used to activate the fluorogen. The fluorescent light radiates out in all directions, so the fluorescence detector can be positioned at an angle from the incident laser light.

Figure 50.6.4.4 shows the obscuration bar in front of the forward-scatter detector that prevents laser light from hitting the detector. As a cell passes through the laser bar, the forward-scatter detector detects light scattered around the obscuration bar. The scattered light is transformed into a voltage pulse, and the cytometer counts a cell. The fluorescence from a labeled cell is detected by the side-scatter detectors. The light passes through various dichroic mirrors such that the light emitted from the fluorophore is received by the correct detector.

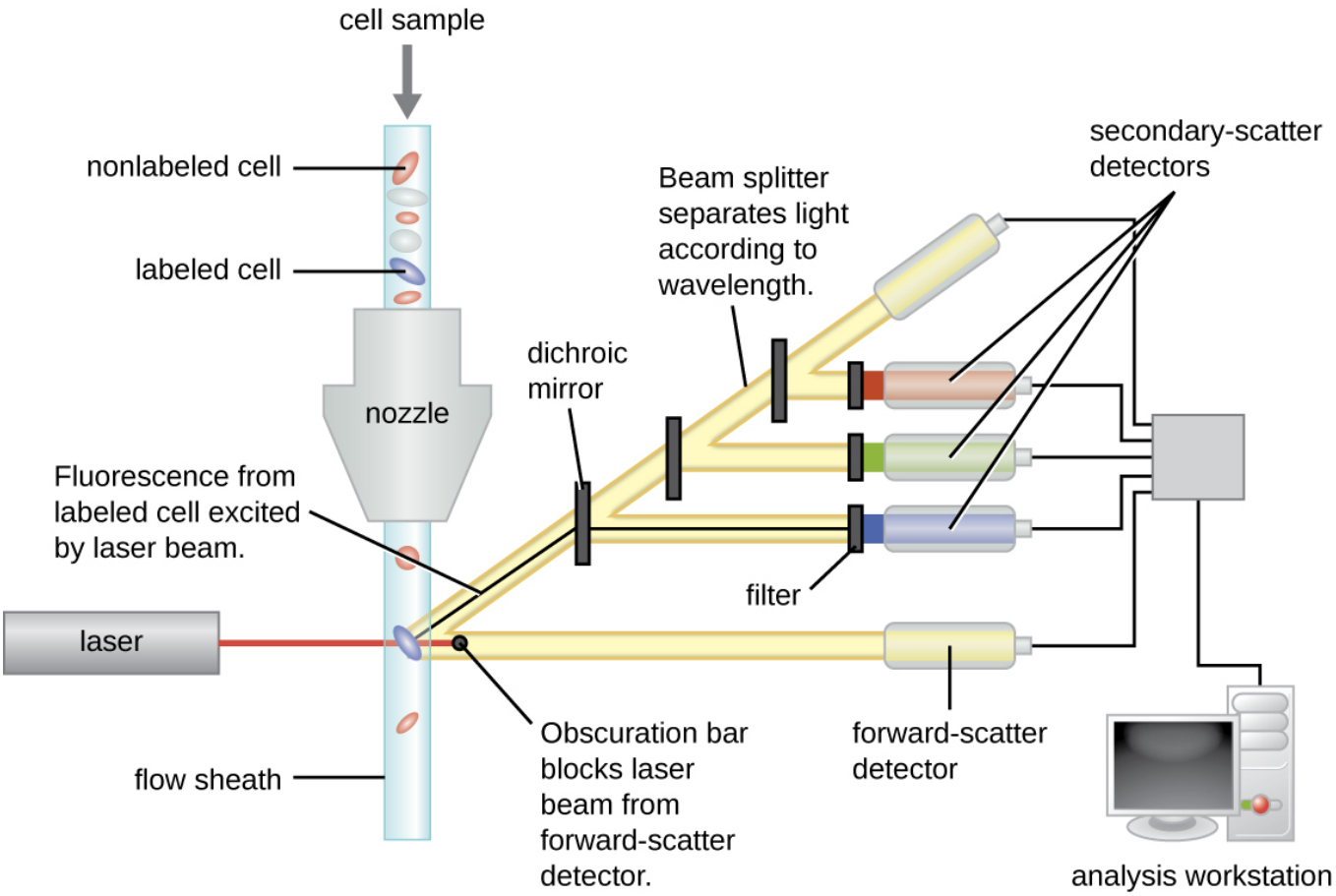


Figure 50.6.4.4: In flow cytometry, a mixture of fluorescently labeled and unlabeled cells passes through a narrow capillary. A laser excites the fluorogen, and the fluorescence intensity of each cell is measured by a detector. (credit: modification of work by "Kierano"/Wikimedia Commons)

Data are collected from both the forward- and side-scatter detectors. One way these data can be presented is in the form of a histogram. The forward scatter is placed on the *y*-axis (to represent the number of cells), and the side scatter is placed on the *x*-axis (to represent the fluoresence of each cell). The scaling for the *x*-axis is logarithmic, so fluorescence intensity increases by a factor of 10 with each unit increase along the axis. Figure 50.6.4.5 depicts an example in which a culture of cells is combined with an antibody attached to a fluorophore to detect CD8 cells and then analyzed by flow cytometry. The histogram has two peaks. The peak on the left has lower fluorescence readings, representing the subset of the cell population (approximately 30 cells) that does not fluoresce; hence, they are not bound by antibody and therefore do not express CD8. The peak on the right has higher fluorescence readings, representing the subset of the cell population (approximately 100 cells) that show fluorescence; hence, they are bound by the antibody and therefore do express CD8.

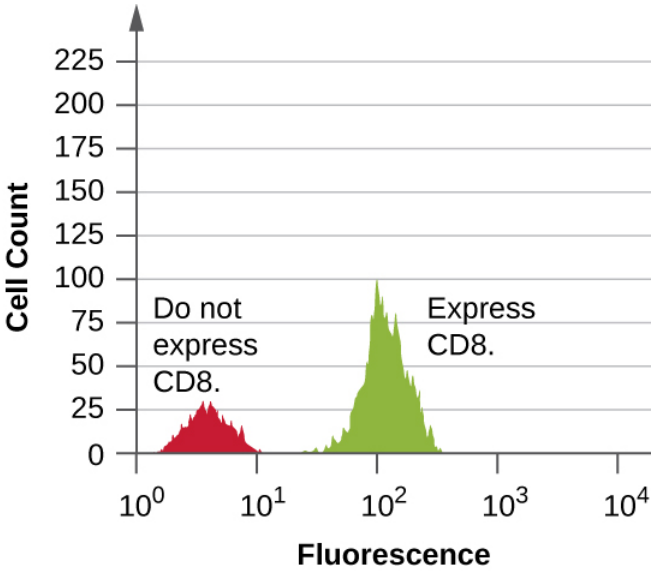


Figure 50.6.4.5: Flow cytometry data are often compiled as a histogram. In the histogram, the area under each peak is proportional to the number of cells in each population. The *x*-axis is the relative fluorescence expressed by the cells (on a log scale), and the *y*-axis represents the number of cells at a particular level of fluorescence.

? Exercise 50.6.4.3

1. What is the purpose of the laser in a flow cytometer?
2. In the output from a flow cytometer, the area under the histogram is equivalent to what?

Clinical Focus: Resolution

After notifying all 1300 patients, the hospital begins scheduling HIV screening. Appointments were scheduled a minimum of 3 weeks after the patient's last hospital visit to minimize the risk of false negatives. Because some false positives were anticipated, the public health physician set up a counseling protocol for any patient whose indirect ELISA came back positive.

Of the 1300 patients, eight tested positive using the ELISA. Five of these tests were invalidated by negative western blot tests, but one western blot came back positive, confirming that the patient had indeed contracted HIV. The two remaining western blots came back indeterminate. These individuals had to submit to a third test, a PCR, to confirm the presence or absence of HIV sequences. Luckily, both patients tested negative.

As for the lone patient confirmed to have HIV, the tests cannot prove or disprove any connection to the syringes compromised by the former hospital employee. Even so, the hospital's insurance will fully cover the patient's treatment, which began immediately.

Although we now have drugs that are typically effective at controlling the progression of HIV and AIDS, there is still no cure. If left untreated, or if the drug regimen fails, the patient will experience a gradual decline in the number of CD4 helper T cells, resulting in severe impairment of all adaptive immune functions. Even moderate declines of helper T cell numbers can result in immunodeficiency, leaving the patient susceptible to opportunistic infections. To monitor the status of the patient's helper T cells, the hospital will use flow cytometry. This sensitive test allows physicians to precisely determine the number of helper T cells so they can adjust treatment if the number falls below 500 cells/μL.

Cell Sorting Using Immunofluorescence

The flow cytometer and immunofluorescence can also be modified to sort cells from a single sample into purified subpopulations of cells for research purposes. This modification of the flow cytometer is called a fluorescence-activated cell sorter (FACS). In a FACS, fluorescence by a cell induces the device to put a charge on a droplet of the transporting fluid containing that cell. The charge is specific to the wavelength of the fluorescent light, which allows for differential sorting by those different charges. The

sorting is accomplished by an electrostatic deflector that moves the charged droplet containing the cell into one collecting vessel or another. The process results in highly purified subpopulations of cells.

One limitation of a FACS is that it only works on isolated cells. Thus, the method would work in sorting white blood cells, since they exist as isolated cells. But for cells in a tissue, flow cytometry can only be applied if we can excise the tissue and separate it into single cells (using proteases to cleave cell-cell adhesion molecules) without disrupting cell integrity. This method may be used on tumors, but more often, immunohistochemistry and immunocytochemistry are used to study cells in tissues.

Link to Learning

Watch videos to learn more about how flow cytometry and a FACS work.

Exercise 50.6.4.4

In fluorescence activated cell sorting, what characteristic of the target cells allows them to be separated?

Table **50.6.4.1** compares the mechanisms of the fluorescent antibody techniques discussed in this section.

Table **50.6.4.1**: Fluorescent Antibody Techniques

Type of Assay	Mechanism	Examples
Direct fluorescent antibody (DFA)	Uses fluorogen-antibody conjugates to label bacteria from patient samples	Visualizing *Legionella pneumophila* from a throat swab
Indirect fluorescent antibody (IFA)	Detects disease-specific antibodies in patent serum	Diagnosing syphilis; detecting antinuclear antibodies (ANA) for lupus and other autoimmune diseases
Flow cytometry	Labels cell membranes with fluorogen-antibody conjugate markers excited by a laser; machine counts the cell and records the relative fluorescence	Counting the number of fluorescently labeled CD4 or CD8 cells in a sample
Fluorescence activated cell sorter (FACS)	Form of flow cytometry that both counts cells and physically separates them into pools of high and low fluorescence cells	Sorting cancer cells

Key Concepts and Summary

- **Immunofluorescence** assays use antibody-fluorogen conjugates to illuminate antigens for easy, rapid detection.
- **Direct immunofluorescence** can be used to detect the presence of bacteria in clinical samples such as sputum.
- **Indirect immunofluorescence** detects the presence of antigen-specific antibodies in patient sera. The fluorescent antibody binds to the antigen-specific antibody rather than the antigen.
- The use of indirect immunofluorescence assays to detect **antinuclear antibodies** is an important tool in the diagnosis of several autoimmune diseases.
- **Flow cytometry** uses fluorescent mAbs against cell-membrane proteins to quantify specific subsets of cells in complex mixtures.
- **Fluorescence-activated cell sorters** are an extension of flow cytometry in which fluorescence intensity is used to physically separate cells into high and low fluorescence populations.

Footnotes

1. 1 Gill, James M., ANNA M. Quisel, PETER V. Rocca, and DENE T. Walters. “Diagnosis of systemic lupus erythematosus.” *American family physician* 68, no. 11 (2003): 2179-2186.

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50.7: Pathogens that Evade the Immune System

Skills to Develop

- Identify major viral illnesses that affect humans
- Compare vaccinations and anti-viral drugs as medical approaches to viruses

Viruses cause a variety of diseases in animals, including humans, ranging from the common cold to potentially fatal illnesses like meningitis (Figure 50.7.1). These diseases can be treated by antiviral drugs or by vaccines, but some viruses, such as HIV, are capable of both avoiding the immune response and mutating to become resistant to antiviral drugs.

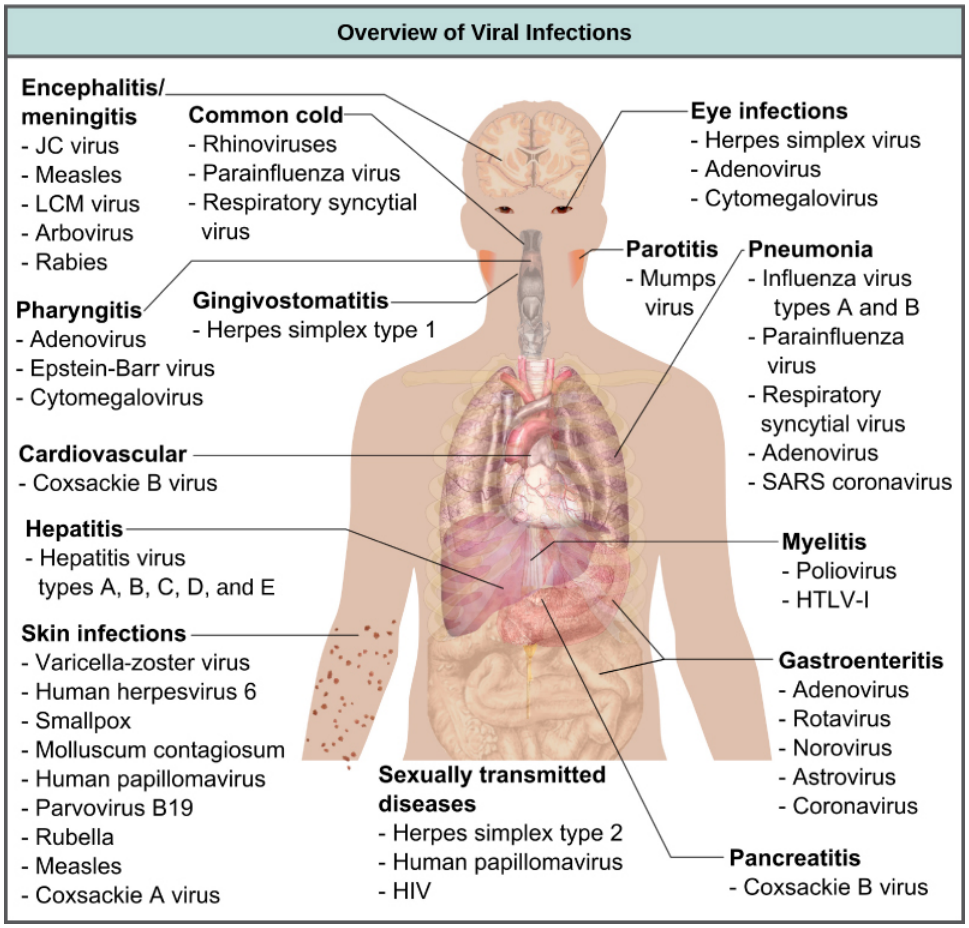


Figure 50.7.1: Viruses can cause dozens of ailments in humans, ranging from mild illnesses to serious diseases. (credit: modification of work by Mikael Häggström)

Vaccines for Prevention

While we do have limited numbers of effective antiviral drugs, such as those used to treat HIV and influenza, the primary method of controlling viral disease is by vaccination, which is intended to prevent outbreaks by building immunity to a virus or virus family (Figure 50.7.1). Vaccines may be prepared using live viruses, killed viruses, or molecular subunits of the virus. The killed viral vaccines and subunit viruses are both incapable of causing disease.

Live viral vaccines are designed in the laboratory to cause few symptoms in recipients while giving them protective immunity against future infections. Polio was one disease that represented a milestone in the use of vaccines. Mass immunization campaigns in the 1950s (killed vaccine) and 1960s (live vaccine) significantly reduced the incidence of the disease, which caused muscle paralysis in children and generated a great amount of fear in the general population when regional epidemics occurred. The success of the polio vaccine paved the way for the routine dispensation of childhood vaccines against measles, mumps, rubella, chickenpox, and other diseases.

The danger of using live vaccines, which are usually more effective than killed vaccines, is the low but significant danger that these viruses will revert to their disease-causing form by back mutations. Live vaccines are usually made by attenuating (weakening) the "wild-type" (disease-causing) virus by growing it in the laboratory in tissues or at temperatures different from what the virus is accustomed to in the host. Adaptations to these new cells or temperatures induce mutations in the genomes of the virus, allowing it to grow better in the laboratory while inhibiting its ability to cause disease when reintroduced into conditions found in the host. These attenuated viruses thus still cause infection, but they do not grow very well, allowing the immune response to develop in time to prevent major disease. Back mutations occur when the vaccine undergoes mutations in the host such that it readapts to the host and can again cause disease, which can then be spread to other humans in an epidemic. This type of scenario happened as recently as 2007 in Nigeria where mutations in a polio vaccine led to an epidemic of polio in that country.

Some vaccines are in continuous development because certain viruses, such as influenza and HIV, have a high mutation rate compared to other viruses and normal host cells. With influenza, mutations in the surface molecules of the virus help the organism evade the protective immunity that may have been obtained in a previous influenza season, making it necessary for individuals to get vaccinated every year. Other viruses, such as those that cause the childhood diseases measles, mumps, and rubella, mutate so infrequently that the same vaccine is used year after year.



Figure **50.7.2**: Vaccinations are designed to boost immunity to a virus to prevent infection. (credit: USACE Europe District)

Link to Learning



Watch this NOVA video to learn how microbiologists are attempting to replicate the deadly 1918 Spanish influenza virus so they can understand more about virology.

Vaccines and Anti-viral Drugs for Treatment

In some cases, vaccines can be used to treat an active viral infection. The concept behind this is that by giving the vaccine, immunity is boosted without adding more disease-causing virus. In the case of rabies, a fatal neurological disease transmitted via the saliva of rabies virus-infected animals, the progression of the disease from the time of the animal bite to the time it enters the central nervous system may be 2 weeks or longer. This is enough time to vaccinate an individual who suspects that they have been bitten by a rabid animal, and their boosted immune response is sufficient to prevent the virus from entering nervous tissue. Thus, the potentially fatal neurological consequences of the disease are averted, and the individual only has to recover from the infected bite. This approach is also being used for the treatment of Ebola, one of the fastest and most deadly viruses on earth. Transmitted by bats and great apes, this disease can cause death in 70–90 percent of infected humans within 2 weeks. Using newly developed vaccines that boost the immune response in this way, there is hope that affected individuals will be better able to control the virus, potentially saving a greater percentage of infected persons from a rapid and very painful death.

Another way of treating viral infections is the use of antiviral drugs. These drugs often have limited success in curing viral disease, but in many cases, they have been used to control and reduce symptoms for a wide variety of viral diseases. For most viruses, these drugs can inhibit the virus by blocking the actions of one or more of its proteins. It is important that the targeted proteins be encoded by viral genes and that these molecules are not present in a healthy host cell. In this way, viral growth is inhibited without damaging the host. There are large numbers of antiviral drugs available to treat infections, some specific for a particular virus and others that can affect multiple viruses.

Antivirals have been developed to treat genital herpes (herpes simplex II) and influenza. For genital herpes, drugs such as acyclovir can reduce the number and duration of episodes of active viral disease, during which patients develop viral lesions in their skin cells. As the virus remains latent in nervous tissue of the body for life, this drug is not curative but can make the symptoms of the disease more manageable. For influenza, drugs like Tamiflu (oseltamivir) (Figure **50.7.3**) can reduce the duration of “flu” symptoms by 1 or 2 days, but the drug does not prevent symptoms entirely. Tamiflu works by inhibiting an enzyme (viral neuraminidase) that allows new virions to leave their infected cells. Thus, Tamiflu inhibits the spread of virus from infected to uninfected cells. Other antiviral drugs, such as Ribavirin, have been used to treat a variety of viral infections, although its mechanism of action against certain viruses remains unclear.

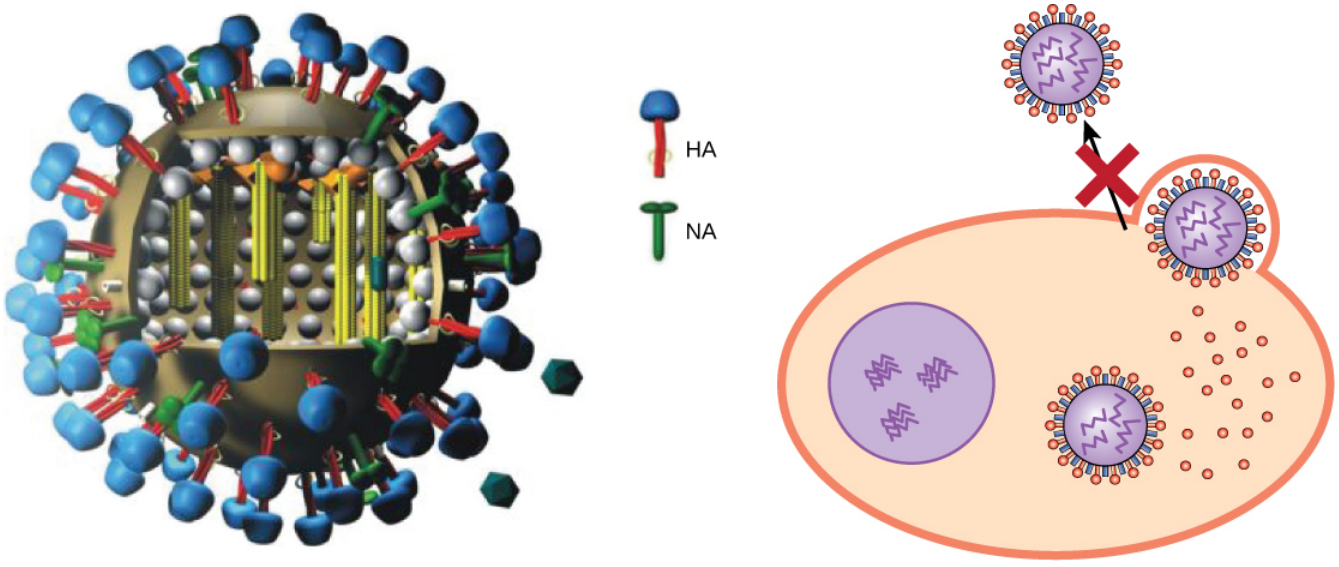


Figure **50.7.3**: (a) Tamiflu inhibits a viral enzyme called neuraminidase (NA) found in the influenza viral envelope. (b) Neuraminidase cleaves the connection between viral hemagglutinin (HA), also found in the viral envelope, and glycoproteins on the host cell surface. Inhibition of neuraminidase prevents the virus from detaching from the host cell, thereby blocking further infection. (credit a: modification of work by M. Eickmann)

By far, the most successful use of antivirals has been in the treatment of the retrovirus HIV, which causes a disease that, if untreated, is usually fatal within 10–12 years after infection. Anti-HIV drugs have been able to control viral replication to the point that individuals receiving these drugs survive for a significantly longer time than the untreated.

Anti-HIV drugs inhibit viral replication at many different phases of the HIV replicative cycle (Figure **50.7.4**). Drugs have been developed that inhibit the fusion of the HIV viral envelope with the plasma membrane of the host cell (fusion inhibitors), the conversion of its RNA genome into double-stranded DNA (reverse transcriptase inhibitors), the integration of the viral DNA into the host genome (integrase inhibitors), and the processing of viral proteins (protease inhibitors).

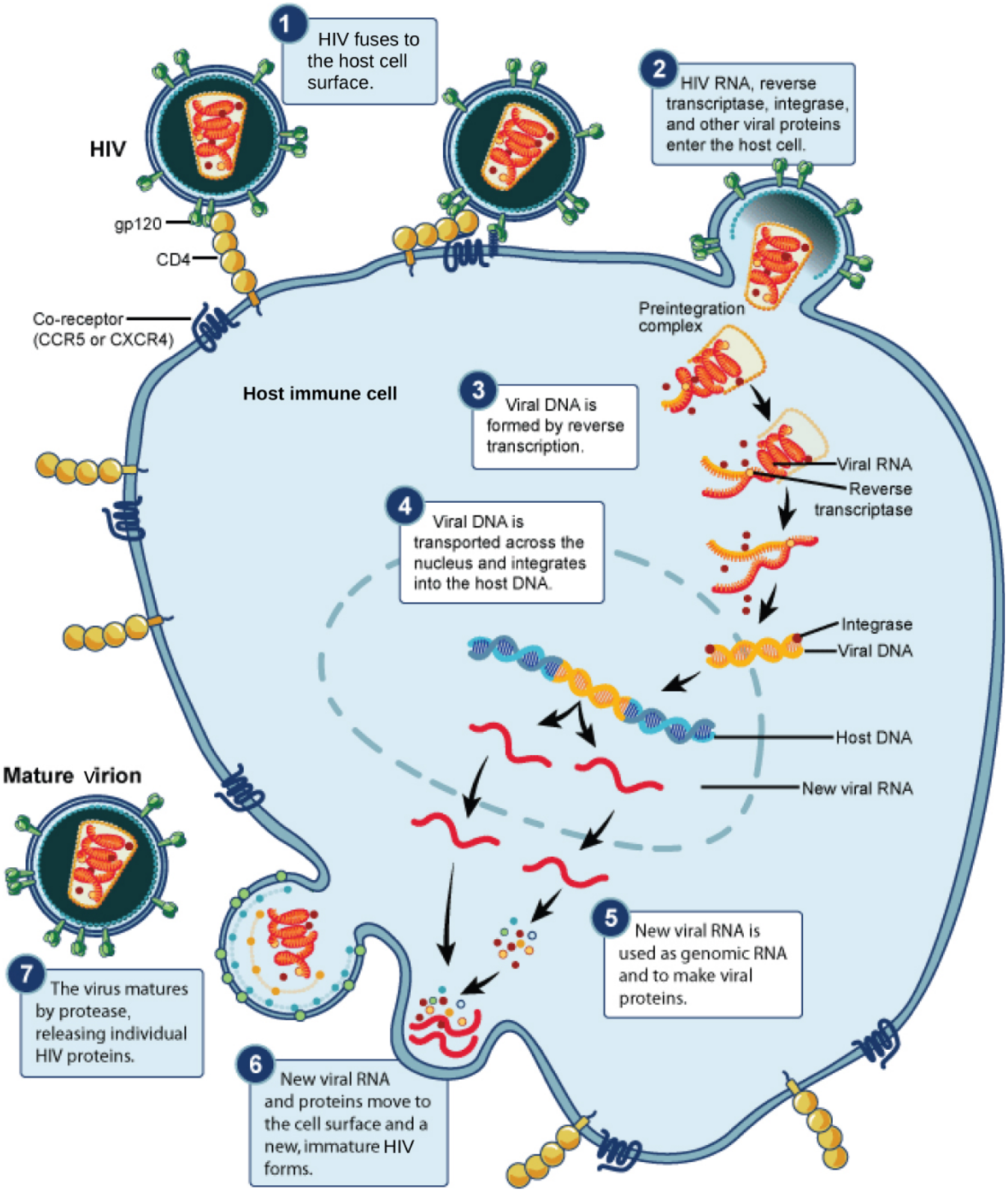


Figure **50.7.4**: HIV, an enveloped, icosahedral virus, attaches to the CD4 receptor of an immune cell and fuses with the cell membrane. Viral contents are released into the cell, where viral enzymes convert the single-stranded RNA genome into DNA and incorporate it into the host genome. (credit: NIAID, NIH)

When any of these drugs are used individually, the high mutation rate of the virus allows it to easily and rapidly develop resistance to the drug, limiting the drug's effectiveness. The breakthrough in the treatment of HIV was the development of HAART, highly active anti-retroviral therapy, which involves a mixture of different drugs, sometimes called a drug "cocktail." By attacking the

virus at different stages of its replicative cycle, it is much more difficult for the virus to develop resistance to multiple drugs at the same time. Still, even with the use of combination HAART therapy, there is concern that, over time, the virus will develop resistance to this therapy. Thus, new anti-HIV drugs are constantly being developed with the hope of continuing the battle against this highly fatal virus.

Everyday Connection: Applied Virology

The study of viruses has led to the development of a variety of new ways to treat non-viral diseases. Viruses have been used in gene therapy. Gene therapy is used to treat genetic diseases such as severe combined immunodeficiency (SCID), a heritable, recessive disease in which children are born with severely compromised immune systems. One common type of SCID is due to the lack of an enzyme, adenosine deaminase (ADA), which breaks down purine bases. To treat this disease by gene therapy, bone marrow cells are taken from a SCID patient and the ADA gene is inserted. This is where viruses come in, and their use relies on their ability to penetrate living cells and bring genes in with them. Viruses such as adenovirus, an upper respiratory human virus, are modified by the addition of the ADA gene, and the virus then transports this gene into the cell. The modified cells, now capable of making ADA, are then given back to the patients in the hope of curing them. Gene therapy using viruses as carrier of genes (viral vectors), although still experimental, holds promise for the treatment of many genetic diseases. Still, many technological problems need to be solved for this approach to be a viable method for treating genetic disease.

Another medical use for viruses relies on their specificity and ability to kill the cells they infect. Oncolytic viruses are engineered in the laboratory specifically to attack and kill cancer cells. A genetically modified adenovirus known as H101 has been used since 2005 in clinical trials in China to treat head and neck cancers. The results have been promising, with a greater short-term response rate to the combination of chemotherapy and viral therapy than to chemotherapy treatment alone. This ongoing research may herald the beginning of a new age of cancer therapy, where viruses are engineered to find and specifically kill cancer cells, regardless of where in the body they may have spread.

A third use of viruses in medicine relies on their specificity and involves using bacteriophages in the treatment of bacterial infections. Bacterial diseases have been treated with antibiotics since the 1940s. However, over time, many bacteria have developed resistance to antibiotics. A good example is methicillin-resistant *Staphylococcus aureus* (MRSA, pronounced “mersa”), an infection commonly acquired in hospitals. This bacterium is resistant to a variety of antibiotics, making it difficult to treat. The use of bacteriophages specific for such bacteria would bypass their resistance to antibiotics and specifically kill them. Although phage therapy is in use in the Republic of Georgia to treat antibiotic-resistant bacteria, its use to treat human diseases has not been approved in most countries. However, the safety of the treatment was confirmed in the United States when the U.S. Food and Drug Administration approved spraying meats with bacteriophages to destroy the food pathogen *Listeria*. As more and more antibiotic-resistant strains of bacteria evolve, the use of bacteriophages might be a potential solution to the problem, and the development of phage therapy is of much interest to researchers worldwide.

Summary

Viruses cause a variety of diseases in humans. Many of these diseases can be prevented by the use of viral vaccines, which stimulate protective immunity against the virus without causing major disease. Viral vaccines may also be used in active viral infections, boosting the ability of the immune system to control or destroy the virus. A series of antiviral drugs that target enzymes and other protein products of viral genes have been developed and used with mixed success. Combinations of anti-HIV drugs have been used to effectively control the virus, extending the lifespans of infected individuals. Viruses have many uses in medicines, such as in the treatment of genetic disorders, cancer, and bacterial infections.

Glossary

attenuation

weakening of a virus during vaccine development

back mutation

when a live virus vaccine reverts back to it disease-causing phenotype

gene therapy
treatment of genetic disease by adding genes, using viruses to carry the new genes inside the cell

oncolytic virus
virus engineered to specifically infect and kill cancer cells

phage therapy
treatment of bacterial diseases using bacteriophages specific to a particular bacterium

vaccine
weakened solution of virus components, viruses, or other agents that produce an immune response

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CHAPTER OVERVIEW

51: The Reproductive System

51.1: Animal Reproductive Strategies

51.2: Vertebrate Fertilization and Development

51.3: Structure and Function of the Human Male Reproductive System

51.3.1: Hormonal Control of Human Reproduction

51.4: Structure and Function of the Female Reproductive System

51.4.1: Hormonal Control of Human Reproduction

51.4.2: Human Pregnancy and Birth

51.5: Contraception and Fertility Treatments

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51.1: Animal Reproductive Strategies

Skills to Develop

- Describe advantages and disadvantages of asexual and sexual reproduction
- Discuss asexual reproduction methods
- Discuss sexual reproduction methods

Animals produce offspring through asexual and/or sexual reproduction. Both methods have advantages and disadvantages. Asexual reproduction produces offspring that are genetically identical to the parent because the offspring are all clones of the original parent. A single individual can produce offspring asexually and large numbers of offspring can be produced quickly. In a stable or predictable environment, asexual reproduction is an effective means of reproduction because all the offspring will be adapted to that environment. In an unstable or unpredictable environment asexually-reproducing species may be at a disadvantage because all the offspring are genetically identical and may not have the genetic variation to survive in new or different conditions. On the other hand, the rapid rates of asexual reproduction may allow for a speedy response to environmental changes if individuals have mutations. An additional advantage of asexual reproduction is that colonization of new habitats may be easier when an individual does not need to find a mate to reproduce.

During sexual reproduction the genetic material of two individuals is combined to produce genetically diverse offspring that differ from their parents. The genetic diversity of sexually produced offspring is thought to give species a better chance of surviving in an unpredictable or changing environment. Species that reproduce sexually must maintain two different types of individuals, males and females, which can limit the ability to colonize new habitats as both sexes must be present.

Asexual Reproduction

Asexual reproduction occurs in prokaryotic microorganisms (bacteria) and in some eukaryotic single-celled and multi-celled organisms. There are a number of ways that animals reproduce asexually.

Fission

Fission, also called binary fission, occurs in prokaryotic microorganisms and in some invertebrate, multi-celled organisms. After a period of growth, an organism splits into two separate organisms. Some unicellular eukaryotic organisms undergo binary fission by mitosis. In other organisms, part of the individual separates and forms a second individual. This process occurs, for example, in many asteroid echinoderms through splitting of the central disk. Some sea anemones and some coral polyps (Figure **51.1.1**) also reproduce through fission.



Figure **51.1.1**: Coral polyps reproduce asexually by fission. (credit: G. P. Schmahl, NOAA FGBNMS Manager)

Budding

Budding is a form of asexual reproduction that results from the outgrowth of a part of a cell or body region leading to a separation from the original organism into two individuals. Budding occurs commonly in some invertebrate animals such as corals and hydras. In hydras, a bud forms that develops into an adult and breaks away from the main body, as illustrated in Figure **51.1.2**, whereas in coral budding, the bud does not detach and multiplies as part of a new colony.

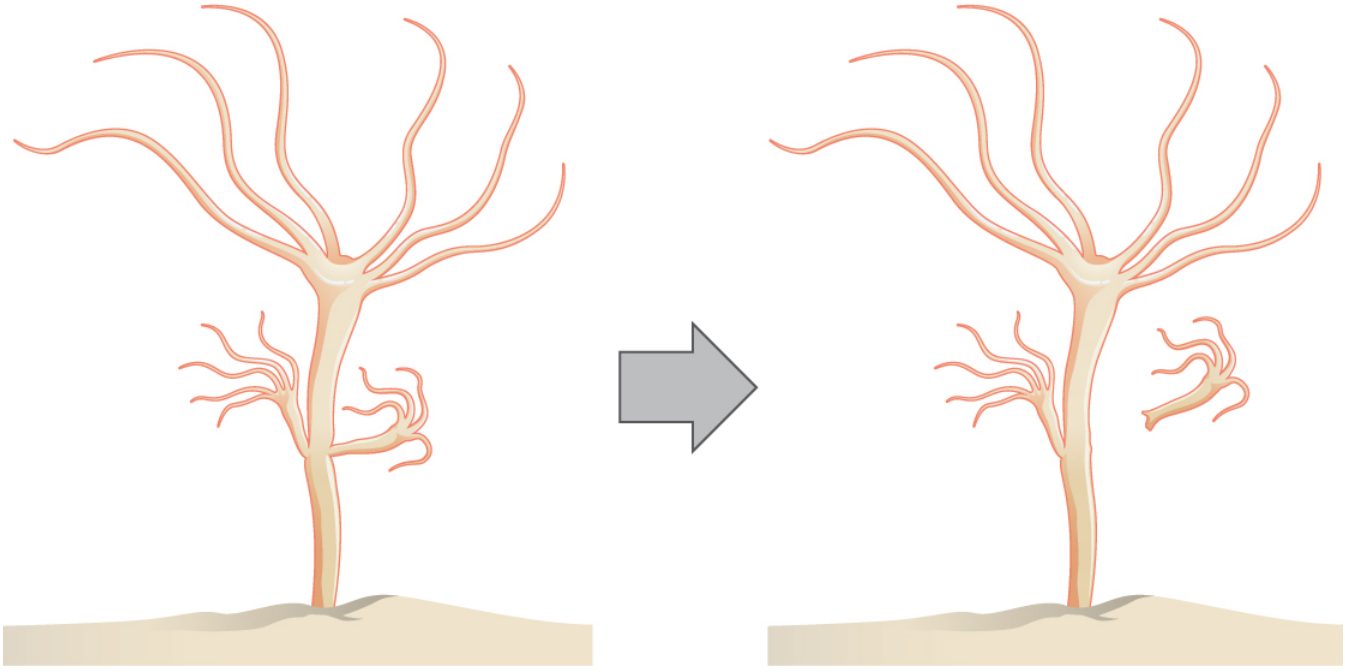
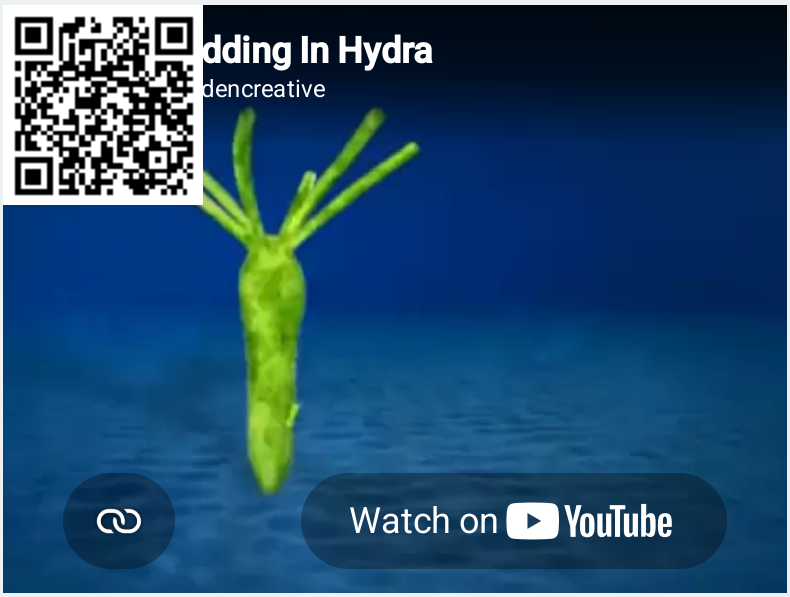


Figure **51.1.2**: Hydra reproduce asexually through budding.

Link to Learning



Watch a video of a hydra budding.

Fragmentation

Fragmentation is the breaking of the body into two parts with subsequent regeneration. If the animal is capable of fragmentation, and the part is big enough, a separate individual will regrow.

For example, in many sea stars, asexual reproduction is accomplished by fragmentation. Figure **51.1.3** illustrates a sea star for which an arm of the individual is broken off and regenerates a new sea star. Fisheries workers have been known to try to kill the sea stars eating their clam or oyster beds by cutting them in half and throwing them back into the ocean. Unfortunately for the workers, the two parts can each regenerate a new half, resulting in twice as many sea stars to prey upon the oysters and clams. Fragmentation also occurs in annelid worms, turbellarians, and poriferans.



Figure **51.1.3**: Sea stars can reproduce through fragmentation. The large arm, a fragment from another sea star, is developing into a new individual.

Note that in fragmentation, there is generally a noticeable difference in the size of the individuals, whereas in fission, two individuals of approximate size are formed.

Parthenogenesis

Parthenogenesis is a form of asexual reproduction where an egg develops into a complete individual without being fertilized. The resulting offspring can be either haploid or diploid, depending on the process and the species. Parthenogenesis occurs in invertebrates such as water flees, rotifers, aphids, stick insects, some ants, wasps, and bees. Bees use parthenogenesis to produce haploid males (drones) and diploid females (workers). If an egg is fertilized, a queen is produced. The queen bee controls the reproduction of the hive bees to regulate the type of bee produced.

Some vertebrate animals—such as certain reptiles, amphibians, and fish—also reproduce through parthenogenesis. Although more common in plants, parthenogenesis has been observed in animal species that were segregated by sex in terrestrial or marine zoos. Two female Komodo dragons, a hammerhead shark, and a blacktop shark have produced parthenogenic young when the females have been isolated from males.

Sexual Reproduction

Sexual reproduction is the combination of (usually haploid) reproductive cells from two individuals to form a third (usually diploid) unique offspring. Sexual reproduction produces offspring with novel combinations of genes. This can be an adaptive advantage in unstable or unpredictable environments. As humans, we are used to thinking of animals as having two separate sexes—male and female—determined at conception. However, in the animal kingdom, there are many variations on this theme.

Hermaphroditism

Hermaphroditism occurs in animals where one individual has both male and female reproductive parts. Invertebrates such as earthworms, slugs, tapeworms and snails, shown in Figure **51.1.4**, are often hermaphroditic. Hermaphrodites may self-fertilize or may mate with another of their species, fertilizing each other and both producing offspring. Self fertilization is common in animals that have limited mobility or are not motile, such as barnacles and clams.



Figure **51.1.4**: Many snails are hermaphrodites. When two individuals mate, they can produce up to one hundred eggs each. (credit: Assaf Shtilman)

Sex Determination

Mammalian sex determination is determined genetically by the presence of X and Y chromosomes. Individuals homozygous for X (XX) are female and heterozygous individuals (XY) are male. The presence of a Y chromosome causes the development of male characteristics and its absence results in female characteristics. The XY system is also found in some insects and plants.

Avian sex determination is dependent on the presence of Z and W chromosomes. Homozygous for Z (ZZ) results in a male and heterozygous (ZW) results in a female. The W appears to be essential in determining the sex of the individual, similar to the Y chromosome in mammals. Some fish, crustaceans, insects (such as butterflies and moths), and reptiles use this system.

The sex of some species is not determined by genetics but by some aspect of the environment. Sex determination in some crocodiles and turtles, for example, is often dependent on the temperature during critical periods of egg development. This is referred to as environmental sex determination, or more specifically as temperature-dependent sex determination. In many turtles,

cooler temperatures during egg incubation produce males and warm temperatures produce females. In some crocodiles, moderate temperatures produce males and both warm and cool temperatures produce females. In some species, sex is both genetic- and temperature-dependent.

Individuals of some species change their sex during their lives, alternating between male and female. If the individual is female first, it is termed protogyny or “first female,” if it is male first, its termed protandry or “first male.” Oysters, for example, are born male, grow, and become female and lay eggs; some oyster species change sex multiple times.

Summary

Reproduction may be asexual when one individual produces genetically identical offspring, or sexual when the genetic material from two individuals is combined to produce genetically diverse offspring. Asexual reproduction occurs through fission, budding, and fragmentation. Sexual reproduction may mean the joining of sperm and eggs within animals’ bodies or it may mean the release of sperm and eggs into the environment. An individual may be one sex, or both; it may start out as one sex and switch during its life, or it may stay male or female.

Glossary

asexual reproduction
: form of reproduction that produces offspring that are genetically identical to the parent

budding
: form of asexual reproduction that results from the outgrowth of a part of a cell leading to a separation from the original animal into two individuals

fission
: (also, binary fission) method by which multicellular organisms increase in size or asexual reproduction in which a unicellular organism splits into two separate organisms by mitosis

fragmentation
: cutting or fragmenting of the original animal into parts and the growth of a separate animal from each part

hermaphroditism
: state of having both male and female reproductive parts within the same individual

parthenogenesis
: form of asexual reproduction where an egg develops into a complete individual without being fertilized

sexual reproduction
: mixing of genetic material from two individuals to produce genetically unique offspring

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51.2: Vertebrate Fertilization and Development

Skills to Develop

- Discuss internal and external methods of fertilization
- Describe the methods used by animals for development of offspring during gestation
- Describe the anatomical adaptions that occurred in animals to facilitate reproduction

Sexual reproduction starts with the combination of a sperm and an egg in a process called fertilization. This can occur either inside (internal fertilization) or outside (external fertilization) the body of the female. Humans provide an example of the former whereas seahorse reproduction is an example of the latter.

External Fertilization

External fertilization usually occurs in aquatic environments where both eggs and sperm are released into the water. After the sperm reaches the egg, fertilization takes place. Most external fertilization happens during the process of spawning where one or several females release their eggs and the male(s) release sperm in the same area, at the same time. The release of the reproductive material may be triggered by water temperature or the length of daylight. Nearly all fish spawn, as do crustaceans (such as crabs and shrimp), mollusks (such as oysters), squid, and echinoderms (such as sea urchins and sea cucumbers). Figure 51.2.1 shows salmon spawning in a shallow stream. Frogs, like those shown in Figure 51.2.2, corals, molluscs, and sea cucumbers also spawn.



Figure 51.2.1: Salmon reproduce through spawning. (credit: Dan Bennett)



Figure **51.2.2**: During sexual reproduction in toads, the male grasps the female from behind and externally fertilizes the eggs as they are deposited. (credit: "OakleyOriginals"/Flickr)

Pairs of fish that are not broadcast spawners may exhibit courtship behavior. This allows the female to select a particular male. The trigger for egg and sperm release (spawning) causes the egg and sperm to be placed in a small area, enhancing the possibility of fertilization.

External fertilization in an aquatic environment protects the eggs from drying out. Broadcast spawning can result in a greater mixture of the genes within a group, leading to higher genetic diversity and a greater chance of species survival in a hostile environment. For sessile aquatic organisms like sponges, broadcast spawning is the only mechanism for fertilization and colonization of new environments. The presence of the fertilized eggs and developing young in the water provides opportunities for predation resulting in a loss of offspring. Therefore, millions of eggs must be produced by individuals, and the offspring produced through this method must mature rapidly. The survival rate of eggs produced through broadcast spawning is low.

Internal Fertilization

Internal fertilization occurs most often in land-based animals, although some aquatic animals also use this method. There are three ways that offspring are produced following internal fertilization. In oviparity, fertilized eggs are laid outside the female's body and develop there, receiving nourishment from the yolk that is a part of the egg. This occurs in most bony fish, many reptiles, some cartilaginous fish, most amphibians, two mammals, and all birds. Reptiles and insects produce leathery eggs, while birds and turtles produce eggs with high concentrations of calcium carbonate in the shell, making them hard. Chicken eggs are an example of this second type.

In ovoviparity, fertilized eggs are retained in the female, but the embryo obtains its nourishment from the egg's yolk and the young are fully developed when they are hatched. This occurs in some bony fish (like the guppy *Lebistes reticulatus*), some sharks, some lizards, some snakes (such as the garter snake *Thamnophis sirtalis*), some vipers, and some invertebrate animals (like the Madagascar hissing cockroach *Gromphadorhina portentosa*).

In viviparity the young develop within the female, receiving nourishment from the mother's blood through a placenta. The offspring develops in the female and is born alive. This occurs in most mammals, some cartilaginous fish, and a few reptiles.

Internal fertilization has the advantage of protecting the fertilized egg from dehydration on land. The embryo is isolated within the female, which limits predation on the young. Internal fertilization enhances the fertilization of eggs by a specific male. Fewer offspring are produced through this method, but their survival rate is higher than that for external fertilization.

The Evolution of Reproduction

Once multicellular organisms evolved and developed specialized cells, some also developed tissues and organs with specialized functions. An early development in reproduction occurred in the Annelids. These organisms produce sperm and eggs from undifferentiated cells in their coelom and store them in that cavity. When the coelom becomes filled, the cells are released through an excretory opening or by the body splitting open. Reproductive organs evolved with the development of gonads that produce sperm and eggs. These cells went through meiosis, an adaption of mitosis, which reduced the number of chromosomes in each reproductive cell by half, while increasing the number of cells through cell division.

Complete reproductive systems were developed in insects, with separate sexes. Sperm are made in testes and then travel through coiled tubes to the epididymis for storage. Eggs mature in the ovary. When they are released from the ovary, they travel to the uterine tubes for fertilization. Some insects have a specialized sac, called a spermatheca, which stores sperm for later use, sometimes up to a year. Fertilization can be timed with environmental or food conditions that are optimal for offspring survival.

Vertebrates have similar structures, with a few differences. Non-mammals, such as birds and reptiles, have a common body opening, called a cloaca, for the digestive, excretory and reproductive systems. Coupling between birds usually involves positioning the cloaca openings opposite each other for transfer of sperm. Mammals have separate openings for the systems in the female and a uterus for support of developing offspring. The uterus has two chambers in species that produce large numbers of offspring at a time, while species that produce one offspring, such as primates, have a single uterus.

Sperm transfer from the male to the female during reproduction ranges from releasing the sperm into the watery environment for external fertilization, to the joining of cloaca in birds, to the development of a penis for direct delivery into the female's vagina in mammals.

Summary

Sexual reproduction starts with the combination of a sperm and an egg in a process called fertilization. This can occur either outside the bodies or inside the female. Both methods have advantages and disadvantages. Once fertilized, the eggs can develop inside the female or outside. If the egg develops outside the body, it usually has a protective covering over it. Animal anatomy evolved various ways to fertilize, hold, or expel the egg. The method of fertilization varies among animals. Some species release the egg and sperm into the environment, some species retain the egg and receive the sperm into the female body and then expel the developing embryo covered with shell, while still other species retain the developing offspring through the gestation period.

Glossary

cloaca
: common body opening for the digestive, excretory, and reproductive systems found in non-mammals, such as birds

external fertilization
: fertilization of egg by sperm outside animal body, often during spawning

internal fertilization
: fertilization of egg by sperm inside the body of the female

oviparity
: process by which fertilized eggs are laid outside the female's body and develop there, receiving nourishment from the yolk that is a part of the egg

ovoviparity
: process by which fertilized eggs are retained within the female; the embryo obtains its nourishment from the egg's yolk and the young are fully developed when they are hatched

spermatheca
: specialized sac that stores sperm for later use

viviparity

process in which the young develop within the female, receiving nourishment from the mother’s blood through a placenta

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51.3: Structure and Function of the Human Male Reproductive System

Skills to Develop

- Describe human male and female reproductive anatomies
- Discuss the human sexual response
- Describe spermatogenesis and oogenesis and discuss their differences and similarities

As animals became more complex, specific organs and organ systems developed to support specific functions for the organism. The reproductive structures that evolved in land animals allow males and females to mate, fertilize internally, and support the growth and development of offspring.

Human Reproductive Anatomy

The reproductive tissues of male and female humans develop similarly *in utero* until a low level of the hormone testosterone is released from male gonads. Testosterone causes the undeveloped tissues to differentiate into male sexual organs. When testosterone is absent, the tissues develop into female sexual tissues. Primitive gonads become testes or ovaries. Tissues that produce a penis in males produce a clitoris in females. The tissue that will become the scrotum in a male becomes the labia in a female; that is, they are homologous structures.

Male Reproductive Anatomy

In the male reproductive system, the scrotum houses the testicles or testes (singular: testis), including providing passage for blood vessels, nerves, and muscles related to testicular function. The testes are a pair of male reproductive organs that produce sperm and some reproductive hormones. Each testis is approximately 2.5 by 3.8 cm (1.5 by 1 in) in size and divided into wedge-shaped lobules by connective tissue called septa. Coiled in each wedge are seminiferous tubules that produce sperm.

Sperm are immobile at body temperature; therefore, the scrotum and penis are external to the body, as illustrated in Figure **51.3.1** so that a proper temperature is maintained for motility. In land mammals, the pair of testes must be suspended outside the body at about 2° C lower than body temperature to produce viable sperm. Infertility can occur in land mammals when the testes do not descend through the abdominal cavity during fetal development.

Art Connection

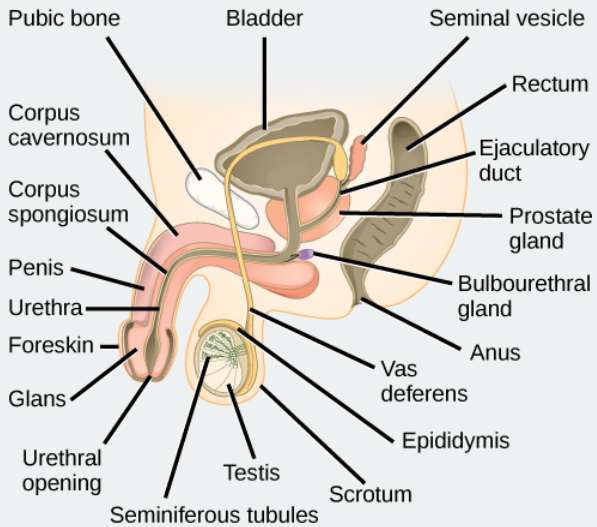


Figure **51.3.1**: The reproductive structures of the human male are shown.

Which of the following statements about the male reproductive system is false?

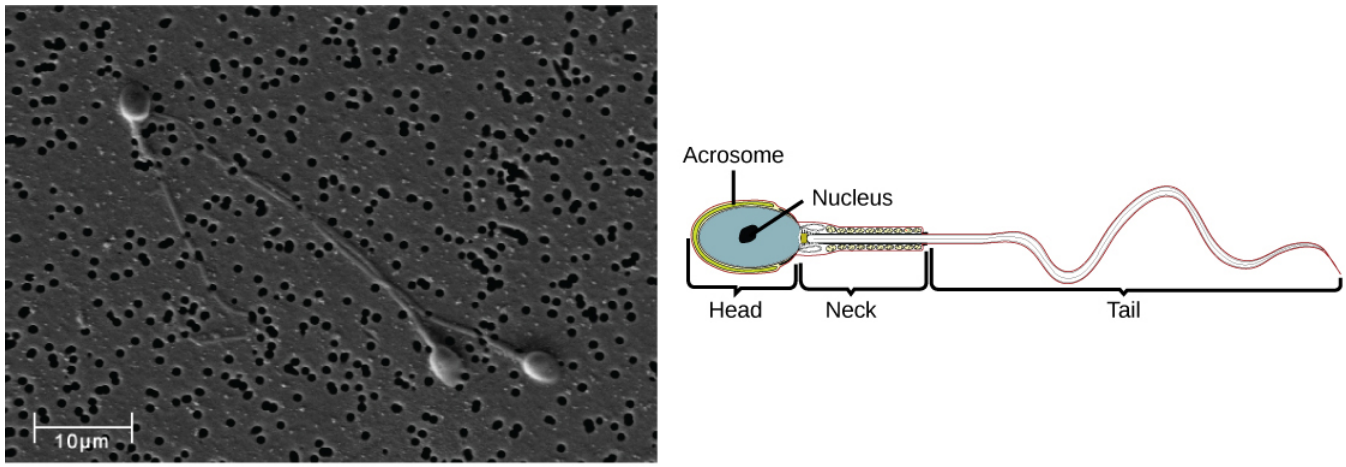
A. The vas deferens carries sperm from the testes to the penis.
B. Sperm mature in seminiferous tubules in the testes.
C. Both the prostate and the bulbourethral glands produce components of the semen.

D. The prostate gland is located in the testes.

Sperm mature in seminiferous tubules that are coiled inside the testes, as illustrated in Figure **51.3.1**. The walls of the seminiferous tubules are made up of the developing sperm cells, with the least developed sperm at the periphery of the tubule and the fully developed sperm in the lumen. The sperm cells are mixed with “nursemaid” cells called Sertoli cells which protect the germ cells and promote their development. Other cells mixed in the wall of the tubules are the interstitial cells of Leydig. These cells produce high levels of testosterone once the male reaches adolescence.

When the sperm have developed flagella and are nearly mature, they leave the testicles and enter the epididymis, shown in Figure **51.3.1**. This structure resembles a comma and lies along the top and posterior portion of the testes; it is the site of sperm maturation. The sperm leave the epididymis and enter the vas deferens (or ductus deferens), which carries the sperm, behind the bladder, and forms the ejaculatory duct with the duct from the seminal vesicles. During a vasectomy, a section of the vas deferens is removed, preventing sperm from being passed out of the body during ejaculation and preventing fertilization.

Semen is a mixture of sperm and spermatic duct secretions (about 10 percent of the total) and fluids from accessory glands that contribute most of the semen’s volume. Sperm are haploid cells, consisting of a flagellum as a tail, a neck that contains the cell’s energy-producing mitochondria, and a head that contains the genetic material. Figure **51.3.2** shows a micrograph of human sperm as well as a diagram of the parts of the sperm. An acrosome is found at the top of the head of the sperm. This structure contains lysosomal enzymes that can digest the protective coverings that surround the egg to help the sperm penetrate and fertilize the egg. An ejaculate will contain from two to five milliliters of fluid with from 50–120 million sperm per milliliter.



(a) (b)

Figure **51.3.2**: Human sperm, visualized using scanning electron microscopy, have a flagellum, neck, and head. (credit b: modification of work by Mariana Ruiz Villareal; scale-bar data from Matt Russell)

The bulk of the semen comes from the accessory glands associated with the male reproductive system. These are the seminal vesicles, the prostate gland, and the bulbourethral gland, all of which are illustrated in Figure **51.3.1**. The seminal vesicles are a pair of glands that lie along the posterior border of the urinary bladder. The glands make a solution that is thick, yellowish, and alkaline. As sperm are only motile in an alkaline environment, a basic pH is important to reverse the acidity of the vaginal environment. The solution also contains mucus, fructose (a sperm mitochondrial nutrient), a coagulating enzyme, ascorbic acid, and local-acting hormones called prostaglandins. The seminal vesicle glands account for 60 percent of the bulk of semen.

The penis, illustrated in Figure **51.3.1**, is an organ that drains urine from the renal bladder and functions as a copulatory organ during intercourse. The penis contains three tubes of erectile tissue running through the length of the organ. These consist of a pair of tubes on the dorsal side, called the corpus cavernosum, and a single tube of tissue on the ventral side, called the corpus spongiosum. This tissue will become engorged with blood, becoming erect and hard, in preparation for intercourse. The organ is inserted into the vagina culminating with an ejaculation. During intercourse, the smooth muscle sphincters at the opening to the renal bladder close and prevent urine from entering the penis. An orgasm is a two-stage process: first, glands and accessory organs connected to the testes contract, then semen (containing sperm) is expelled through the urethra during ejaculation. After intercourse, the blood drains from the erectile tissue and the penis becomes flaccid.

The walnut-shaped prostate gland surrounds the urethra, the connection to the urinary bladder. It has a series of short ducts that directly connect to the urethra. The gland is a mixture of smooth muscle and glandular tissue. The muscle provides much of the force needed for ejaculation to occur. The glandular tissue makes a thin, milky fluid that contains citrate (a nutrient), enzymes, and prostate specific antigen (PSA). PSA is a proteolytic enzyme that helps to liquefy the ejaculate several minutes after release from the male. Prostate gland secretions account for about 30 percent of the bulk of semen.

The bulbourethral gland, or Cowper's gland, releases its secretion prior to the release of the bulk of the semen. It neutralizes any acid residue in the urethra left over from urine. This usually accounts for a couple of drops of fluid in the total ejaculate and may contain a few sperm. Withdrawal of the penis from the vagina before ejaculation to prevent pregnancy may not work if sperm are present in the bulbourethral gland secretions. The location and functions of the male reproductive organs are summarized in Table **51.3.1**.

Table 51.3.1: Male Reproductive Anatomy

Organ	Location	Function
Scrotum	External	Carry and support testes
Penis	External	Deliver urine, copulating organ
Testes	Internal	Produce sperm and male hormones
Seminal Vesicles	Internal	Contribute to semen production
Prostate Gland	Internal	Contribute to semen production
Bulbourethral Glands	Internal	Clean urethra at ejaculation

Female Reproductive Anatomy

A number of reproductive structures are exterior to the female's body. These include the breasts and the vulva, which consists of the mons pubis, clitoris, labia majora, labia minora, and the vestibular glands, all illustrated in Figure **51.3.3**. The location and functions of the female reproductive organs are summarized in Table **51.3.2**. The vulva is an area associated with the vestibule which includes the structures found in the inguinal (groin) area of women. The mons pubis is a round, fatty area that overlies the pubic symphysis. The clitoris is a structure with erectile tissue that contains a large number of sensory nerves and serves as a source of stimulation during intercourse. The labia majora are a pair of elongated folds of tissue that run posterior from the mons pubis and enclose the other components of the vulva. The labia majora derive from the same tissue that produces the scrotum in a male. The labia minora are thin folds of tissue centrally located within the labia majora. These labia protect the openings to the vagina and urethra. The mons pubis and the anterior portion of the labia majora become covered with hair during adolescence; the labia minora is hairless. The greater vestibular glands are found at the sides of the vaginal opening and provide lubrication during intercourse.

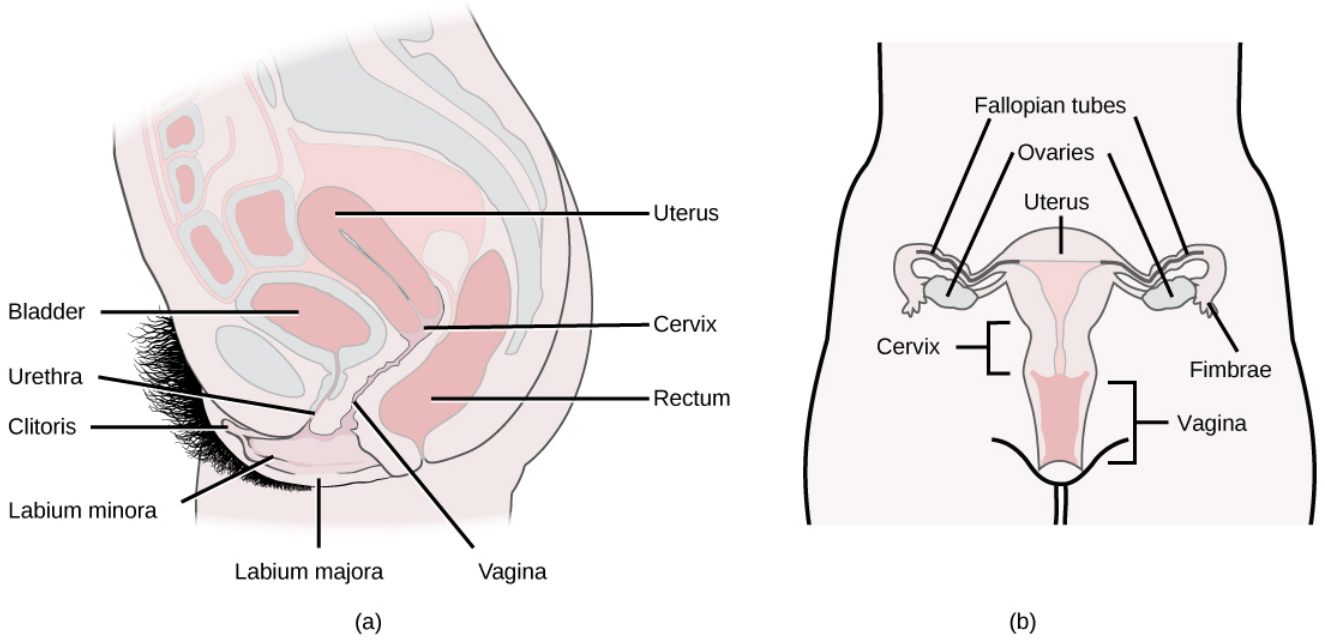


Figure **51.3.3**: The reproductive structures of the human female are shown. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by CDC)

Table 51.3.2: Female Reproductive Anatomy

Organ	Location	Function
Clitoris	External	Sensory organ
Mons pubis	External	Fatty area overlying pubic bone
Labia majora	External	Covers labia minora
Labia minora	External	Covers vestibule
Greater vestibular glands	External	Secrete mucus; lubricate vagina
Breast	External	Produce and deliver milk
Ovaries	Internal	Carry and develop eggs
Oviducts (Fallopian tubes)	Internal	Transport egg to uterus
Uterus	Internal	Support developing embryo
Vagina	Internal	Common tube for intercourse, birth canal, passing menstrual flow

The breasts consist of mammary glands and fat. The size of the breast is determined by the amount of fat deposited behind the gland. Each gland consists of 15 to 25 lobes that have ducts that empty at the nipple and that supply the nursing child with nutrient- and antibody-rich milk to aid development and protect the child.

Internal female reproductive structures include ovaries, oviducts, the uterus, and the vagina, shown in Figure **51.3.3**. The pair of ovaries is held in place in the abdominal cavity by a system of ligaments. Ovaries consist of a medulla and cortex: the medulla contains nerves and blood vessels to supply the cortex with nutrients and remove waste. The outer layers of cells of the cortex are the functional parts of the ovaries. The cortex is made up of follicular cells that surround eggs that develop during fetal development *in utero*. During the menstrual period, a batch of follicular cells develops and prepares the eggs for release. At ovulation, one follicle ruptures and one egg is released, as illustrated in Figure **51.3.4**.

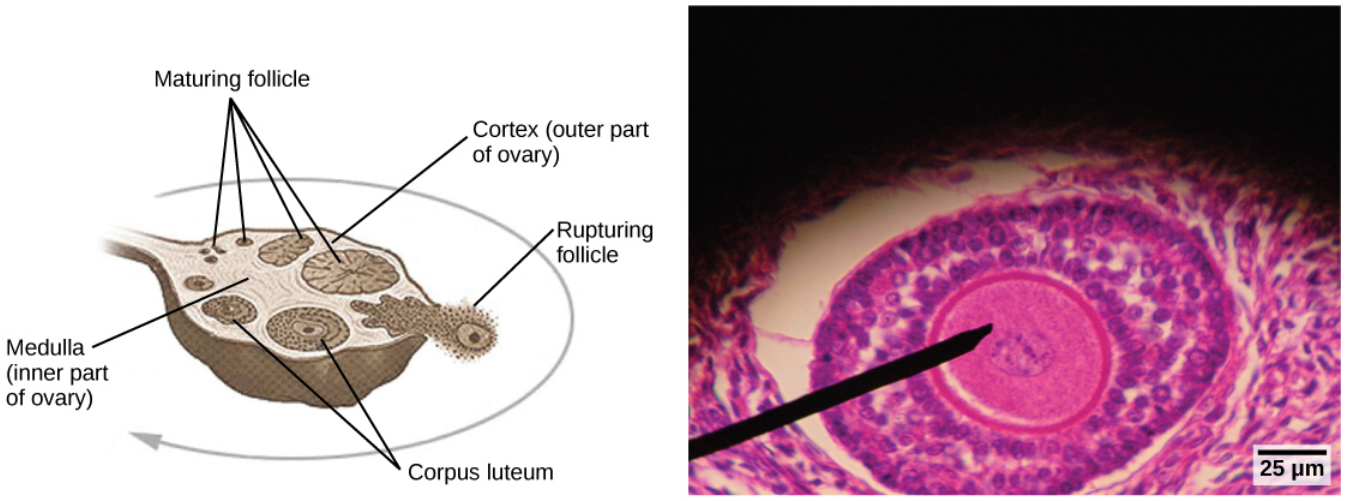


Figure **51.3.4**: Oocytes develop in (a) follicles, located in the ovary. At the beginning of the menstrual cycle, the follicle matures. At ovulation, the follicle ruptures, releasing the egg. The follicle becomes a corpus luteum, which eventually degenerates. The (b) follicle in this light micrograph has an oocyte at its center. (credit a: modification of work by NIH; scale-bar data from Matt Russell)

The oviducts, or fallopian tubes, extend from the uterus in the lower abdominal cavity to the ovaries, but they are not in contact with the ovaries. The lateral ends of the oviducts flare out into a trumpet-like structure and have a fringe of finger-like projections called fimbriae, illustrated in Figure **51.3.4**. When an egg is released at ovulation, the fimbrae help the non-motile egg enter into the tube and passage to the uterus. The walls of the oviducts are ciliated and are made up mostly of smooth muscle. The cilia beat toward the middle, and the smooth muscle contracts in the same direction, moving the egg toward the uterus. Fertilization usually takes place within the oviducts and the developing embryo is moved toward the uterus for development. It usually takes the egg or embryo a week to travel through the oviduct. Sterilization in women is called a tubal ligation; it is analogous to a vasectomy in males in that the oviducts are severed and sealed.

The uterus is a structure about the size of a woman's fist. This is lined with an endometrium rich in blood vessels and mucus glands. The uterus supports the developing embryo and fetus during gestation. The thickest portion of the wall of the uterus is made of smooth muscle. Contractions of the smooth muscle in the uterus aid in passing the baby through the vagina during labor. A portion of the lining of the uterus sloughs off during each menstrual period, and then builds up again in preparation for an implantation. Part of the uterus, called the cervix, protrudes into the top of the vagina. The cervix functions as the birth canal.

The vagina is a muscular tube that serves several purposes. It allows menstrual flow to leave the body. It is the receptacle for the penis during intercourse and the vessel for the delivery of offspring. It is lined by stratified squamous epithelial cells to protect the underlying tissue.

Sexual Response during Intercourse

The sexual response in humans is both psychological and physiological. Both sexes experience sexual arousal through psychological and physical stimulation. There are four phases of the sexual response. During phase one, called excitement, vasodilation leads to vasocongestion in erectile tissues in both men and women. The nipples, clitoris, labia, and penis engorge with blood and become enlarged. Vaginal secretions are released to lubricate the vagina to facilitate intercourse. During the second phase, called the plateau, stimulation continues, the outer third of the vaginal wall enlarges with blood, and breathing and heart rate increase.

During phase three, or orgasm, rhythmic, involuntary contractions of muscles occur in both sexes. In the male, the reproductive accessory glands and tubules constrict placing semen in the urethra, then the urethra contracts expelling the semen through the penis. In women, the uterus and vaginal muscles contract in waves that may last slightly less than a second each. During phase four, or resolution, the processes described in the first three phases reverse themselves and return to their normal state. Men experience a refractory period in which they cannot maintain an erection or ejaculate for a period of time ranging from minutes to hours.

Gametogenesis (Spermatogenesis and Oogenesis)

Gametogenesis, the production of sperm and eggs, takes place through the process of meiosis. During meiosis, two cell divisions separate the paired chromosomes in the nucleus and then separate the chromatids that were made during an earlier stage of the cell's life cycle. Meiosis produces haploid cells with half of each pair of chromosomes normally found in diploid cells. The production of sperm is called spermatogenesis and the production of eggs is called oogenesis.

Spermatogenesis

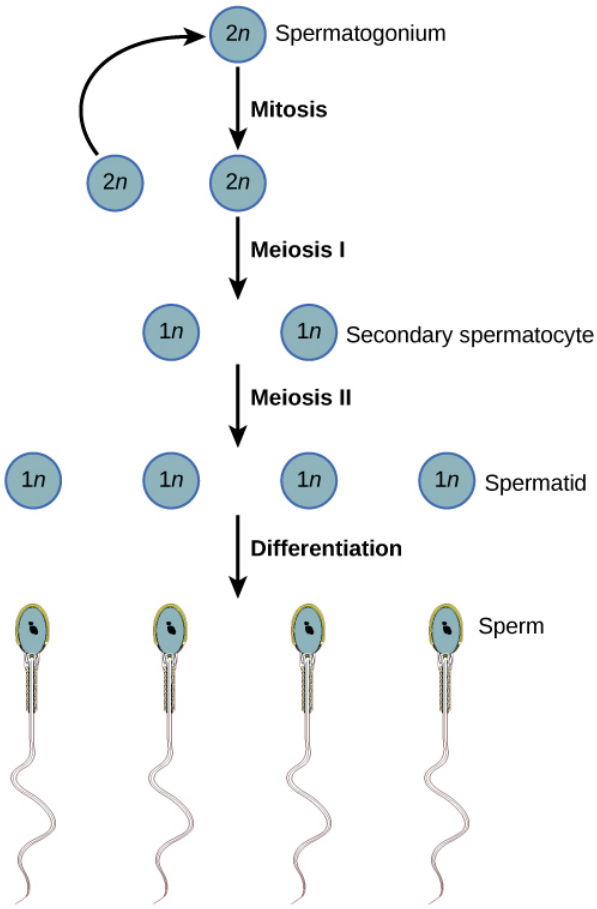


Figure **51.3.5**: During spermatogenesis, four sperm result from each primary spermatocyte.

Spermatogenesis, illustrated in Figure **51.3.5**, occurs in the wall of the seminiferous tubules, with stem cells at the periphery of the tube and the spermatozoa at the lumen of the tube. Immediately under the capsule of the tubule are diploid, undifferentiated cells. These stem cells, called spermatogonia (singular: spermatagonium), go through mitosis with one offspring going on to differentiate into a sperm cell and the other giving rise to the next generation of sperm.

Meiosis starts with a cell called a primary spermatocyte. At the end of the first meiotic division, a haploid cell is produced called a secondary spermatocyte. This cell is haploid and must go through another meiotic cell division. The cell produced at the end of meiosis is called a spermatid and when it reaches the lumen of the tubule and grows a flagellum, it is called a sperm cell. Four sperm result from each primary spermatocyte that goes through meiosis.

Stem cells are deposited during gestation and are present at birth through the beginning of adolescence, but in an inactive state. During adolescence, gonadotropic hormones from the anterior pituitary cause the activation of these cells and the production of viable sperm. This continues into old age.

Link to Learning



Visit this site to see the process of spermatogenesis.

Oogenesis

Oogenesis, illustrated in Figure **51.3.6**, occurs in the outermost layers of the ovaries. As with sperm production, oogenesis starts with a germ cell, called an oogonium (plural: oogonia), but this cell undergoes mitosis to increase in number, eventually resulting in up to about one to two million cells in the embryo.

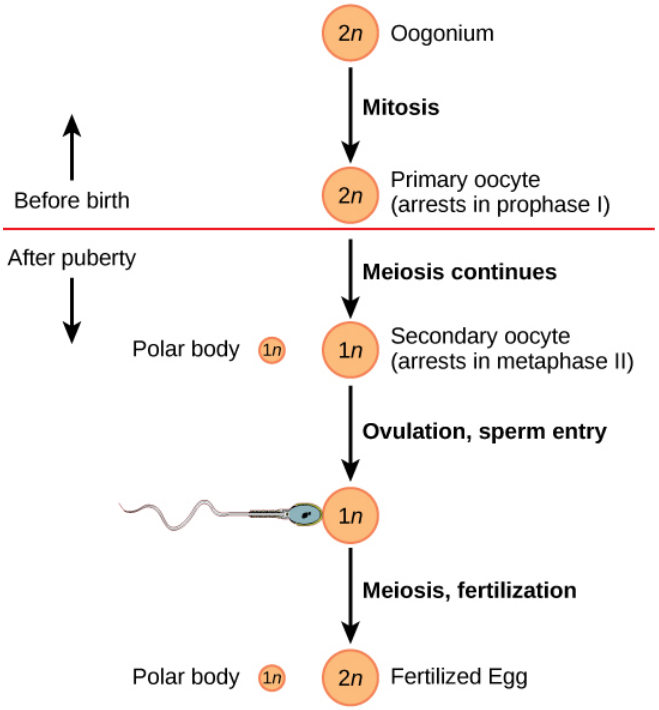


Figure **51.3.6**: The process of oogenesis occurs in the ovary's outermost layer.

The cell starting meiosis is called a primary oocyte, as shown in Figure **51.3.6**. This cell will start the first meiotic division and be arrested in its progress in the first prophase stage. At the time of birth, all future eggs are in the prophase stage. At adolescence, anterior pituitary hormones cause the development of a number of follicles in an ovary. This results in the primary oocyte finishing the first meiotic division. The cell divides unequally, with most of the cellular material and organelles going to one cell, called a secondary oocyte, and only one set of chromosomes and a small amount of cytoplasm going to the other cell. This second cell is called a polar body and usually dies. A secondary meiotic arrest occurs, this time at the metaphase II stage. At ovulation, this secondary oocyte will be released and travel toward the uterus through the oviduct. If the secondary oocyte is fertilized, the cell

continues through the meiosis II, producing a second polar body and a fertilized egg containing all 46 chromosomes of a human being, half of them coming from the sperm.

Egg production begins before birth, is arrested during meiosis until puberty, and then individual cells continue through at each menstrual cycle. One egg is produced from each meiotic process, with the extra chromosomes and chromatids going into polar bodies that degenerate and are reabsorbed by the body.

Summary

As animals became more complex, specific organs and organ systems developed to support specific functions for the organism. The reproductive structures that evolved in land animals allow males and females to mate, fertilize internally, and support the growth and development of offspring. Processes developed to produce reproductive cells that had exactly half the number of chromosomes of each parent so that new combinations would have the appropriate amount of genetic material. Gametogenesis, the production of sperm (spermatogenesis) and eggs (oogenesis), takes place through the process of meiosis.

Figure **51.3.1**: Which of the following statements about the male reproductive system is false?

A. The vas deferens carries sperm from the testes to the penis.
B. Sperm mature in seminiferous tubules in the testes.
C. Both the prostate and the bulbourethral glands produce components of the semen.
D. The prostate gland is located in the testes.

Answer

D

Glossary

bulbourethral gland
secretion that cleanses the urethra prior to ejaculation

clitoris
sensory structure in females; stimulated during sexual arousal

labia majora
large folds of tissue covering the inguinal area

labia minora
smaller folds of tissue within the labia majora

oogenesis
process of producing haploid eggs

oviduct
(also, fallopian tube) muscular tube connecting the uterus with the ovary area

penis
male reproductive structure for urine elimination and copulation

prostate gland
structure that is a mixture of smooth muscle and glandular material and that contributes to semen

scrotum
sac containing testes; exterior to the body

semen
fluid mixture of sperm and supporting materials

seminal vesicle
secretory accessory gland in males; contributes to semen

seminiferous tubule
site of sperm production in testes

spermatogenesis
process of producing haploid sperm

testes
pair of reproductive organs in males

uterus
environment for developing embryo and fetus

vagina
muscular tube for the passage of menstrual flow, copulation, and birth of offspring

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51.3.1: Hormonal Control of Human Reproduction

Skills to Develop

- Describe the roles of male and female reproductive hormones
- Discuss the interplay of the ovarian and menstrual cycles
- Describe the process of menopause

The human male and female reproductive cycles are controlled by the interaction of hormones from the hypothalamus and anterior pituitary with hormones from reproductive tissues and organs. In both sexes, the hypothalamus monitors and causes the release of hormones from the pituitary gland. When the reproductive hormone is required, the hypothalamus sends a gonadotropin-releasing hormone (GnRH) to the anterior pituitary. This causes the release of follicle stimulating hormone (FSH) and luteinizing hormone (LH) from the anterior pituitary into the blood. Note that the body must reach puberty for the adrenals to release the hormones that must be present for GnRH to be produced. Although FSH and LH are named after their functions in female reproduction, they are produced in both sexes and play important roles in controlling reproduction. Other hormones have specific functions in the male and female reproductive systems.

Male Hormones

At the onset of puberty, the hypothalamus causes the release of FSH and LH into the male system for the first time. FSH enters the testes and stimulates the Sertoli cells to begin facilitating spermatogenesis using negative feedback, as illustrated in Figure **51.3.1.1**. LH also enters the testes and stimulates the interstitial cells of Leydig to make and release testosterone into the testes and the blood.

Testosterone, the hormone responsible for the secondary sexual characteristics that develop in the male during adolescence, stimulates spermatogenesis. These secondary sex characteristics include a deepening of the voice, the growth of facial, axillary, and pubic hair, and the beginnings of the sex drive.

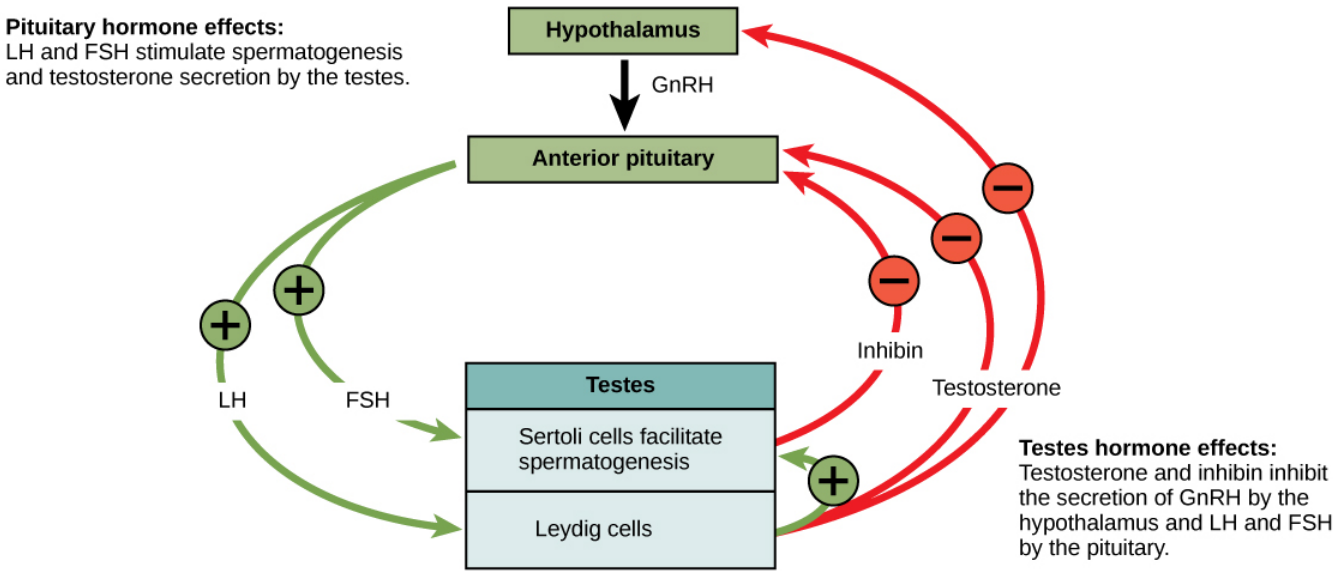


Figure **51.3.1.1**: Hormones control sperm production in a negative feedback system.

A negative feedback system occurs in the male with rising levels of testosterone acting on the hypothalamus and anterior pituitary to inhibit the release of GnRH, FSH, and LH. The Sertoli cells produce the hormone inhibin, which is released into the blood when the sperm count is too high. This inhibits the release of GnRH and FSH, which will cause spermatogenesis to slow down. If the sperm count reaches 20 million/ml, the Sertoli cells cease the release of inhibin, and the sperm count increases.

Female Hormones

The control of reproduction in females is more complex. As with the male, the anterior pituitary hormones cause the release of the hormones FSH and LH. In addition, estrogens and progesterone are released from the developing follicles. Estrogen is the

reproductive hormone in females that assists in endometrial regrowth, ovulation, and calcium absorption; it is also responsible for the secondary sexual characteristics of females. These include breast development, flaring of the hips, and a shorter period necessary for bone maturation. Progesterone assists in endometrial re-growth and inhibition of FSH and LH release.

In females, FSH stimulates development of egg cells, called ova, which develop in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production. LH also plays a role in the development of ova, induction of ovulation, and stimulation of estradiol and progesterone production by the ovaries. Estradiol and progesterone are steroid hormones that prepare the body for pregnancy. Estradiol produces secondary sex characteristics in females, while both estradiol and progesterone regulate the menstrual cycle.

The Ovarian Cycle and the Menstrual Cycle

The ovarian cycle governs the preparation of endocrine tissues and release of eggs, while the menstrual cycle governs the preparation and maintenance of the uterine lining. These cycles occur concurrently and are coordinated over a 22–32 day cycle, with an average length of 28 days.

The first half of the ovarian cycle is the follicular phase shown in Figure **51.3.1.2**. Slowly rising levels of FSH and LH cause the growth of follicles on the surface of the ovary. This process prepares the egg for ovulation. As the follicles grow, they begin releasing estrogens and a low level of progesterone. Progesterone maintains the endometrium to help ensure pregnancy. The trip through the fallopian tube takes about seven days. At this stage of development, called the *morula*, there are 30-60 cells. If pregnancy implantation does not occur, the lining is sloughed off. After about five days, estrogen levels rise and the menstrual cycle enters the proliferative phase. The endometrium begins to regrow, replacing the blood vessels and glands that deteriorated during the end of the last cycle.

Art Connection

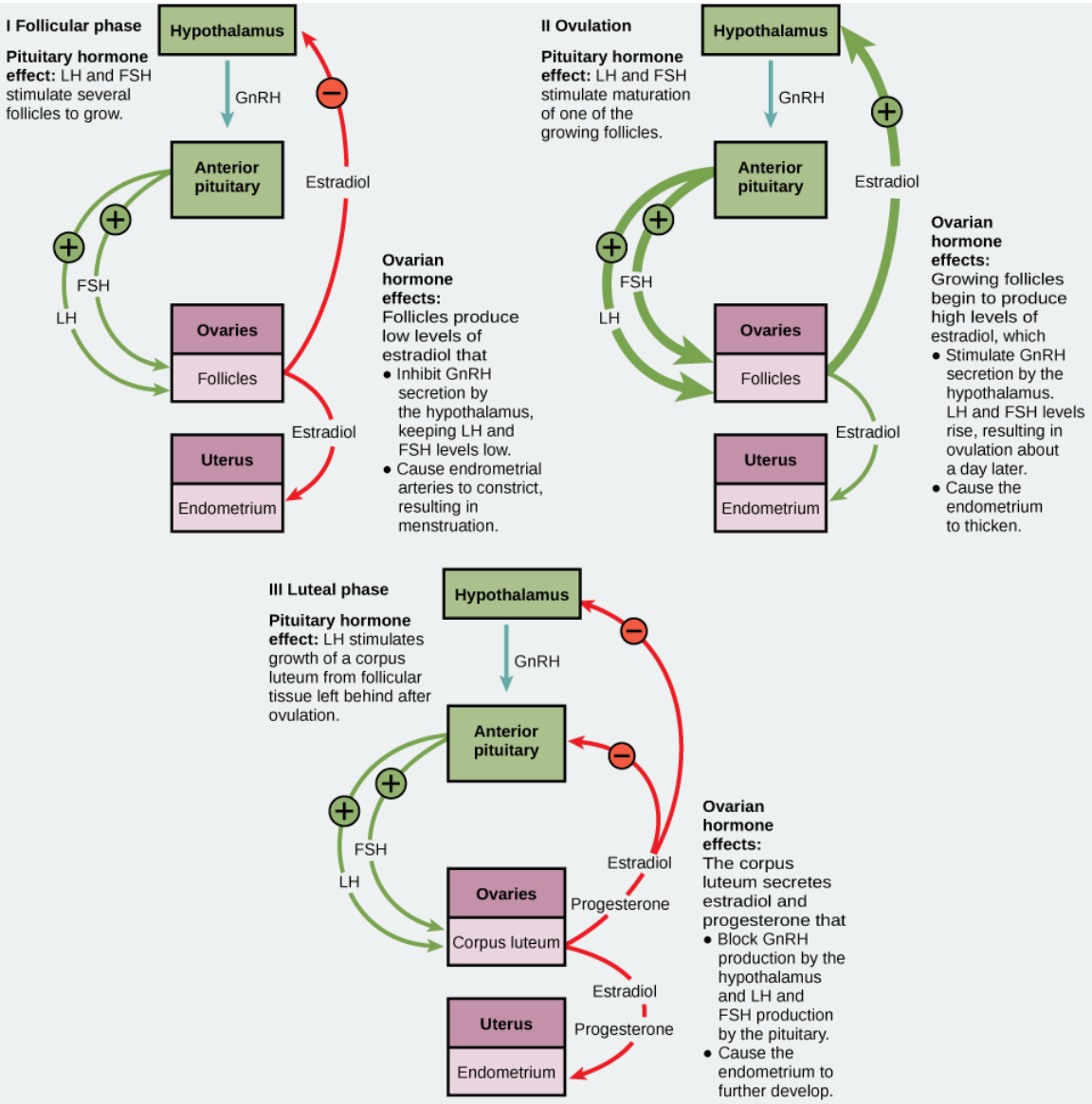


Figure **51.3.1.2**: The ovarian and menstrual cycles of female reproduction are regulated by hormones produced by the hypothalamus, pituitary, and ovaries.

Which of the following statements about hormone regulation of the female reproductive cycle is false?

A. LH and FSH are produced in the pituitary, and estradiol and progesterone are produced in the ovaries.
B. Estradiol and progesterone secreted from the corpus luteum cause the endometrium to thicken.
C. Both progesterone and estradiol are produced by the follicles.
D. Secretion of GnRH by the hypothalamus is inhibited by low levels of estradiol but stimulated by high levels of estradiol.

Just prior to the middle of the cycle (approximately day 14), the high level of estrogen causes FSH and especially LH to rise rapidly, then fall. The spike in LH causes ovulation: the most mature follicle, like that shown in Figure **51.3.1.3**, ruptures and releases its egg. The follicles that did not rupture degenerate and their eggs are lost. The level of estrogen decreases when the extra follicles degenerate.



Figure **51.3.1.3**: This mature egg follicle may rupture and release an egg. (credit: scale-bar data from Matt Russell)

Following ovulation, the ovarian cycle enters its luteal phase, illustrated in Figure **51.3.1.4** and the menstrual cycle enters its secretory phase, both of which run from about day 15 to 28. The luteal and secretory phases refer to changes in the ruptured follicle. The cells in the follicle undergo physical changes and produce a structure called a corpus luteum. The corpus luteum produces estrogen and progesterone. The progesterone facilitates the regrowth of the uterine lining and inhibits the release of further FSH and LH. The uterus is being prepared to accept a fertilized egg, should it occur during this cycle. The inhibition of FSH and LH prevents any further eggs and follicles from developing, while the progesterone is elevated. The level of estrogen produced by the corpus luteum increases to a steady level for the next few days.

If no fertilized egg is implanted into the uterus, the corpus luteum degenerates and the levels of estrogen and progesterone decrease. The endometrium begins to degenerate as the progesterone levels drop, initiating the next menstrual cycle. The decrease in progesterone also allows the hypothalamus to send GnRH to the anterior pituitary, releasing FSH and LH and starting the cycles again. Figure **51.3.1.4** visually compares the ovarian and uterine cycles as well as the commensurate hormone levels.

Art Connection

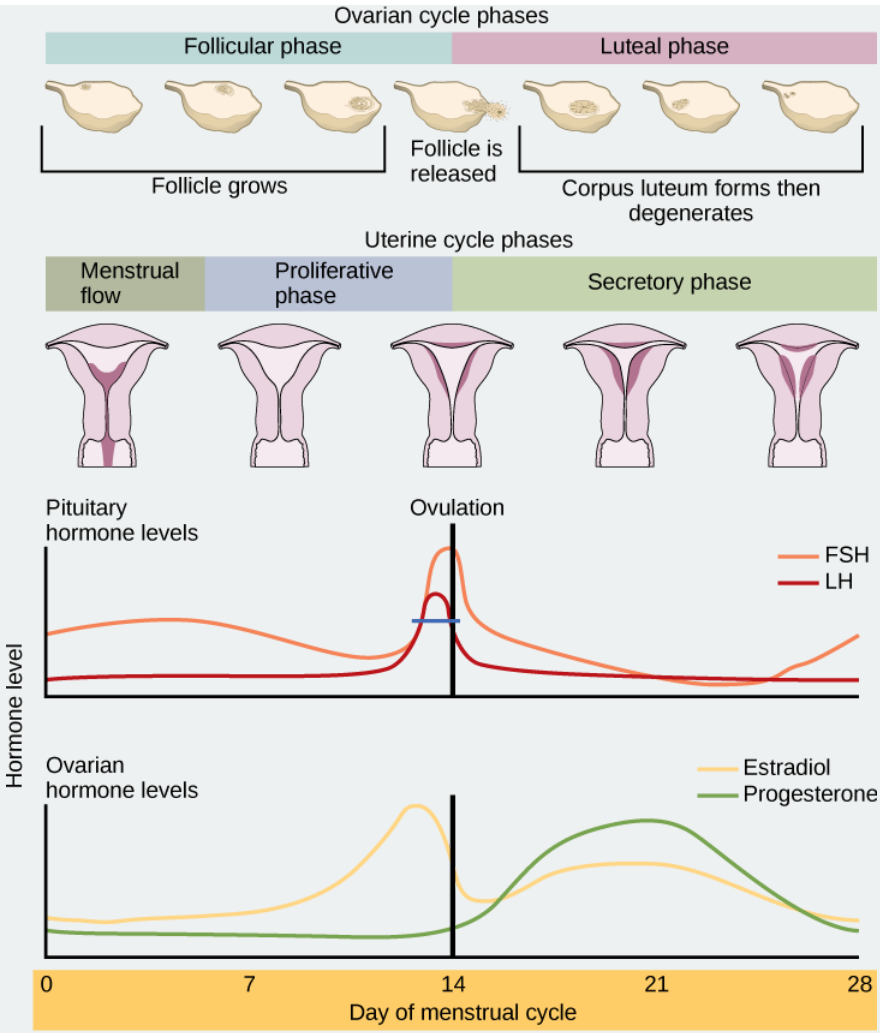


Figure 51.3.1.4: Rising and falling hormone levels result in progression of the ovarian and menstrual cycles. (credit: modification of work by Mikael Häggström)

Which of the following statements about the menstrual cycle is false?

A. Progesterone levels rise during the luteal phase of the ovarian cycle and the secretory phase of the uterine cycle.
B. Menstruation occurs just after LH and FSH levels peak.
C. Menstruation occurs after progesterone levels drop.
D. Estrogen levels rise before ovulation, while progesterone levels rise after.

Menopause

As women approach their mid-40s to mid-50s, their ovaries begin to lose their sensitivity to FSH and LH. Menstrual periods become less frequent and finally cease; this is menopause. There are still eggs and potential follicles on the ovaries, but without the stimulation of FSH and LH, they will not produce a viable egg to be released. The outcome of this is the inability to have children.

The side effects of menopause include hot flashes, heavy sweating (especially at night), headaches, some hair loss, muscle pain, vaginal dryness, insomnia, depression, weight gain, and mood swings. Estrogen is involved in calcium metabolism and, without it, blood levels of calcium decrease. To replenish the blood, calcium is lost from bone which may decrease the bone density and lead to osteoporosis. Supplementation of estrogen in the form of hormone replacement therapy (HRT) can prevent bone loss, but the therapy can have negative side effects. While HRT is thought to give some protection from colon cancer, osteoporosis, heart disease, macular degeneration, and possibly depression, its negative side effects include increased risk of: stroke or heart attack, blood clots, breast cancer, ovarian cancer, endometrial cancer, gall bladder disease, and possibly dementia.

Career Connection: Reproductive Endocrinologist

A reproductive endocrinologist is a physician who treats a variety of hormonal disorders related to reproduction and infertility in both men and women. The disorders include menstrual problems, infertility, pregnancy loss, sexual dysfunction, and menopause. Doctors may use fertility drugs, surgery, or assisted reproductive techniques (ART) in their therapy. ART involves the use of procedures to manipulate the egg or sperm to facilitate reproduction, such as *in vitro* fertilization.

Reproductive endocrinologists undergo extensive medical training, first in a four-year residency in obstetrics and gynecology, then in a three-year fellowship in reproductive endocrinology. To be board certified in this area, the physician must pass written and oral exams in both areas.

Summary

The male and female reproductive cycles are controlled by hormones released from the hypothalamus and anterior pituitary as well as hormones from reproductive tissues and organs. The hypothalamus monitors the need for the FSH and LH hormones made and released from the anterior pituitary. FSH and LH affect reproductive structures to cause the formation of sperm and the preparation of eggs for release and possible fertilization. In the male, FSH and LH stimulate Sertoli cells and interstitial cells of Leydig in the testes to facilitate sperm production. The Leydig cells produce testosterone, which also is responsible for the secondary sexual characteristics of males. In females, FSH and LH cause estrogen and progesterone to be produced. They regulate the female reproductive system which is divided into the ovarian cycle and the menstrual cycle. Menopause occurs when the ovaries lose their sensitivity to FSH and LH and the female reproductive cycles slow to a stop.

Art Connections

Figure **51.3.1.2**: Which of the following statements about hormone regulation of the female reproductive cycle is false?

A. LH and FSH are produced in the pituitary, and estradiol and progesterone are produced in the ovaries.
B. Estradiol and progesterone secreted from the corpus luteum cause the endometrium to thicken.
C. Both progesterone and estradiol are produced by the follicles.
D. Secretion of GnRH by the hypothalamus is inhibited by low levels of estradiol but stimulated by high levels of estradiol.

Answer

C

Figure **51.3.1.4**: Which of the following statements about the menstrual cycle is false?

A. Progesterone levels rise during the luteal phase of the ovarian cycle and the secretory phase of the uterine cycle.
B. Menstruation occurs just after LH and FSH levels peak.
C. Menstruation occurs after progesterone levels drop.
D. Estrogen levels rise before ovulation, while progesterone levels rise after.

Answer

B

Glossary

estrogen

reproductive hormone in females that assists in endometrial regrowth, ovulation, and calcium absorption

follicle stimulating hormone (FSH)

reproductive hormone that causes sperm production in men and follicle development in women

gonadotropin-releasing hormone (GnRH)

hormone from the hypothalamus that causes the release of FSH and LH from the anterior pituitary

inhibin
hormone made by Sertoli cells; provides negative feedback to hypothalamus in control of FSH and GnRH release

interstitial cell of Leydig
cell in seminiferous tubules that makes testosterone

luteinizing hormone (LH)
reproductive hormone in both men and women, causes testosterone production in men and ovulation and lactation in women

menopause
loss of reproductive capacity in women due to decreased sensitivity of the ovaries to FSH and LH

menstrual cycle
cycle of the degradation and re-growth of the endometrium

ovarian cycle
cycle of preparation of egg for ovulation and the conversion of the follicle to the corpus luteum

ovulation
release of the egg by the most mature follicle

progesterone
reproductive hormone in women; assists in endometrial re-growth and inhibition of FSH and LH release

Sertoli cell
cell in seminiferous tubules that assists developing sperm and makes inhibin

testosterone
reproductive hormone in men that assists in sperm production and promoting secondary sexual characteristics

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51.4: Structure and Function of the Female Reproductive System

Skills to Develop

- Describe human male and female reproductive anatomies
- Discuss the human sexual response
- Describe spermatogenesis and oogenesis and discuss their differences and similarities

As animals became more complex, specific organs and organ systems developed to support specific functions for the organism. The reproductive structures that evolved in land animals allow males and females to mate, fertilize internally, and support the growth and development of offspring.

Human Reproductive Anatomy

The reproductive tissues of male and female humans develop similarly *in utero* until a low level of the hormone testosterone is released from male gonads. Testosterone causes the undeveloped tissues to differentiate into male sexual organs. When testosterone is absent, the tissues develop into female sexual tissues. Primitive gonads become testes or ovaries. Tissues that produce a penis in males produce a clitoris in females. The tissue that will become the scrotum in a male becomes the labia in a female; that is, they are homologous structures.

Male Reproductive Anatomy

In the male reproductive system, the scrotum houses the testicles or testes (singular: testis), including providing passage for blood vessels, nerves, and muscles related to testicular function. The testes are a pair of male reproductive organs that produce sperm and some reproductive hormones. Each testis is approximately 2.5 by 3.8 cm (1.5 by 1 in) in size and divided into wedge-shaped lobules by connective tissue called septa. Coiled in each wedge are seminiferous tubules that produce sperm.

Sperm are immobile at body temperature; therefore, the scrotum and penis are external to the body, as illustrated in Figure **51.4.1** so that a proper temperature is maintained for motility. In land mammals, the pair of testes must be suspended outside the body at about 2° C lower than body temperature to produce viable sperm. Infertility can occur in land mammals when the testes do not descend through the abdominal cavity during fetal development.

Art Connection

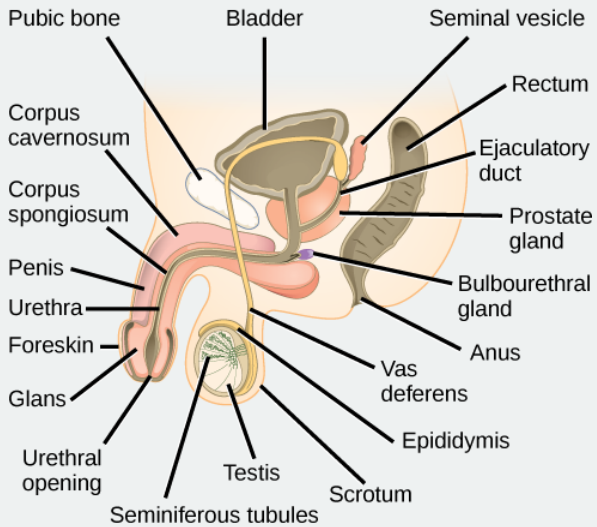


Figure **51.4.1**: The reproductive structures of the human male are shown.

Which of the following statements about the male reproductive system is false?

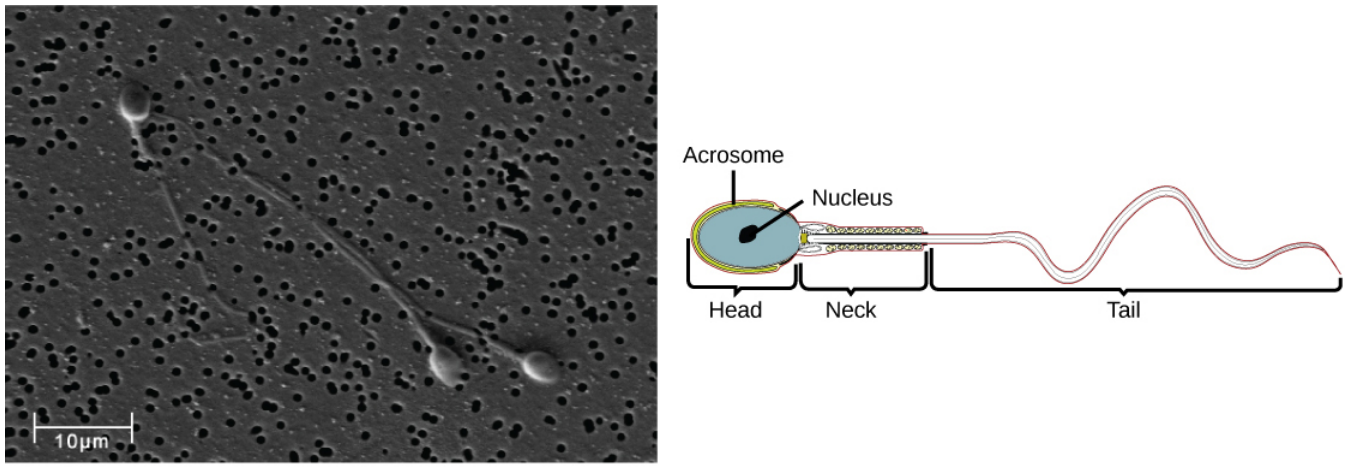
A. The vas deferens carries sperm from the testes to the penis.
B. Sperm mature in seminiferous tubules in the testes.
C. Both the prostate and the bulbourethral glands produce components of the semen.

D. The prostate gland is located in the testes.

Sperm mature in seminiferous tubules that are coiled inside the testes, as illustrated in Figure **51.4.1**. The walls of the seminiferous tubules are made up of the developing sperm cells, with the least developed sperm at the periphery of the tubule and the fully developed sperm in the lumen. The sperm cells are mixed with "nursemaid" cells called Sertoli cells which protect the germ cells and promote their development. Other cells mixed in the wall of the tubules are the interstitial cells of Leydig. These cells produce high levels of testosterone once the male reaches adolescence.

When the sperm have developed flagella and are nearly mature, they leave the testicles and enter the epididymis, shown in Figure **51.4.1**. This structure resembles a comma and lies along the top and posterior portion of the testes; it is the site of sperm maturation. The sperm leave the epididymis and enter the vas deferens (or ductus deferens), which carries the sperm, behind the bladder, and forms the ejaculatory duct with the duct from the seminal vesicles. During a vasectomy, a section of the vas deferens is removed, preventing sperm from being passed out of the body during ejaculation and preventing fertilization.

Semen is a mixture of sperm and spermatic duct secretions (about 10 percent of the total) and fluids from accessory glands that contribute most of the semen's volume. Sperm are haploid cells, consisting of a flagellum as a tail, a neck that contains the cell's energy-producing mitochondria, and a head that contains the genetic material. Figure **51.4.2** shows a micrograph of human sperm as well as a diagram of the parts of the sperm. An acrosome is found at the top of the head of the sperm. This structure contains lysosomal enzymes that can digest the protective coverings that surround the egg to help the sperm penetrate and fertilize the egg. An ejaculate will contain from two to five milliliters of fluid with from 50–120 million sperm per milliliter.



(a) (b)

Figure **51.4.2**: Human sperm, visualized using scanning electron microscopy, have a flagellum, neck, and head. (credit b: modification of work by Mariana Ruiz Villareal; scale-bar data from Matt Russell)

The bulk of the semen comes from the accessory glands associated with the male reproductive system. These are the seminal vesicles, the prostate gland, and the bulbourethral gland, all of which are illustrated in Figure **51.4.1**. The seminal vesicles are a pair of glands that lie along the posterior border of the urinary bladder. The glands make a solution that is thick, yellowish, and alkaline. As sperm are only motile in an alkaline environment, a basic pH is important to reverse the acidity of the vaginal environment. The solution also contains mucus, fructose (a sperm mitochondrial nutrient), a coagulating enzyme, ascorbic acid, and local-acting hormones called prostaglandins. The seminal vesicle glands account for 60 percent of the bulk of semen.

The penis, illustrated in Figure **51.4.1**, is an organ that drains urine from the renal bladder and functions as a copulatory organ during intercourse. The penis contains three tubes of erectile tissue running through the length of the organ. These consist of a pair of tubes on the dorsal side, called the corpus cavernosum, and a single tube of tissue on the ventral side, called the corpus spongiosum. This tissue will become engorged with blood, becoming erect and hard, in preparation for intercourse. The organ is inserted into the vagina culminating with an ejaculation. During intercourse, the smooth muscle sphincters at the opening to the renal bladder close and prevent urine from entering the penis. An orgasm is a two-stage process: first, glands and accessory organs connected to the testes contract, then semen (containing sperm) is expelled through the urethra during ejaculation. After intercourse, the blood drains from the erectile tissue and the penis becomes flaccid.

The walnut-shaped prostate gland surrounds the urethra, the connection to the urinary bladder. It has a series of short ducts that directly connect to the urethra. The gland is a mixture of smooth muscle and glandular tissue. The muscle provides much of the force needed for ejaculation to occur. The glandular tissue makes a thin, milky fluid that contains citrate (a nutrient), enzymes, and prostate specific antigen (PSA). PSA is a proteolytic enzyme that helps to liquefy the ejaculate several minutes after release from the male. Prostate gland secretions account for about 30 percent of the bulk of semen.

The bulbourethral gland, or Cowper's gland, releases its secretion prior to the release of the bulk of the semen. It neutralizes any acid residue in the urethra left over from urine. This usually accounts for a couple of drops of fluid in the total ejaculate and may contain a few sperm. Withdrawal of the penis from the vagina before ejaculation to prevent pregnancy may not work if sperm are present in the bulbourethral gland secretions. The location and functions of the male reproductive organs are summarized in Table **51.4.1**.

Table 51.4.1: Male Reproductive Anatomy

Organ	Location	Function
Scrotum	External	Carry and support testes
Penis	External	Deliver urine, copulating organ
Testes	Internal	Produce sperm and male hormones
Seminal Vesicles	Internal	Contribute to semen production
Prostate Gland	Internal	Contribute to semen production
Bulbourethral Glands	Internal	Clean urethra at ejaculation

Female Reproductive Anatomy

A number of reproductive structures are exterior to the female's body. These include the breasts and the vulva, which consists of the mons pubis, clitoris, labia majora, labia minora, and the vestibular glands, all illustrated in Figure **51.4.3**. The location and functions of the female reproductive organs are summarized in Table **51.4.2**. The vulva is an area associated with the vestibule which includes the structures found in the inguinal (groin) area of women. The mons pubis is a round, fatty area that overlies the pubic symphysis. The clitoris is a structure with erectile tissue that contains a large number of sensory nerves and serves as a source of stimulation during intercourse. The labia majora are a pair of elongated folds of tissue that run posterior from the mons pubis and enclose the other components of the vulva. The labia majora derive from the same tissue that produces the scrotum in a male. The labia minora are thin folds of tissue centrally located within the labia majora. These labia protect the openings to the vagina and urethra. The mons pubis and the anterior portion of the labia majora become covered with hair during adolescence; the labia minora is hairless. The greater vestibular glands are found at the sides of the vaginal opening and provide lubrication during intercourse.

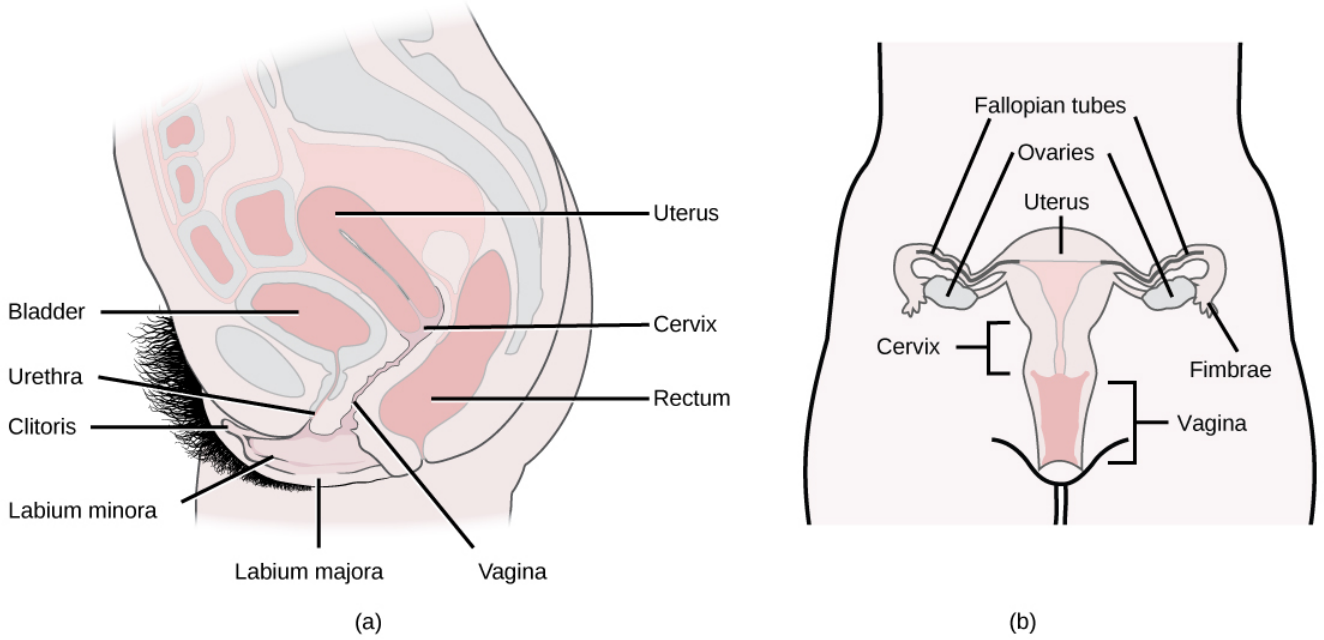


Figure 51.4.3: The reproductive structures of the human female are shown. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by CDC)

Table 51.4.2: Female Reproductive Anatomy

Organ	Location	Function
Clitoris	External	Sensory organ
Mons pubis	External	Fatty area overlying pubic bone
Labia majora	External	Covers labia minora
Labia minora	External	Covers vestibule
Greater vestibular glands	External	Secrete mucus; lubricate vagina
Breast	External	Produce and deliver milk
Ovaries	Internal	Carry and develop eggs
Oviducts (Fallopian tubes)	Internal	Transport egg to uterus
Uterus	Internal	Support developing embryo
Vagina	Internal	Common tube for intercourse, birth canal, passing menstrual flow

The breasts consist of mammary glands and fat. The size of the breast is determined by the amount of fat deposited behind the gland. Each gland consists of 15 to 25 lobes that have ducts that empty at the nipple and that supply the nursing child with nutrient- and antibody-rich milk to aid development and protect the child.

Internal female reproductive structures include ovaries, oviducts, the uterus, and the vagina, shown in Figure 51.4.3. The pair of ovaries is held in place in the abdominal cavity by a system of ligaments. Ovaries consist of a medulla and cortex: the medulla contains nerves and blood vessels to supply the cortex with nutrients and remove waste. The outer layers of cells of the cortex are the functional parts of the ovaries. The cortex is made up of follicular cells that surround eggs that develop during fetal development *in utero*. During the menstrual period, a batch of follicular cells develops and prepares the eggs for release. At ovulation, one follicle ruptures and one egg is released, as illustrated in Figure 51.4.4.

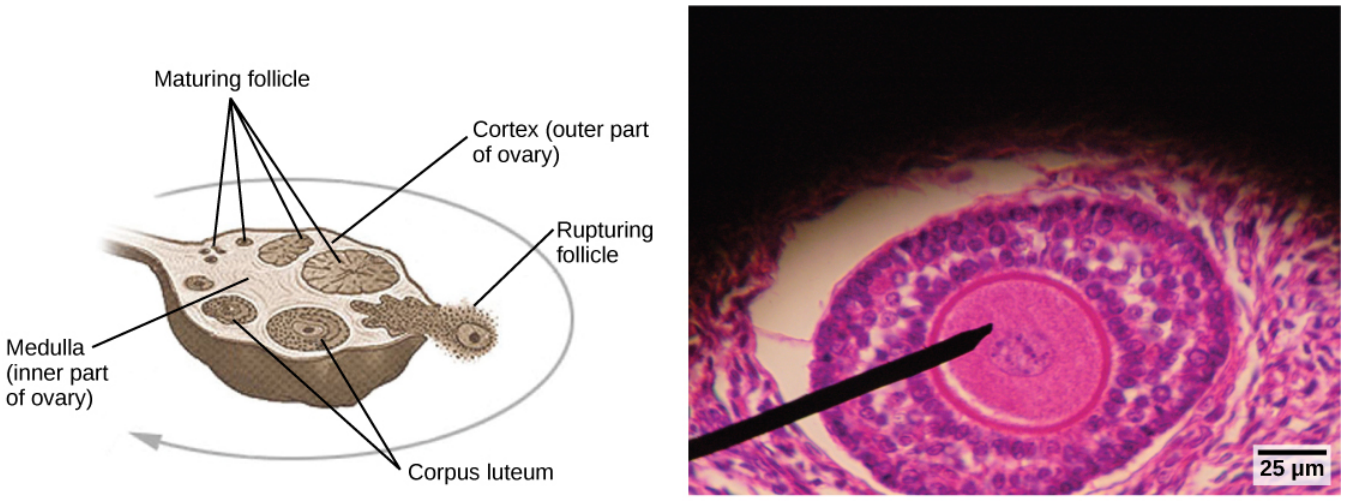


Figure 51.4.4: Oocytes develop in (a) follicles, located in the ovary. At the beginning of the menstrual cycle, the follicle matures. At ovulation, the follicle ruptures, releasing the egg. The follicle becomes a corpus luteum, which eventually degenerates. The (b) follicle in this light micrograph has an oocyte at its center. (credit a: modification of work by NIH; scale-bar data from Matt Russell)

The oviducts, or fallopian tubes, extend from the uterus in the lower abdominal cavity to the ovaries, but they are not in contact with the ovaries. The lateral ends of the oviducts flare out into a trumpet-like structure and have a fringe of finger-like projections called fimbriae, illustrated in Figure 51.4.4. When an egg is released at ovulation, the fimbrae help the non-motile egg enter into the tube and passage to the uterus. The walls of the oviducts are ciliated and are made up mostly of smooth muscle. The cilia beat toward the middle, and the smooth muscle contracts in the same direction, moving the egg toward the uterus. Fertilization usually takes place within the oviducts and the developing embryo is moved toward the uterus for development. It usually takes the egg or embryo a week to travel through the oviduct. Sterilization in women is called a tubal ligation; it is analogous to a vasectomy in males in that the oviducts are severed and sealed.

The uterus is a structure about the size of a woman's fist. This is lined with an endometrium rich in blood vessels and mucus glands. The uterus supports the developing embryo and fetus during gestation. The thickest portion of the wall of the uterus is made of smooth muscle. Contractions of the smooth muscle in the uterus aid in passing the baby through the vagina during labor. A portion of the lining of the uterus sloughs off during each menstrual period, and then builds up again in preparation for an implantation. Part of the uterus, called the cervix, protrudes into the top of the vagina. The cervix functions as the birth canal.

The vagina is a muscular tube that serves several purposes. It allows menstrual flow to leave the body. It is the receptacle for the penis during intercourse and the vessel for the delivery of offspring. It is lined by stratified squamous epithelial cells to protect the underlying tissue.

Sexual Response during Intercourse

The sexual response in humans is both psychological and physiological. Both sexes experience sexual arousal through psychological and physical stimulation. There are four phases of the sexual response. During phase one, called excitement, vasodilation leads to vasocongestion in erectile tissues in both men and women. The nipples, clitoris, labia, and penis engorge with blood and become enlarged. Vaginal secretions are released to lubricate the vagina to facilitate intercourse. During the second phase, called the plateau, stimulation continues, the outer third of the vaginal wall enlarges with blood, and breathing and heart rate increase.

During phase three, or orgasm, rhythmic, involuntary contractions of muscles occur in both sexes. In the male, the reproductive accessory glands and tubules constrict placing semen in the urethra, then the urethra contracts expelling the semen through the penis. In women, the uterus and vaginal muscles contract in waves that may last slightly less than a second each. During phase four, or resolution, the processes described in the first three phases reverse themselves and return to their normal state. Men experience a refractory period in which they cannot maintain an erection or ejaculate for a period of time ranging from minutes to hours.

Gametogenesis (Spermatogenesis and Oogenesis)

Gametogenesis, the production of sperm and eggs, takes place through the process of meiosis. During meiosis, two cell divisions separate the paired chromosomes in the nucleus and then separate the chromatids that were made during an earlier stage of the cell's life cycle. Meiosis produces haploid cells with half of each pair of chromosomes normally found in diploid cells. The production of sperm is called spermatogenesis and the production of eggs is called oogenesis.

Spermatogenesis

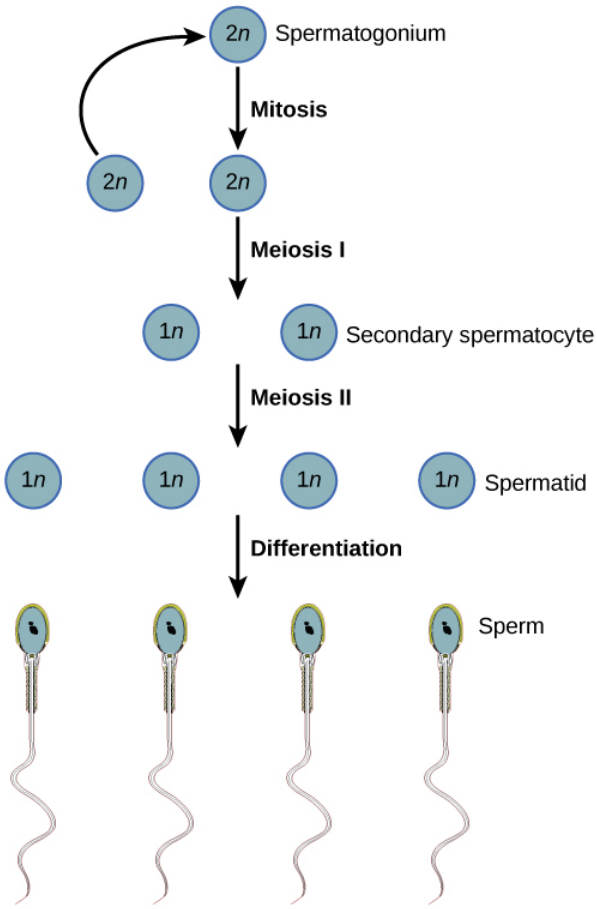


Figure **51.4.5**: During spermatogenesis, four sperm result from each primary spermatocyte.

Spermatogenesis, illustrated in Figure **51.4.5**, occurs in the wall of the seminiferous tubules, with stem cells at the periphery of the tube and the spermatozoa at the lumen of the tube. Immediately under the capsule of the tubule are diploid, undifferentiated cells. These stem cells, called spermatogonia (singular: spermatagonium), go through mitosis with one offspring going on to differentiate into a sperm cell and the other giving rise to the next generation of sperm.

Meiosis starts with a cell called a primary spermatocyte. At the end of the first meiotic division, a haploid cell is produced called a secondary spermatocyte. This cell is haploid and must go through another meiotic cell division. The cell produced at the end of meiosis is called a spermatid and when it reaches the lumen of the tubule and grows a flagellum, it is called a sperm cell. Four sperm result from each primary spermatocyte that goes through meiosis.

Stem cells are deposited during gestation and are present at birth through the beginning of adolescence, but in an inactive state. During adolescence, gonadotropic hormones from the anterior pituitary cause the activation of these cells and the production of viable sperm. This continues into old age.

Link to Learning



Visit this site to see the process of spermatogenesis.

Oogenesis

Oogenesis, illustrated in Figure **51.4.6**, occurs in the outermost layers of the ovaries. As with sperm production, oogenesis starts with a germ cell, called an oogonium (plural: oogonia), but this cell undergoes mitosis to increase in number, eventually resulting in up to about one to two million cells in the embryo.

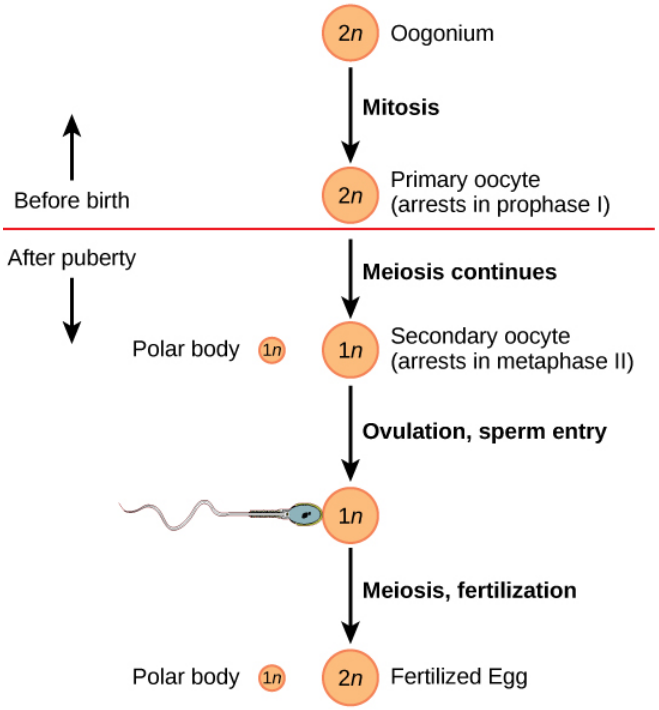


Figure **51.4.6**: The process of oogenesis occurs in the ovary's outermost layer.

The cell starting meiosis is called a primary oocyte, as shown in Figure **51.4.6**. This cell will start the first meiotic division and be arrested in its progress in the first prophase stage. At the time of birth, all future eggs are in the prophase stage. At adolescence, anterior pituitary hormones cause the development of a number of follicles in an ovary. This results in the primary oocyte finishing the first meiotic division. The cell divides unequally, with most of the cellular material and organelles going to one cell, called a secondary oocyte, and only one set of chromosomes and a small amount of cytoplasm going to the other cell. This second cell is called a polar body and usually dies. A secondary meiotic arrest occurs, this time at the metaphase II stage. At ovulation, this secondary oocyte will be released and travel toward the uterus through the oviduct. If the secondary oocyte is fertilized, the cell

continues through the meiosis II, producing a second polar body and a fertilized egg containing all 46 chromosomes of a human being, half of them coming from the sperm.

Egg production begins before birth, is arrested during meiosis until puberty, and then individual cells continue through at each menstrual cycle. One egg is produced from each meiotic process, with the extra chromosomes and chromatids going into polar bodies that degenerate and are reabsorbed by the body.

Summary

As animals became more complex, specific organs and organ systems developed to support specific functions for the organism. The reproductive structures that evolved in land animals allow males and females to mate, fertilize internally, and support the growth and development of offspring. Processes developed to produce reproductive cells that had exactly half the number of chromosomes of each parent so that new combinations would have the appropriate amount of genetic material. Gametogenesis, the production of sperm (spermatogenesis) and eggs (oogenesis), takes place through the process of meiosis.

Figure **51.4.1**: Which of the following statements about the male reproductive system is false?

A. The vas deferens carries sperm from the testes to the penis.
B. Sperm mature in seminiferous tubules in the testes.
C. Both the prostate and the bulbourethral glands produce components of the semen.
D. The prostate gland is located in the testes.

Answer

D

Glossary

bulbourethral gland
secretion that cleanses the urethra prior to ejaculation

clitoris
sensory structure in females; stimulated during sexual arousal

labia majora
large folds of tissue covering the inguinal area

labia minora
smaller folds of tissue within the labia majora

oogenesis
process of producing haploid eggs

oviduct
(also, fallopian tube) muscular tube connecting the uterus with the ovary area

penis
male reproductive structure for urine elimination and copulation

prostate gland
structure that is a mixture of smooth muscle and glandular material and that contributes to semen

scrotum
sac containing testes; exterior to the body

semen
fluid mixture of sperm and supporting materials

seminal vesicle
secretory accessory gland in males; contributes to semen

seminiferous tubule
site of sperm production in testes

spermatogenesis
process of producing haploid sperm

testes
pair of reproductive organs in males

uterus
environment for developing embryo and fetus

vagina
muscular tube for the passage of menstrual flow, copulation, and birth of offspring

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51.4.1: Hormonal Control of Human Reproduction

Skills to Develop

- Describe the roles of male and female reproductive hormones
- Discuss the interplay of the ovarian and menstrual cycles
- Describe the process of menopause

The human male and female reproductive cycles are controlled by the interaction of hormones from the hypothalamus and anterior pituitary with hormones from reproductive tissues and organs. In both sexes, the hypothalamus monitors and causes the release of hormones from the pituitary gland. When the reproductive hormone is required, the hypothalamus sends a gonadotropin-releasing hormone (GnRH) to the anterior pituitary. This causes the release of follicle stimulating hormone (FSH) and luteinizing hormone (LH) from the anterior pituitary into the blood. Note that the body must reach puberty for the adrenals to release the hormones that must be present for GnRH to be produced. Although FSH and LH are named after their functions in female reproduction, they are produced in both sexes and play important roles in controlling reproduction. Other hormones have specific functions in the male and female reproductive systems.

Male Hormones

At the onset of puberty, the hypothalamus causes the release of FSH and LH into the male system for the first time. FSH enters the testes and stimulates the Sertoli cells to begin facilitating spermatogenesis using negative feedback, as illustrated in Figure **51.4.1.1**. LH also enters the testes and stimulates the interstitial cells of Leydig to make and release testosterone into the testes and the blood.

Testosterone, the hormone responsible for the secondary sexual characteristics that develop in the male during adolescence, stimulates spermatogenesis. These secondary sex characteristics include a deepening of the voice, the growth of facial, axillary, and pubic hair, and the beginnings of the sex drive.

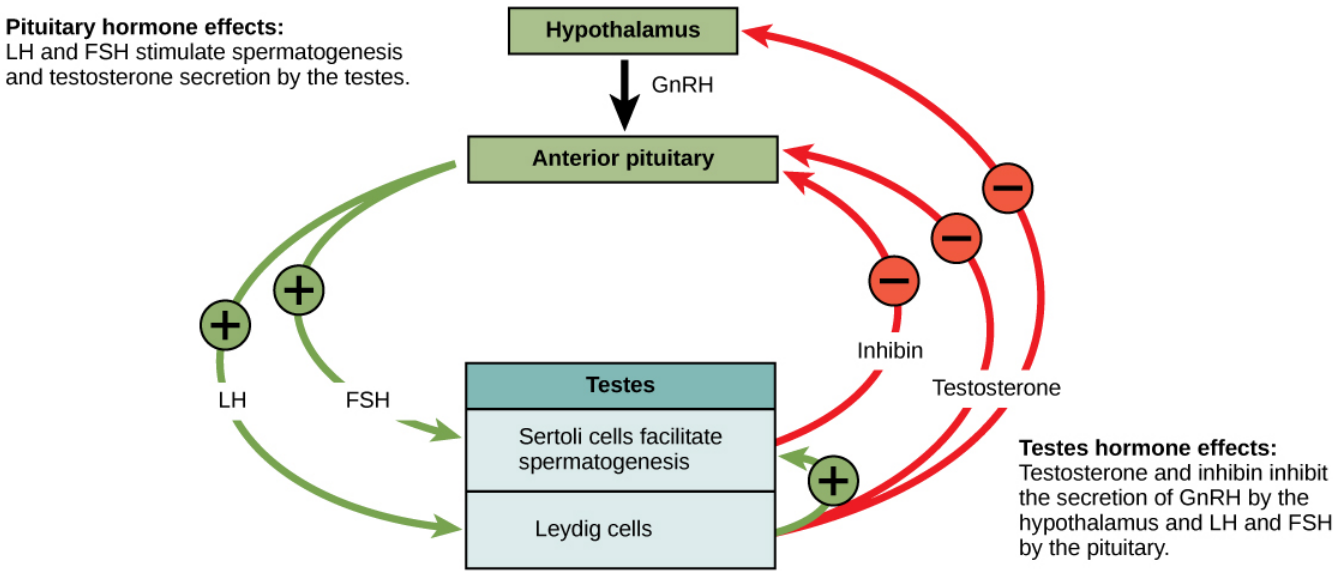


Figure **51.4.1.1**: Hormones control sperm production in a negative feedback system.

A negative feedback system occurs in the male with rising levels of testosterone acting on the hypothalamus and anterior pituitary to inhibit the release of GnRH, FSH, and LH. The Sertoli cells produce the hormone inhibin, which is released into the blood when the sperm count is too high. This inhibits the release of GnRH and FSH, which will cause spermatogenesis to slow down. If the sperm count reaches 20 million/ml, the Sertoli cells cease the release of inhibin, and the sperm count increases.

Female Hormones

The control of reproduction in females is more complex. As with the male, the anterior pituitary hormones cause the release of the hormones FSH and LH. In addition, estrogens and progesterone are released from the developing follicles. Estrogen is the

reproductive hormone in females that assists in endometrial regrowth, ovulation, and calcium absorption; it is also responsible for the secondary sexual characteristics of females. These include breast development, flaring of the hips, and a shorter period necessary for bone maturation. Progesterone assists in endometrial re-growth and inhibition of FSH and LH release.

In females, FSH stimulates development of egg cells, called ova, which develop in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production. LH also plays a role in the development of ova, induction of ovulation, and stimulation of estradiol and progesterone production by the ovaries. Estradiol and progesterone are steroid hormones that prepare the body for pregnancy. Estradiol produces secondary sex characteristics in females, while both estradiol and progesterone regulate the menstrual cycle.

The Ovarian Cycle and the Menstrual Cycle

The ovarian cycle governs the preparation of endocrine tissues and release of eggs, while the menstrual cycle governs the preparation and maintenance of the uterine lining. These cycles occur concurrently and are coordinated over a 22–32 day cycle, with an average length of 28 days.

The first half of the ovarian cycle is the follicular phase shown in Figure **51.4.1.2**. Slowly rising levels of FSH and LH cause the growth of follicles on the surface of the ovary. This process prepares the egg for ovulation. As the follicles grow, they begin releasing estrogens and a low level of progesterone. Progesterone maintains the endometrium to help ensure pregnancy. The trip through the fallopian tube takes about seven days. At this stage of development, called the *morula*, there are 30-60 cells. If pregnancy implantation does not occur, the lining is sloughed off. After about five days, estrogen levels rise and the menstrual cycle enters the proliferative phase. The endometrium begins to regrow, replacing the blood vessels and glands that deteriorated during the end of the last cycle.

Art Connection

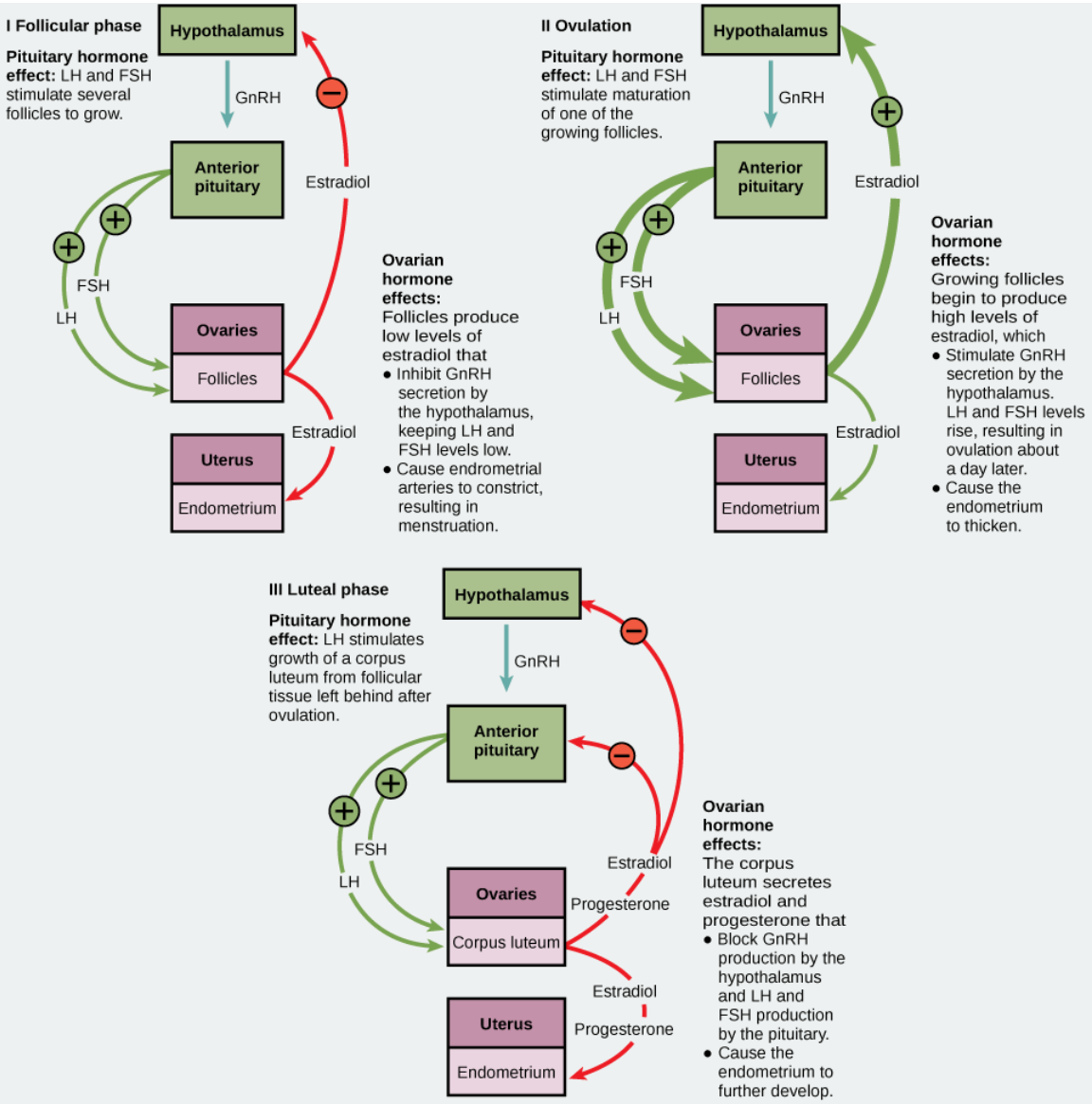


Figure **51.4.1.2**: The ovarian and menstrual cycles of female reproduction are regulated by hormones produced by the hypothalamus, pituitary, and ovaries.

Which of the following statements about hormone regulation of the female reproductive cycle is false?

A. LH and FSH are produced in the pituitary, and estradiol and progesterone are produced in the ovaries.
B. Estradiol and progesterone secreted from the corpus luteum cause the endometrium to thicken.
C. Both progesterone and estradiol are produced by the follicles.
D. Secretion of GnRH by the hypothalamus is inhibited by low levels of estradiol but stimulated by high levels of estradiol.

Just prior to the middle of the cycle (approximately day 14), the high level of estrogen causes FSH and especially LH to rise rapidly, then fall. The spike in LH causes ovulation: the most mature follicle, like that shown in Figure **51.4.1.3**, ruptures and releases its egg. The follicles that did not rupture degenerate and their eggs are lost. The level of estrogen decreases when the extra follicles degenerate.



Figure **51.4.1.3**: This mature egg follicle may rupture and release an egg. (credit: scale-bar data from Matt Russell)

Following ovulation, the ovarian cycle enters its luteal phase, illustrated in Figure **51.4.1.4** and the menstrual cycle enters its secretory phase, both of which run from about day 15 to 28. The luteal and secretory phases refer to changes in the ruptured follicle. The cells in the follicle undergo physical changes and produce a structure called a corpus luteum. The corpus luteum produces estrogen and progesterone. The progesterone facilitates the regrowth of the uterine lining and inhibits the release of further FSH and LH. The uterus is being prepared to accept a fertilized egg, should it occur during this cycle. The inhibition of FSH and LH prevents any further eggs and follicles from developing, while the progesterone is elevated. The level of estrogen produced by the corpus luteum increases to a steady level for the next few days.

If no fertilized egg is implanted into the uterus, the corpus luteum degenerates and the levels of estrogen and progesterone decrease. The endometrium begins to degenerate as the progesterone levels drop, initiating the next menstrual cycle. The decrease in progesterone also allows the hypothalamus to send GnRH to the anterior pituitary, releasing FSH and LH and starting the cycles again. Figure **51.4.1.4** visually compares the ovarian and uterine cycles as well as the commensurate hormone levels.

Art Connection

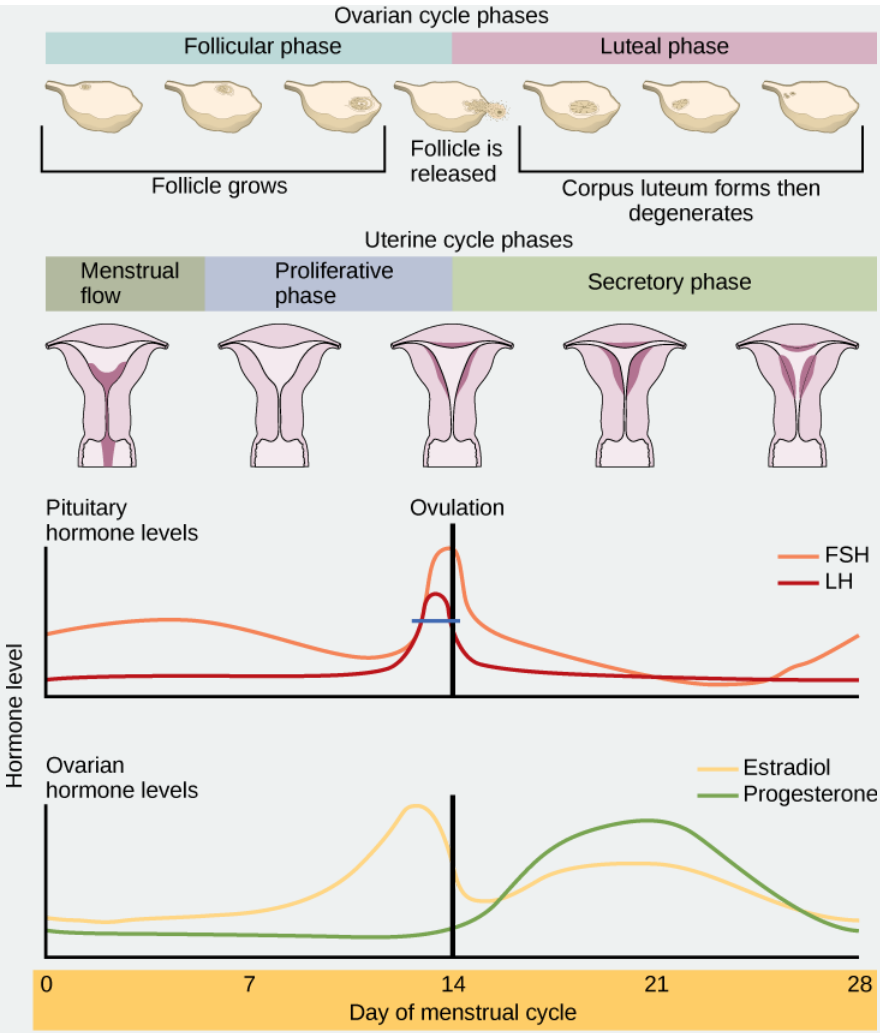


Figure 51.4.1.4: Rising and falling hormone levels result in progression of the ovarian and menstrual cycles. (credit: modification of work by Mikael Häggström)

Which of the following statements about the menstrual cycle is false?

A. Progesterone levels rise during the luteal phase of the ovarian cycle and the secretory phase of the uterine cycle.
B. Menstruation occurs just after LH and FSH levels peak.
C. Menstruation occurs after progesterone levels drop.
D. Estrogen levels rise before ovulation, while progesterone levels rise after.

Menopause

As women approach their mid-40s to mid-50s, their ovaries begin to lose their sensitivity to FSH and LH. Menstrual periods become less frequent and finally cease; this is menopause. There are still eggs and potential follicles on the ovaries, but without the stimulation of FSH and LH, they will not produce a viable egg to be released. The outcome of this is the inability to have children.

The side effects of menopause include hot flashes, heavy sweating (especially at night), headaches, some hair loss, muscle pain, vaginal dryness, insomnia, depression, weight gain, and mood swings. Estrogen is involved in calcium metabolism and, without it, blood levels of calcium decrease. To replenish the blood, calcium is lost from bone which may decrease the bone density and lead to osteoporosis. Supplementation of estrogen in the form of hormone replacement therapy (HRT) can prevent bone loss, but the therapy can have negative side effects. While HRT is thought to give some protection from colon cancer, osteoporosis, heart disease, macular degeneration, and possibly depression, its negative side effects include increased risk of: stroke or heart attack, blood clots, breast cancer, ovarian cancer, endometrial cancer, gall bladder disease, and possibly dementia.

Career Connection: Reproductive Endocrinologist

A reproductive endocrinologist is a physician who treats a variety of hormonal disorders related to reproduction and infertility in both men and women. The disorders include menstrual problems, infertility, pregnancy loss, sexual dysfunction, and menopause. Doctors may use fertility drugs, surgery, or assisted reproductive techniques (ART) in their therapy. ART involves the use of procedures to manipulate the egg or sperm to facilitate reproduction, such as *in vitro* fertilization.

Reproductive endocrinologists undergo extensive medical training, first in a four-year residency in obstetrics and gynecology, then in a three-year fellowship in reproductive endocrinology. To be board certified in this area, the physician must pass written and oral exams in both areas.

Summary

The male and female reproductive cycles are controlled by hormones released from the hypothalamus and anterior pituitary as well as hormones from reproductive tissues and organs. The hypothalamus monitors the need for the FSH and LH hormones made and released from the anterior pituitary. FSH and LH affect reproductive structures to cause the formation of sperm and the preparation of eggs for release and possible fertilization. In the male, FSH and LH stimulate Sertoli cells and interstitial cells of Leydig in the testes to facilitate sperm production. The Leydig cells produce testosterone, which also is responsible for the secondary sexual characteristics of males. In females, FSH and LH cause estrogen and progesterone to be produced. They regulate the female reproductive system which is divided into the ovarian cycle and the menstrual cycle. Menopause occurs when the ovaries lose their sensitivity to FSH and LH and the female reproductive cycles slow to a stop.

Art Connections

Figure **51.4.1.2**: Which of the following statements about hormone regulation of the female reproductive cycle is false?

A. LH and FSH are produced in the pituitary, and estradiol and progesterone are produced in the ovaries.
B. Estradiol and progesterone secreted from the corpus luteum cause the endometrium to thicken.
C. Both progesterone and estradiol are produced by the follicles.
D. Secretion of GnRH by the hypothalamus is inhibited by low levels of estradiol but stimulated by high levels of estradiol.

Answer

C

Figure **51.4.1.4**: Which of the following statements about the menstrual cycle is false?

A. Progesterone levels rise during the luteal phase of the ovarian cycle and the secretory phase of the uterine cycle.
B. Menstruation occurs just after LH and FSH levels peak.
C. Menstruation occurs after progesterone levels drop.
D. Estrogen levels rise before ovulation, while progesterone levels rise after.

Answer

B

Glossary

estrogen

reproductive hormone in females that assists in endometrial regrowth, ovulation, and calcium absorption

follicle stimulating hormone (FSH)

reproductive hormone that causes sperm production in men and follicle development in women

gonadotropin-releasing hormone (GnRH)

hormone from the hypothalamus that causes the release of FSH and LH from the anterior pituitary

inhibin
hormone made by Sertoli cells; provides negative feedback to hypothalamus in control of FSH and GnRH release

interstitial cell of Leydig
cell in seminiferous tubules that makes testosterone

luteinizing hormone (LH)
reproductive hormone in both men and women, causes testosterone production in men and ovulation and lactation in women

menopause
loss of reproductive capacity in women due to decreased sensitivity of the ovaries to FSH and LH

menstrual cycle
cycle of the degradation and re-growth of the endometrium

ovarian cycle
cycle of preparation of egg for ovulation and the conversion of the follicle to the corpus luteum

ovulation
release of the egg by the most mature follicle

progesterone
reproductive hormone in women; assists in endometrial re-growth and inhibition of FSH and LH release

Sertoli cell
cell in seminiferous tubules that assists developing sperm and makes inhibin

testosterone
reproductive hormone in men that assists in sperm production and promoting secondary sexual characteristics

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51.4.2: Human Pregnancy and Birth

Skills to Develop

- Explain fetal development during the three trimesters of gestation
- Describe labor and delivery
- Compare the efficacy and duration of various types of contraception
- Discuss causes of infertility and the therapeutic options available

Pregnancy begins with the fertilization of an egg and continues through to the birth of the individual. The length of time of gestation varies among animals, but is very similar among the great apes: human gestation is 266 days, while chimpanzee gestation is 237 days, a gorilla's is 257 days, and orangutan gestation is 260 days long. The fox has a 57-day gestation. Dogs and cats have similar gestations averaging 60 days. The longest gestation for a land mammal is an African elephant at 640 days. The longest gestations among marine mammals are the beluga and sperm whales at 460 days.

Human Gestation

Twenty-four hours before fertilization, the egg has finished meiosis and becomes a mature oocyte. When fertilized (at conception) the egg becomes known as a zygote. The zygote travels through the oviduct to the uterus (Figure 51.4.2.1). The developing embryo must implant into the wall of the uterus within seven days, or it will deteriorate and die. The outer layers of the zygote (blastocyst) grow into the endometrium by digesting the endometrial cells, and wound healing of the endometrium closes up the blastocyst into the tissue. Another layer of the blastocyst, the chorion, begins releasing a hormone called human beta chorionic gonadotropin (β-HCG) which makes its way to the corpus luteum and keeps that structure active. This ensures adequate levels of progesterone that will maintain the endometrium of the uterus for the support of the developing embryo. Pregnancy tests determine the level of β-HCG in urine or serum. If the hormone is present, the test is positive.

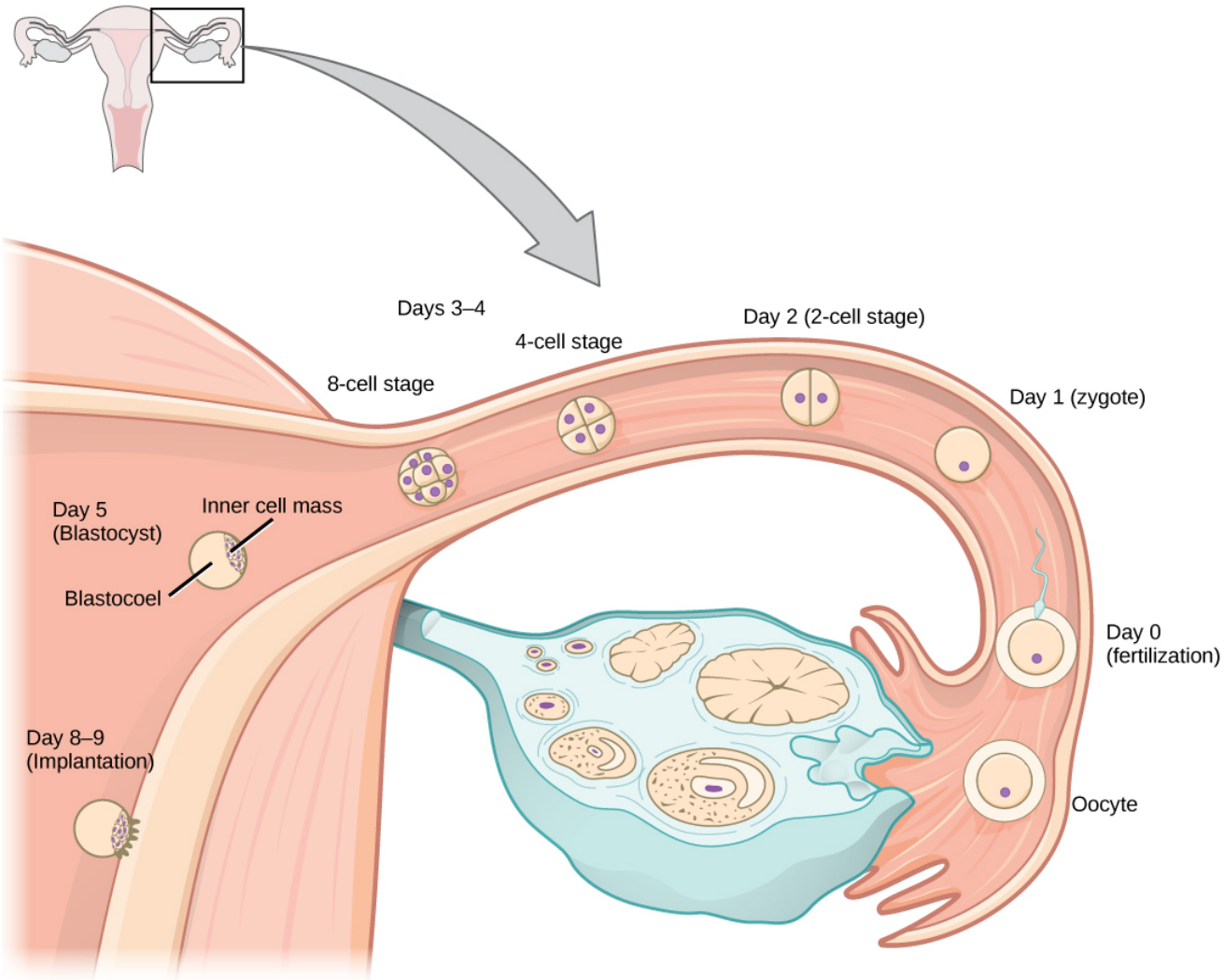


Figure **51.4.2.1**: In humans, fertilization occurs soon after the oocyte leaves the ovary. Implantation occurs eight or nine days later. (credit: Ed Uthman)

The gestation period is divided into three equal periods or trimesters. During the first two to four weeks of the first trimester, nutrition and waste are handled by the endometrial lining through diffusion. As the trimester progresses, the outer layer of the embryo begins to merge with the endometrium, and the placenta forms. This organ takes over the nutrient and waste requirements of the embryo and fetus, with the mother's blood passing nutrients to the placenta and removing waste from it. Chemicals from the fetus, such as bilirubin, are processed by the mother's liver for elimination. Some of the mother's immunoglobulins will pass through the placenta, providing passive immunity against some potential infections.

Internal organs and body structures begin to develop during the first trimester. By five weeks, limb buds, eyes, the heart, and liver have been basically formed. By eight weeks, the term fetus applies, and the body is essentially formed, as shown in Figure **51.4.2.2**. The individual is about five centimeters (two inches) in length and many of the organs, such as the lungs and liver, are not yet functioning. Exposure to any toxins is especially dangerous during the first trimester, as all of the body's organs and structures are going through initial development. Anything that affects that development can have a severe effect on the fetus' survival.



Figure **51.4.2.2**: Fetal development is shown at nine weeks gestation. (credit: Ed Uthman)

During the second trimester, the fetus grows to about 30 cm (12 inches), as shown in Figure **51.4.2.3.** It becomes active and the mother usually feels the first movements. All organs and structures continue to develop. The placenta has taken over the functions of nutrition and waste and the production of estrogen and progesterone from the corpus luteum, which has degenerated. The placenta will continue functioning up through the delivery of the baby.



Figure **51.4.2.3**: This fetus is just entering the second trimester, when the placenta takes over more of the functions performed as the baby develops. (credit: National Museum of Health and Medicine)

During the third trimester, the fetus grows to 3 to 4 kg (6 ½ -8 ½ lbs.) and about 50 cm (19-20 inches) long, as illustrated in Figure **51.4.2.4**. This is the period of the most rapid growth during the pregnancy. Organ development continues to birth (and some systems, such as the nervous system and liver, continue to develop after birth). The mother will be at her most uncomfortable during this trimester. She may urinate frequently due to pressure on the bladder from the fetus. There may also be intestinal blockage and circulatory problems, especially in her legs. Clots may form in her legs due to pressure from the fetus on returning veins as they enter the abdominal cavity.

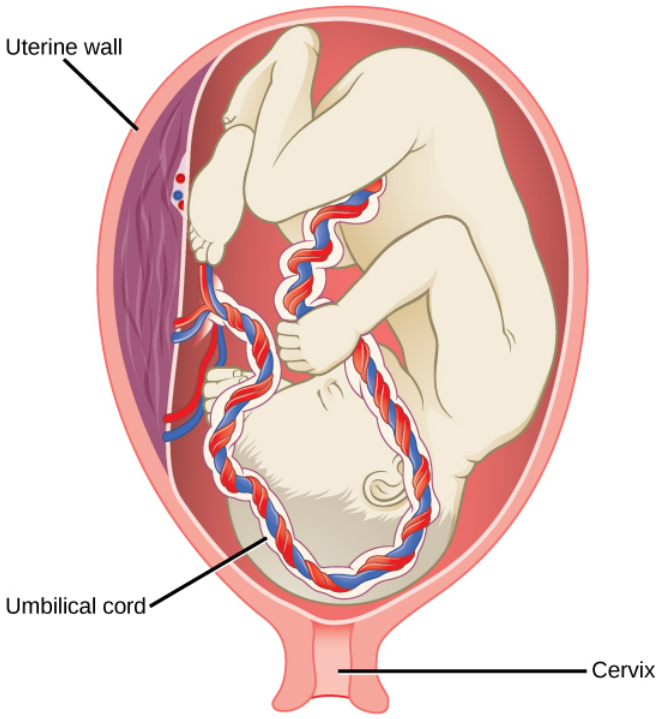


Figure 51.4.2.4: There is rapid fetal growth during the third trimester. (credit: modification of work by Gray's Anatomy)

Link to Learning

Visit this site to see the stages of human fetal development.

Labor and Birth

Labor is the physical efforts of expulsion of the fetus and the placenta from the uterus during birth (parturition). Toward the end of the third trimester, estrogen causes receptors on the uterine wall to develop and bind the hormone oxytocin. At this time, the baby reorients, facing forward and down with the back or crown of the head engaging the cervix (uterine opening). This causes the cervix to stretch and nerve impulses are sent to the hypothalamus, which signals for the release of oxytocin from the posterior pituitary. The oxytocin causes the smooth muscle in the uterine wall to contract. At the same time, the placenta releases prostaglandins into the uterus, increasing the contractions. A positive feedback relay occurs between the uterus, hypothalamus, and the posterior pituitary to assure an adequate supply of oxytocin. As more smooth muscle cells are recruited, the contractions increase in intensity and force.

There are three stages to labor. During stage one, the cervix thins and dilates. This is necessary for the baby and placenta to be expelled during birth. The cervix will eventually dilate to about 10 cm. During stage two, the baby is expelled from the uterus. The uterus contracts and the mother pushes as she compresses her abdominal muscles to aid the delivery. The last stage is the passage of the placenta after the baby has been born and the organ has completely disengaged from the uterine wall. If labor should stop before stage two is reached, synthetic oxytocin, known as Pitocin, can be administered to restart and maintain labor.

An alternative to labor and delivery is the surgical delivery of the baby through a procedure called a Caesarian section. This is major abdominal surgery and can lead to post-surgical complications for the mother, but in some cases it may be the only way to safely deliver the baby.

The mother's mammary glands go through changes during the third trimester to prepare for lactation and breastfeeding. When the baby begins suckling at the breast, signals are sent to the hypothalamus causing the release of prolactin from the anterior pituitary. Prolactin causes the mammary glands to produce milk. Oxytocin is also released, promoting the release of the milk. The milk contains nutrients for the baby's development and growth as well as immunoglobulins to protect the child from bacterial and viral infections.

Contraception and Birth Control

The prevention of a pregnancy comes under the terms contraception or birth control. Strictly speaking, contraception refers to preventing the sperm and egg from joining. Both terms are, however, frequently used interchangeably.

Table 51.4.2.1: Contraceptive Methods

Method	Examples	Failure Rate in Typical Use Over 12 Months
Barrier	male condom, female condom, sponge, cervical cap, diaphragm, spermicides	15 to 24%
Hormonal	oral, patch, vaginal ring	8%
	injection	3%
	implant	less than 1%
Other	natural family planning	12 to 25%
	withdrawal	27%
	sterilization	less than 1%

Table **51.4.2.1** lists common methods of contraception. The failure rates listed are not the ideal rates that could be realized, but the typical rates that occur. A failure rate is the number of pregnancies resulting from the method's use over a twelve-month period. Barrier methods, such as condoms, cervical caps, and diaphragms, block sperm from entering the uterus, preventing fertilization. Spermicides are chemicals that are placed in the vagina that kill sperm. Sponges, which are saturated with spermicides, are placed in the vagina at the cervical opening. Combinations of spermicidal chemicals and barrier methods achieve lower failure rates than do the methods when used separately.

Nearly a quarter of the couples using barrier methods, natural family planning, or withdrawal can expect a failure of the method. Natural family planning is based on the monitoring of the menstrual cycle and having intercourse only during times when the egg is not available. A woman's body temperature may rise a degree Celsius at ovulation and the cervical mucus may increase in volume and become more pliable. These changes give a general indication of when intercourse is more or less likely to result in fertilization. Withdrawal involves the removal of the penis from the vagina during intercourse, before ejaculation occurs. This is a risky method with a high failure rate due to the possible presence of sperm in the bulbourethral gland's secretion, which may enter the vagina prior to removing the penis.

Hormonal methods use synthetic progesterone (sometimes in combination with estrogen), to inhibit the hypothalamus from releasing FSH or LH, and thus prevent an egg from being available for fertilization. The method of administering the hormone affects failure rate. The most reliable method, with a failure rate of less than 1 percent, is the implantation of the hormone under the skin. The same rate can be achieved through the sterilization procedures of vasectomy in the man or of tubal ligation in the woman, or by using an intrauterine device (IUD). IUDs are inserted into the uterus and establish an inflammatory condition that prevents fertilized eggs from implanting into the uterine wall.

Compliance with the contraceptive method is a strong contributor to the success or failure rate of any particular method. The only method that is completely effective at preventing conception is abstinence. The choice of contraceptive method depends on the goals of the woman or couple. Tubal ligation and vasectomy are considered permanent prevention, while other methods are reversible and provide short-term contraception.

Termination of an existing pregnancy can be spontaneous or voluntary. Spontaneous termination is a miscarriage and usually occurs very early in the pregnancy, usually within the first few weeks. This occurs when the fetus cannot develop properly and the gestation is naturally terminated. Voluntary termination of a pregnancy is an abortion. Laws regulating abortion vary between states and tend to view fetal viability as the criteria for allowing or preventing the procedure.

Infertility

Infertility is the inability to conceive a child or carry a child to birth. About 75 percent of causes of infertility can be identified; these include diseases, such as sexually transmitted diseases that can cause scarring of the reproductive tubes in either men or women, or developmental problems frequently related to abnormal hormone levels in one of the individuals. Inadequate nutrition, especially starvation, can delay menstruation. Stress can also lead to infertility. Short-term stress can affect hormone levels, while long-term stress can delay puberty and cause less frequent menstrual cycles. Other factors that affect fertility include toxins (such as cadmium), tobacco smoking, marijuana use, gonadal injuries, and aging.

If infertility is identified, several assisted reproductive technologies (ART) are available to aid conception. A common type of ART is *in vitro* fertilization (IVF) where an egg and sperm are combined outside the body and then placed in the uterus. Eggs are obtained from the woman after extensive hormonal treatments that prepare mature eggs for fertilization and prepare the uterus for implantation of the fertilized egg. Sperm are obtained from the man and they are combined with the eggs and supported through several cell divisions to ensure viability of the zygotes. When the embryos have reached the eight-cell stage, one or more is implanted into the woman's uterus. If fertilization is not accomplished by simple IVF, a procedure that injects the sperm into an egg can be used. This is called intracytoplasmic sperm injection (ICSI) and is shown in Figure **51.4.2.5**. IVF procedures produce a surplus of fertilized eggs and embryos that can be frozen and stored for future use. The procedures can also result in multiple births.

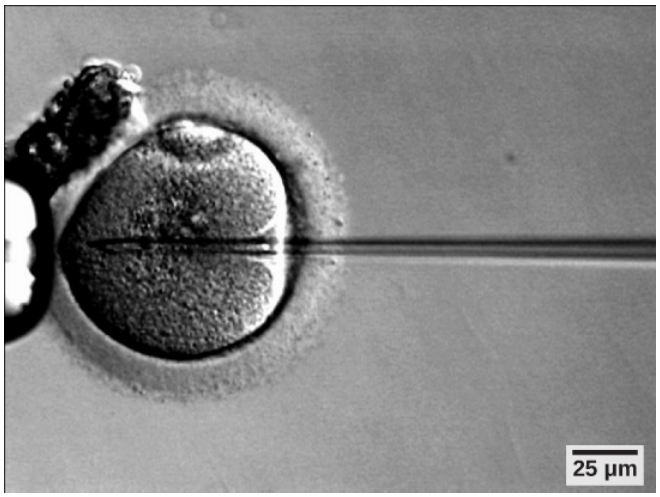


Figure **51.4.2.5**: A sperm is inserted into an egg for fertilization during intracytoplasmic sperm injection (ICSI). (credit: scale-bar data from Matt Russell)

Summary

Human pregnancy begins with fertilization of an egg and proceeds through the three trimesters of gestation. The labor process has three stages (contractions, delivery of the fetus, expulsion of the placenta), each propelled by hormones. The first trimester lays down the basic structures of the body, including the limb buds, heart, eyes, and the liver. The second trimester continues the development of all of the organs and systems. The third trimester exhibits the greatest growth of the fetus and culminates in labor and delivery. Prevention of a pregnancy can be accomplished through a variety of methods including barriers, hormones, or other means. Assisted reproductive technologies may help individuals who have infertility problems.

Glossary

contraception
(also, birth control) various means used to prevent pregnancy

gestation
length of time for fetal development to birth

human beta chorionic gonadotropin (*β*-HCG)
hormone produced by the chorion of the zygote that helps to maintain the corpus luteum and elevated levels of progesterone

infertility
inability to conceive, carry, and deliver children

morning sickness
condition in the mother during the first trimester; includes feelings of nausea

placenta
organ that supports the diffusion of nutrients and waste between the mother's and fetus' blood

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51.5: Contraception and Fertility Treatments

Skills to Develop

- Explain fetal development during the three trimesters of gestation
- Describe labor and delivery
- Compare the efficacy and duration of various types of contraception
- Discuss causes of infertility and the therapeutic options available

Pregnancy begins with the fertilization of an egg and continues through to the birth of the individual. The length of time of gestation varies among animals, but is very similar among the great apes: human gestation is 266 days, while chimpanzee gestation is 237 days, a gorilla's is 257 days, and orangutan gestation is 260 days long. The fox has a 57-day gestation. Dogs and cats have similar gestations averaging 60 days. The longest gestation for a land mammal is an African elephant at 640 days. The longest gestations among marine mammals are the beluga and sperm whales at 460 days.

Human Gestation

Twenty-four hours before fertilization, the egg has finished meiosis and becomes a mature oocyte. When fertilized (at conception) the egg becomes known as a zygote. The zygote travels through the oviduct to the uterus (Figure 51.5.1). The developing embryo must implant into the wall of the uterus within seven days, or it will deteriorate and die. The outer layers of the zygote (blastocyst) grow into the endometrium by digesting the endometrial cells, and wound healing of the endometrium closes up the blastocyst into the tissue. Another layer of the blastocyst, the chorion, begins releasing a hormone called human beta chorionic gonadotropin (β-HCG) which makes its way to the corpus luteum and keeps that structure active. This ensures adequate levels of progesterone that will maintain the endometrium of the uterus for the support of the developing embryo. Pregnancy tests determine the level of β-HCG in urine or serum. If the hormone is present, the test is positive.

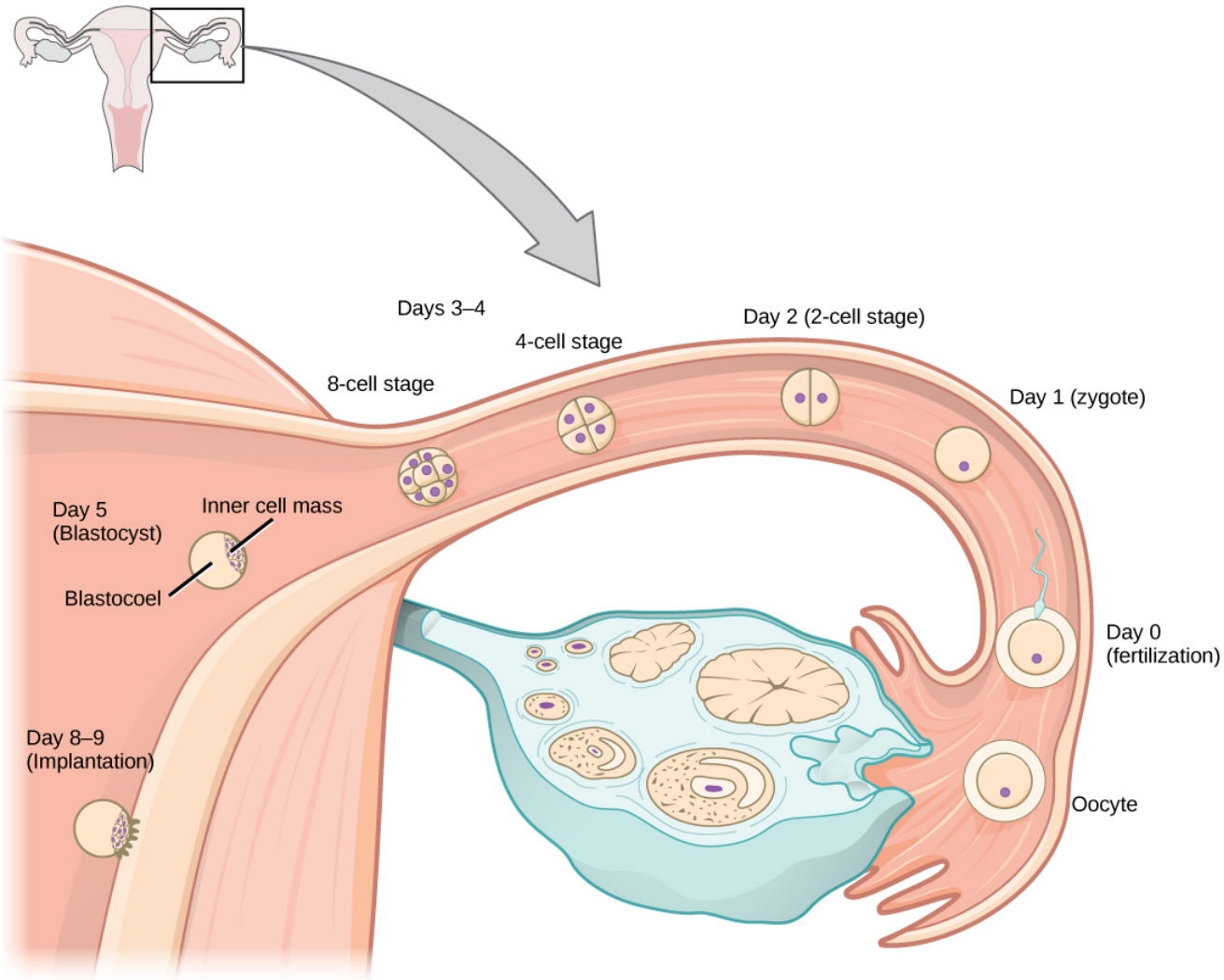


Figure 51.5.1: In humans, fertilization occurs soon after the oocyte leaves the ovary. Implantation occurs eight or nine days later. (credit: Ed Uthman)

The gestation period is divided into three equal periods or trimesters. During the first two to four weeks of the first trimester, nutrition and waste are handled by the endometrial lining through diffusion. As the trimester progresses, the outer layer of the embryo begins to merge with the endometrium, and the placenta forms. This organ takes over the nutrient and waste requirements of the embryo and fetus, with the mother's blood passing nutrients to the placenta and removing waste from it. Chemicals from the fetus, such as bilirubin, are processed by the mother's liver for elimination. Some of the mother's immunoglobulins will pass through the placenta, providing passive immunity against some potential infections.

Internal organs and body structures begin to develop during the first trimester. By five weeks, limb buds, eyes, the heart, and liver have been basically formed. By eight weeks, the term fetus applies, and the body is essentially formed, as shown in Figure 51.5.2. The individual is about five centimeters (two inches) in length and many of the organs, such as the lungs and liver, are not yet functioning. Exposure to any toxins is especially dangerous during the first trimester, as all of the body's organs and structures are going through initial development. Anything that affects that development can have a severe effect on the fetus' survival.



Figure **51.5.2**: Fetal development is shown at nine weeks gestation. (credit: Ed Uthman)

During the second trimester, the fetus grows to about 30 cm (12 inches), as shown in Figure **51.5.3**. It becomes active and the mother usually feels the first movements. All organs and structures continue to develop. The placenta has taken over the functions of nutrition and waste and the production of estrogen and progesterone from the corpus luteum, which has degenerated. The placenta will continue functioning up through the delivery of the baby.



Figure **51.5.3**: This fetus is just entering the second trimester, when the placenta takes over more of the functions performed as the baby develops. (credit: National Museum of Health and Medicine)

During the third trimester, the fetus grows to 3 to 4 kg (6 ½ -8 ½ lbs.) and about 50 cm (19-20 inches) long, as illustrated in Figure **51.5.4**. This is the period of the most rapid growth during the pregnancy. Organ development continues to birth (and some systems, such as the nervous system and liver, continue to develop after birth). The mother will be at her most uncomfortable during this trimester. She may urinate frequently due to pressure on the bladder from the fetus. There may also be intestinal blockage and circulatory problems, especially in her legs. Clots may form in her legs due to pressure from the fetus on returning veins as they enter the abdominal cavity.

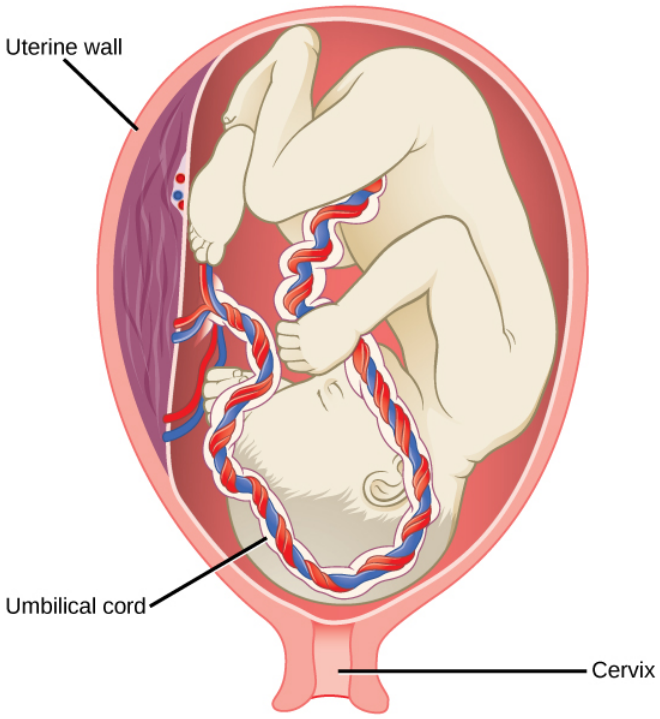


Figure 51.5.4: There is rapid fetal growth during the third trimester. (credit: modification of work by Gray's Anatomy)

Link to Learning

Visit this site to see the stages of human fetal development.

Labor and Birth

Labor is the physical efforts of expulsion of the fetus and the placenta from the uterus during birth (parturition). Toward the end of the third trimester, estrogen causes receptors on the uterine wall to develop and bind the hormone oxytocin. At this time, the baby reorients, facing forward and down with the back or crown of the head engaging the cervix (uterine opening). This causes the cervix to stretch and nerve impulses are sent to the hypothalamus, which signals for the release of oxytocin from the posterior pituitary. The oxytocin causes the smooth muscle in the uterine wall to contract. At the same time, the placenta releases prostaglandins into the uterus, increasing the contractions. A positive feedback relay occurs between the uterus, hypothalamus, and the posterior pituitary to assure an adequate supply of oxytocin. As more smooth muscle cells are recruited, the contractions increase in intensity and force.

There are three stages to labor. During stage one, the cervix thins and dilates. This is necessary for the baby and placenta to be expelled during birth. The cervix will eventually dilate to about 10 cm. During stage two, the baby is expelled from the uterus. The uterus contracts and the mother pushes as she compresses her abdominal muscles to aid the delivery. The last stage is the passage of the placenta after the baby has been born and the organ has completely disengaged from the uterine wall. If labor should stop before stage two is reached, synthetic oxytocin, known as Pitocin, can be administered to restart and maintain labor.

An alternative to labor and delivery is the surgical delivery of the baby through a procedure called a Caesarian section. This is major abdominal surgery and can lead to post-surgical complications for the mother, but in some cases it may be the only way to safely deliver the baby.

The mother's mammary glands go through changes during the third trimester to prepare for lactation and breastfeeding. When the baby begins suckling at the breast, signals are sent to the hypothalamus causing the release of prolactin from the anterior pituitary. Prolactin causes the mammary glands to produce milk. Oxytocin is also released, promoting the release of the milk. The milk contains nutrients for the baby's development and growth as well as immunoglobulins to protect the child from bacterial and viral infections.

Contraception and Birth Control

The prevention of a pregnancy comes under the terms contraception or birth control. Strictly speaking, contraception refers to preventing the sperm and egg from joining. Both terms are, however, frequently used interchangeably.

Table 51.5.1: Contraceptive Methods

Method	Examples	Failure Rate in Typical Use Over 12 Months
Barrier	male condom, female condom, sponge, cervical cap, diaphragm, spermicides	15 to 24%
Hormonal	oral, patch, vaginal ring	8%
	injection	3%
	implant	less than 1%
Other	natural family planning	12 to 25%
	withdrawal	27%
	sterilization	less than 1%

Table 51.5.1 lists common methods of contraception. The failure rates listed are not the ideal rates that could be realized, but the typical rates that occur. A failure rate is the number of pregnancies resulting from the method's use over a twelve-month period. Barrier methods, such as condoms, cervical caps, and diaphragms, block sperm from entering the uterus, preventing fertilization. Spermicides are chemicals that are placed in the vagina that kill sperm. Sponges, which are saturated with spermicides, are placed in the vagina at the cervical opening. Combinations of spermicidal chemicals and barrier methods achieve lower failure rates than do the methods when used separately.

Nearly a quarter of the couples using barrier methods, natural family planning, or withdrawal can expect a failure of the method. Natural family planning is based on the monitoring of the menstrual cycle and having intercourse only during times when the egg is not available. A woman's body temperature may rise a degree Celsius at ovulation and the cervical mucus may increase in volume and become more pliable. These changes give a general indication of when intercourse is more or less likely to result in fertilization. Withdrawal involves the removal of the penis from the vagina during intercourse, before ejaculation occurs. This is a risky method with a high failure rate due to the possible presence of sperm in the bulbourethral gland's secretion, which may enter the vagina prior to removing the penis.

Hormonal methods use synthetic progesterone (sometimes in combination with estrogen), to inhibit the hypothalamus from releasing FSH or LH, and thus prevent an egg from being available for fertilization. The method of administering the hormone affects failure rate. The most reliable method, with a failure rate of less than 1 percent, is the implantation of the hormone under the skin. The same rate can be achieved through the sterilization procedures of vasectomy in the man or of tubal ligation in the woman, or by using an intrauterine device (IUD). IUDs are inserted into the uterus and establish an inflammatory condition that prevents fertilized eggs from implanting into the uterine wall.

Compliance with the contraceptive method is a strong contributor to the success or failure rate of any particular method. The only method that is completely effective at preventing conception is abstinence. The choice of contraceptive method depends on the goals of the woman or couple. Tubal ligation and vasectomy are considered permanent prevention, while other methods are reversible and provide short-term contraception.

Termination of an existing pregnancy can be spontaneous or voluntary. Spontaneous termination is a miscarriage and usually occurs very early in the pregnancy, usually within the first few weeks. This occurs when the fetus cannot develop properly and the gestation is naturally terminated. Voluntary termination of a pregnancy is an abortion. Laws regulating abortion vary between states and tend to view fetal viability as the criteria for allowing or preventing the procedure.

Infertility

Infertility is the inability to conceive a child or carry a child to birth. About 75 percent of causes of infertility can be identified; these include diseases, such as sexually transmitted diseases that can cause scarring of the reproductive tubes in either men or women, or developmental problems frequently related to abnormal hormone levels in one of the individuals. Inadequate nutrition, especially starvation, can delay menstruation. Stress can also lead to infertility. Short-term stress can affect hormone levels, while long-term stress can delay puberty and cause less frequent menstrual cycles. Other factors that affect fertility include toxins (such as cadmium), tobacco smoking, marijuana use, gonadal injuries, and aging.

If infertility is identified, several assisted reproductive technologies (ART) are available to aid conception. A common type of ART is *in vitro* fertilization (IVF) where an egg and sperm are combined outside the body and then placed in the uterus. Eggs are obtained from the woman after extensive hormonal treatments that prepare mature eggs for fertilization and prepare the uterus for implantation of the fertilized egg. Sperm are obtained from the man and they are combined with the eggs and supported through several cell divisions to ensure viability of the zygotes. When the embryos have reached the eight-cell stage, one or more is implanted into the woman's uterus. If fertilization is not accomplished by simple IVF, a procedure that injects the sperm into an egg can be used. This is called intracytoplasmic sperm injection (ICSI) and is shown in Figure **51.5.5**. IVF procedures produce a surplus of fertilized eggs and embryos that can be frozen and stored for future use. The procedures can also result in multiple births.

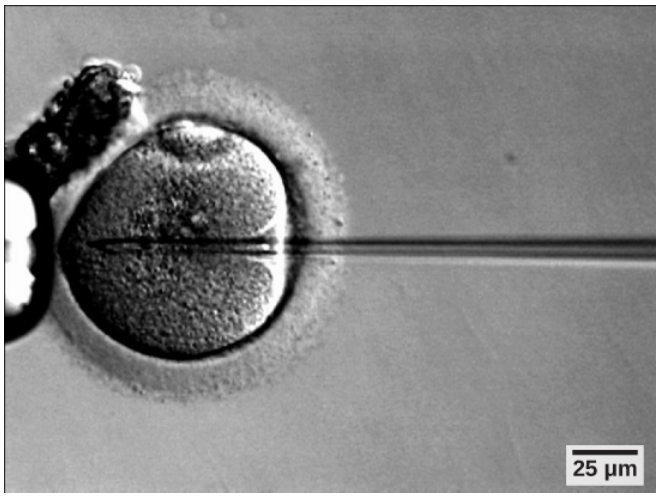


Figure **51.5.5**: A sperm is inserted into an egg for fertilization during intracytoplasmic sperm injection (ICSI). (credit: scale-bar data from Matt Russell)

Summary

Human pregnancy begins with fertilization of an egg and proceeds through the three trimesters of gestation. The labor process has three stages (contractions, delivery of the fetus, expulsion of the placenta), each propelled by hormones. The first trimester lays down the basic structures of the body, including the limb buds, heart, eyes, and the liver. The second trimester continues the development of all of the organs and systems. The third trimester exhibits the greatest growth of the fetus and culminates in labor and delivery. Prevention of a pregnancy can be accomplished through a variety of methods including barriers, hormones, or other means. Assisted reproductive technologies may help individuals who have infertility problems.

Glossary

contraception
(also, birth control) various means used to prevent pregnancy

gestation
length of time for fetal development to birth

human beta chorionic gonadotropin (*β*-HCG)
hormone produced by the chorion of the zygote that helps to maintain the corpus luteum and elevated levels of progesterone

infertility
inability to conceive, carry, and deliver children

morning sickness
condition in the mother during the first trimester; includes feelings of nausea

placenta
organ that supports the diffusion of nutrients and waste between the mother's and fetus' blood

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CHAPTER OVERVIEW

52: Animal Development

52.1: Fertilization

52.2: Cleavage and the Blastula Stage

52.3: Gastrulation

52.4: Organogenesis

52.5: Vertebrate Axis Pattern Formation

52.6: Human Development

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52.1: Fertilization

Skills to Develop

- Discuss how fertilization occurs
- Explain how the embryo forms from the zygote
- Discuss the role of cleavage and gastrulation in animal development

The process in which an organism develops from a single-celled zygote to a multi-cellular organism is complex and well-regulated. The early stages of embryonic development are also crucial for ensuring the fitness of the organism.

Fertilization

Fertilization, pictured in Figure 52.1.1a is the process in which gametes (an egg and sperm) fuse to form a zygote. The egg and sperm each contain one set of chromosomes. To ensure that the offspring has only one complete diploid set of chromosomes, only one sperm must fuse with one egg. In mammals, the egg is protected by a layer of extracellular matrix consisting mainly of glycoproteins called the zona pellucida. When a sperm binds to the zona pellucida, a series of biochemical events, called the acrosomal reactions, take place. In placental mammals, the acrosome contains digestive enzymes that initiate the degradation of the glycoprotein matrix protecting the egg and allowing the sperm plasma membrane to fuse with the egg plasma membrane, as illustrated in Figure 52.1.1b. The fusion of these two membranes creates an opening through which the sperm nucleus is transferred into the ovum. The nuclear membranes of the egg and sperm break down and the two haploid genomes condense to form a diploid genome.

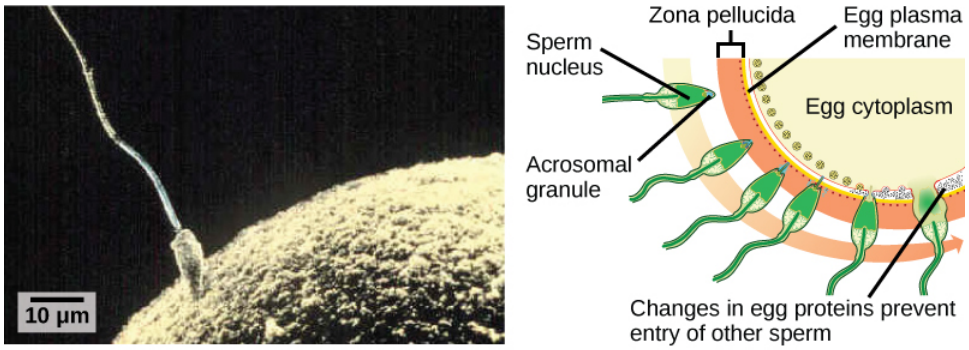


Figure 52.1.1: (a) Fertilization is the process in which sperm and egg fuse to form a zygote. (b) Acrosomal reactions help the sperm degrade the glycoprotein matrix protecting the egg and allow the sperm to transfer its nucleus. (credit: (b) modification of work by Mariana Ruiz Villareal; scale-bar data from Matt Russell)

To ensure that no more than one sperm fertilizes the egg, once the acrosomal reactions take place at one location of the egg membrane, the egg releases proteins in other locations to prevent other sperm from fusing with the egg. If this mechanism fails, multiple sperm can fuse with the egg, resulting in polyspermy. The resulting embryo is not genetically viable and dies within a few days.

Cleavage and Blastula Stage

The development of multi-cellular organisms begins from a single-celled zygote, which undergoes rapid cell division to form the blastula. The rapid, multiple rounds of cell division are termed cleavage. Cleavage is illustrated in (Figure 52.1.2a). After the cleavage has produced over 100 cells, the embryo is called a blastula. The blastula is usually a spherical layer of cells (the blastoderm) surrounding a fluid-filled or yolk-filled cavity (the blastocoel). Mammals at this stage form a structure called the blastocyst, characterized by an inner cell mass that is distinct from the surrounding blastula, shown in Figure 52.1.2b. During cleavage, the cells divide without an increase in mass; that is, one large single-celled zygote divides into multiple smaller cells. Each cell within the blastula is called a blastomere.

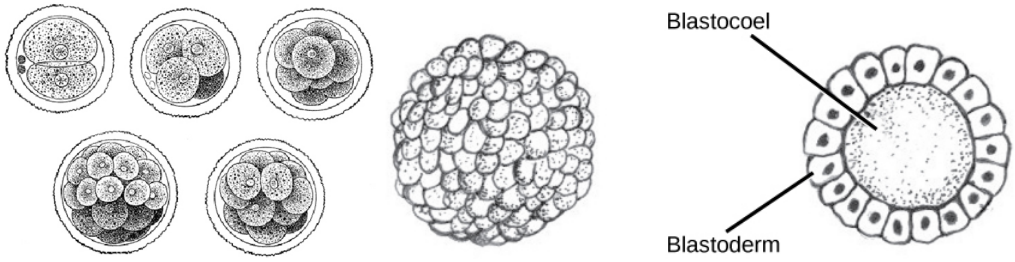


Figure 52.1.2: (a) During cleavage, the zygote rapidly divides into multiple cells without increasing in size. (b) The cells rearrange themselves to form a hollow ball with a fluid-filled or yolk-filled cavity called the blastula. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

Cleavage can take place in two ways: holoblastic (total) cleavage or meroblastic (partial) cleavage. The type of cleavage depends on the amount of yolk in the eggs. In placental mammals (including humans) where nourishment is provided by the mother's body, the eggs have a very small amount of yolk and undergo holoblastic cleavage. Other species, such as birds, with a lot of yolk in the egg to nourish the embryo during development, undergo meroblastic cleavage.

In mammals, the blastula forms the blastocyst in the next stage of development. Here the cells in the blastula arrange themselves in two layers: the inner cell mass, and an outer layer called the trophoblast. The inner cell mass is also known as the embryoblast and this mass of cells will go on to form the embryo. At this stage of development, illustrated in Figure **52.1.3** the inner cell mass consists of embryonic stem cells that will differentiate into the different cell types needed by the organism. The trophoblast will contribute to the placenta and nourish the embryo.

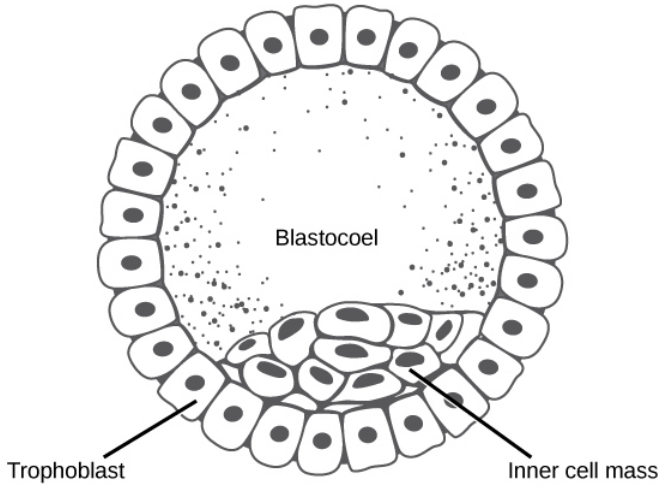


Figure **52.1.3**: The rearrangement of the cells in the mammalian blastula to two layers—the inner cell mass and the trophoblast—results in the formation of the blastocyst.

Link to Learning

Visit the Virtual Human Embryo project at the Endowment for Human Development site to step through an interactive that shows the stages of embryo development, including micrographs and rotating 3-D images.

Gastrulation

The typical blastula is a ball of cells. The next stage in embryonic development is the formation of the body plan. The cells in the blastula rearrange themselves spatially to form three layers of cells. This process is called gastrulation. During gastrulation, the blastula folds upon itself to form the three layers of cells. Each of these layers is called a germ layer and each germ layer differentiates into different organ systems.

The three germs layers, shown in Figure 52.1.4, are the endoderm, the ectoderm, and the mesoderm. The ectoderm gives rise to the nervous system and the epidermis. The mesoderm gives rise to the muscle cells and connective tissue in the body. The endoderm gives rise to columnar cells found in the digestive system and many internal organs.

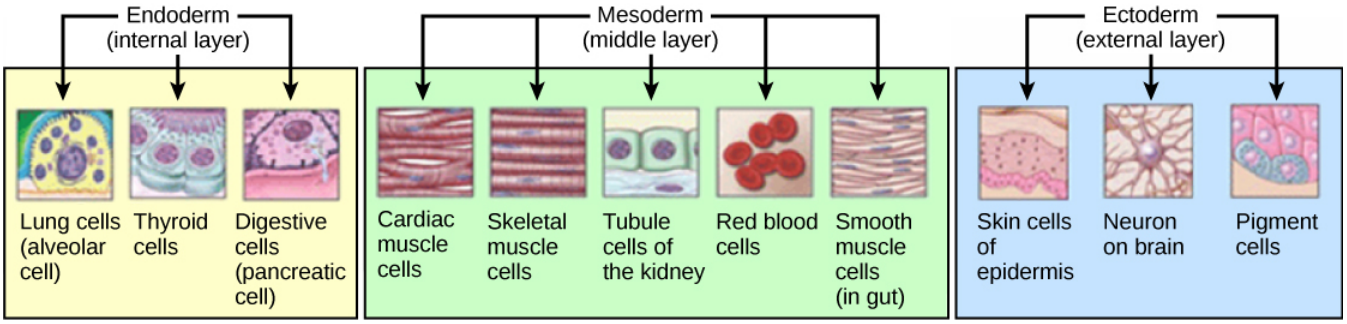


Figure 52.1.4: The three germ layers give rise to different cell types in the animal body. (credit: modification of work by NIH, NCBI)

Everyday Connection: Are Designer Babies in Our Future?

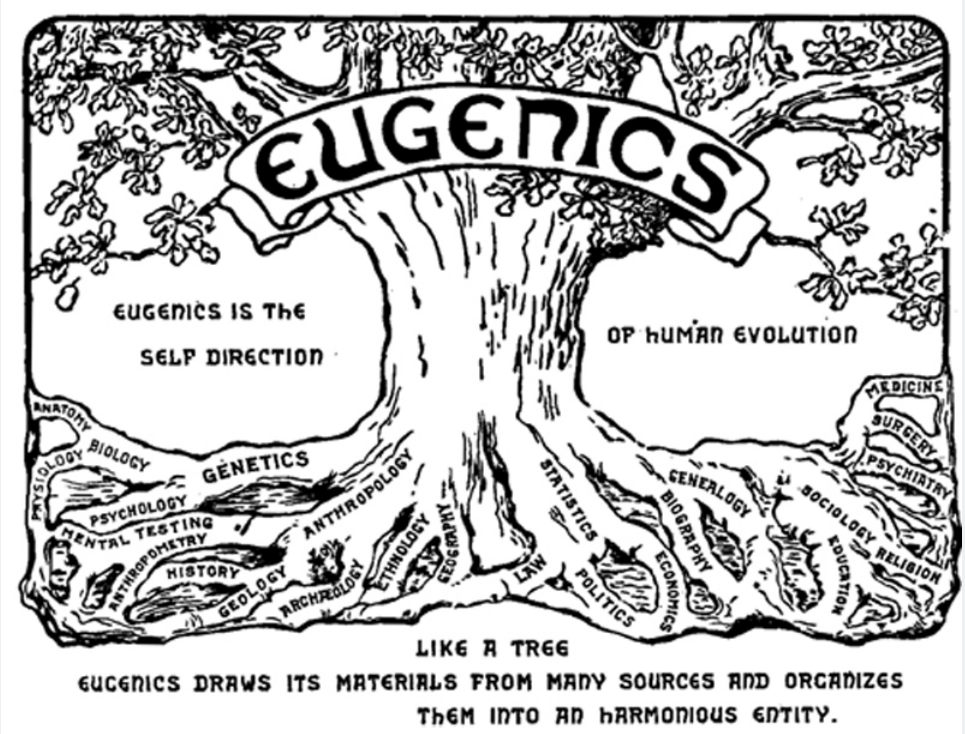


Figure 52.1.5: This logo from the Second International Eugenics Conference in New York City in September of 1921 shows how eugenics attempted to merge several fields of study with the goal of producing a genetically superior human race.

If you could prevent your child from getting a devastating genetic disease, would you do it? Would you select the sex of your child or select for their attractiveness, strength, or intelligence? How far would you go to maximize the possibility of resistance to disease? The genetic engineering of a human child, the production of "designer babies" with desirable phenotypic characteristics, was once a topic restricted to science fiction. This is the case no longer: science fiction is now overlapping into science fact. Many phenotypic choices for offspring are already available, with many more likely to be possible in the not too

distant future. Which traits should be selected and how they should be selected are topics of much debate within the worldwide medical community. The ethical and moral line is not always clear or agreed upon, and some fear that modern reproductive technologies could lead to a new form of eugenics.

Eugenics is the use of information and technology from a variety of sources to improve the genetic makeup of the human race. The goal of creating genetically superior humans was quite prevalent (although controversial) in several countries during the early 20th century, but fell into disrepute when Nazi Germany developed an extensive eugenics program in the 1930's and 40's. As part of their program, the Nazis forcibly sterilized hundreds of thousands of the so-called "unfit" and killed tens of thousands of institutionally disabled people as part of a systematic program to develop a genetically superior race of Germans known as Aryans. Ever since, eugenic ideas have not been as publicly expressed, but there are still those who promote them.

Efforts have been made in the past to control traits in human children using donated sperm from men with desired traits. In fact, eugenicist Robert Klark Graham established a sperm bank in 1980 that included samples exclusively from donors with high IQs. The "genius" sperm bank failed to capture the public's imagination and the operation closed in 1999.

In more recent times, the procedure known as prenatal genetic diagnosis (PGD) has been developed. PGD involves the screening of human embryos as part of the process of *in vitro* fertilization, during which embryos are conceived and grown outside the mother's body for some period of time before they are implanted. The term PGD usually refers to both the diagnosis, selection, and the implantation of the selected embryos.

In the least controversial use of PGD, embryos are tested for the presence of alleles which cause genetic diseases such as sickle cell disease, muscular dystrophy, and hemophilia, in which a single disease-causing allele or pair of alleles has been identified. By excluding embryos containing these alleles from implantation into the mother, the disease is prevented, and the unused embryos are either donated to science or discarded. There are relatively few in the worldwide medical community that question the ethics of this type of procedure, which allows individuals scared to have children because of the alleles they carry to do so successfully. The major limitation to this procedure is its expense. Not usually covered by medical insurance and thus out of reach financially for most couples, only a very small percentage of all live births use such complicated methodologies. Yet, even in cases like these where the ethical issues may seem to be clear-cut, not everyone agrees with the morality of these types of procedures. For example, to those who take the position that human life begins at conception, the discarding of unused embryos, a necessary result of PGD, is unacceptable under any circumstances.

A murkier ethical situation is found in the selection of a child's sex, which is easily performed by PGD. Currently, countries such as Great Britain have banned the selection of a child's sex for reasons other than preventing sex-linked diseases. Other countries allow the procedure for "family balancing", based on the desire of some parents to have at least one child of each sex. Still others, including the United States, have taken a scattershot approach to regulating these practices, essentially leaving it to the individual practicing physician to decide which practices are acceptable and which are not.

Even murkier are rare instances of disabled parents, such as those with deafness or dwarfism, who select embryos via PGD to ensure that they share their disability. These parents usually cite many positive aspects of their disabilities and associated culture as reasons for their choice, which they see as their moral right. To others, to purposely cause a disability in a child violates the basic medical principle of *Primum non nocere*, "first, do no harm." This procedure, although not illegal in most countries, demonstrates the complexity of ethical issues associated with choosing genetic traits in offspring.

Where could this process lead? Will this technology become more affordable and how should it be used? With the ability of technology to progress rapidly and unpredictably, a lack of definitive guidelines for the use of reproductive technologies before they arise might make it difficult for legislators to keep pace once they are in fact realized, assuming the process needs any government regulation at all. Other bioethicists argue that we should only deal with technologies that exist now, and not in some uncertain future. They argue that these types of procedures will always be expensive and rare, so the fears of eugenics and "master" races are unfounded and overstated. The debate continues.

Summary

The early stages of embryonic development begin with fertilization. The process of fertilization is tightly controlled to ensure that only one sperm fuses with one egg. After fertilization, the zygote undergoes cleavage to form the blastula. The blastula, which in some species is a hollow ball of cells, undergoes a process called gastrulation, in which the three germ layers form. The ectoderm

gives rise to the nervous system and the epidermal skin cells, the mesoderm gives rise to the muscle cells and connective tissue in the body, and the endoderm gives rise to columnar cells and internal organs.

Glossary

acrosomal reaction
series of biochemical reactions that the sperm uses to break through the zona pellucida

blastocyst
structure formed when cells in the mammalian blastula separate into an inner and outer layer

gastrulation
process in which the blastula folds over itself to form the three germ layers

holoblastic
complete cleavage; takes place in cells with a small amount of yolk

inner cell mass
inner layer of cells in the blastocyst

meroblastic
partial cleavage; takes place in cells with a large amount of yolk

polyspermy
condition in which one egg is fertilized by multiple sperm

trophoblast
outer layer of cells in the blastocyst

zona pellucida
protective layer of glycoproteins on the mammalian egg

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52.2: Cleavage and the Blastula Stage

Skills to Develop

- Discuss how fertilization occurs
- Explain how the embryo forms from the zygote
- Discuss the role of cleavage and gastrulation in animal development

The process in which an organism develops from a single-celled zygote to a multi-cellular organism is complex and well-regulated. The early stages of embryonic development are also crucial for ensuring the fitness of the organism.

Fertilization

Fertilization, pictured in Figure 52.2.1a is the process in which gametes (an egg and sperm) fuse to form a zygote. The egg and sperm each contain one set of chromosomes. To ensure that the offspring has only one complete diploid set of chromosomes, only one sperm must fuse with one egg. In mammals, the egg is protected by a layer of extracellular matrix consisting mainly of glycoproteins called the zona pellucida. When a sperm binds to the zona pellucida, a series of biochemical events, called the acrosomal reactions, take place. In placental mammals, the acrosome contains digestive enzymes that initiate the degradation of the glycoprotein matrix protecting the egg and allowing the sperm plasma membrane to fuse with the egg plasma membrane, as illustrated in Figure 52.2.1b. The fusion of these two membranes creates an opening through which the sperm nucleus is transferred into the ovum. The nuclear membranes of the egg and sperm break down and the two haploid genomes condense to form a diploid genome.

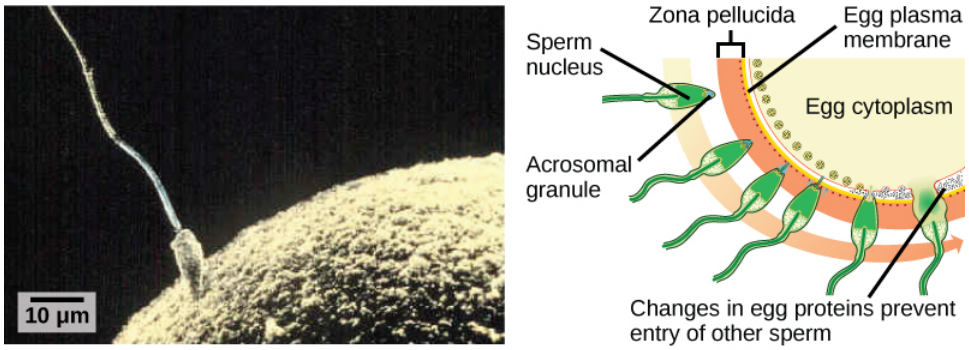


Figure 52.2.1: (a) Fertilization is the process in which sperm and egg fuse to form a zygote. (b) Acrosomal reactions help the sperm degrade the glycoprotein matrix protecting the egg and allow the sperm to transfer its nucleus. (credit: (b) modification of work by Mariana Ruiz Villareal; scale-bar data from Matt Russell)

To ensure that no more than one sperm fertilizes the egg, once the acrosomal reactions take place at one location of the egg membrane, the egg releases proteins in other locations to prevent other sperm from fusing with the egg. If this mechanism fails, multiple sperm can fuse with the egg, resulting in polyspermy. The resulting embryo is not genetically viable and dies within a few days.

Cleavage and Blastula Stage

The development of multi-cellular organisms begins from a single-celled zygote, which undergoes rapid cell division to form the blastula. The rapid, multiple rounds of cell division are termed cleavage. Cleavage is illustrated in (Figure 52.2.2a). After the cleavage has produced over 100 cells, the embryo is called a blastula. The blastula is usually a spherical layer of cells (the blastoderm) surrounding a fluid-filled or yolk-filled cavity (the blastocoel). Mammals at this stage form a structure called the blastocyst, characterized by an inner cell mass that is distinct from the surrounding blastula, shown in Figure 52.2.2b. During cleavage, the cells divide without an increase in mass; that is, one large single-celled zygote divides into multiple smaller cells. Each cell within the blastula is called a blastomere.

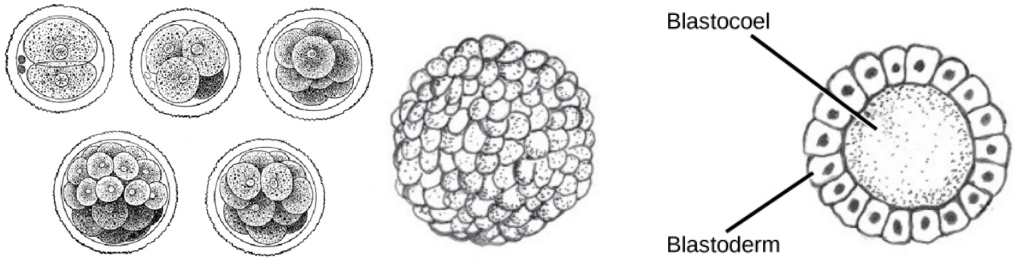


Figure 52.2.2: (a) During cleavage, the zygote rapidly divides into multiple cells without increasing in size. (b) The cells rearrange themselves to form a hollow ball with a fluid-filled or yolk-filled cavity called the blastula. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

Cleavage can take place in two ways: holoblastic (total) cleavage or meroblastic (partial) cleavage. The type of cleavage depends on the amount of yolk in the eggs. In placental mammals (including humans) where nourishment is provided by the mother's body, the eggs have a very small amount of yolk and undergo holoblastic cleavage. Other species, such as birds, with a lot of yolk in the egg to nourish the embryo during development, undergo meroblastic cleavage.

In mammals, the blastula forms the blastocyst in the next stage of development. Here the cells in the blastula arrange themselves in two layers: the inner cell mass, and an outer layer called the trophoblast. The inner cell mass is also known as the embryoblast and this mass of cells will go on to form the embryo. At this stage of development, illustrated in Figure **52.2.3** the inner cell mass consists of embryonic stem cells that will differentiate into the different cell types needed by the organism. The trophoblast will contribute to the placenta and nourish the embryo.

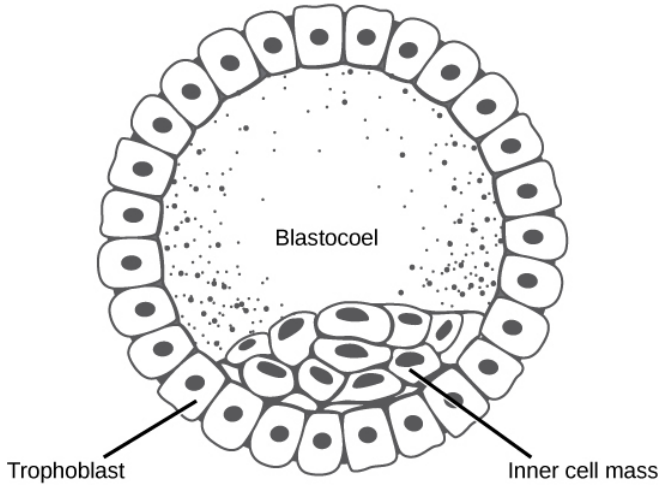


Figure **52.2.3**: The rearrangement of the cells in the mammalian blastula to two layers—the inner cell mass and the trophoblast—results in the formation of the blastocyst.

Link to Learning

Visit the Virtual Human Embryo project at the Endowment for Human Development site to step through an interactive that shows the stages of embryo development, including micrographs and rotating 3-D images.

Gastrulation

The typical blastula is a ball of cells. The next stage in embryonic development is the formation of the body plan. The cells in the blastula rearrange themselves spatially to form three layers of cells. This process is called gastrulation. During gastrulation, the blastula folds upon itself to form the three layers of cells. Each of these layers is called a germ layer and each germ layer differentiates into different organ systems.

The three germs layers, shown in Figure 52.2.4, are the endoderm, the ectoderm, and the mesoderm. The ectoderm gives rise to the nervous system and the epidermis. The mesoderm gives rise to the muscle cells and connective tissue in the body. The endoderm gives rise to columnar cells found in the digestive system and many internal organs.

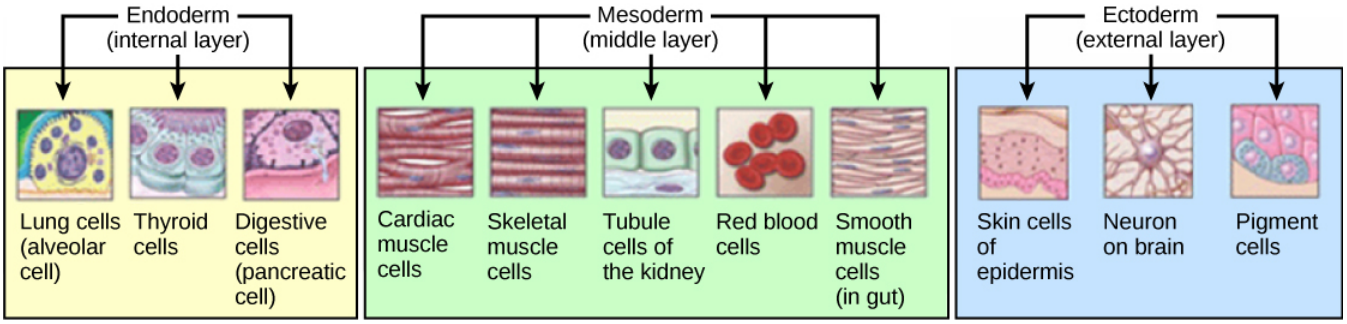


Figure 52.2.4: The three germ layers give rise to different cell types in the animal body. (credit: modification of work by NIH, NCBI)

Everyday Connection: Are Designer Babies in Our Future?

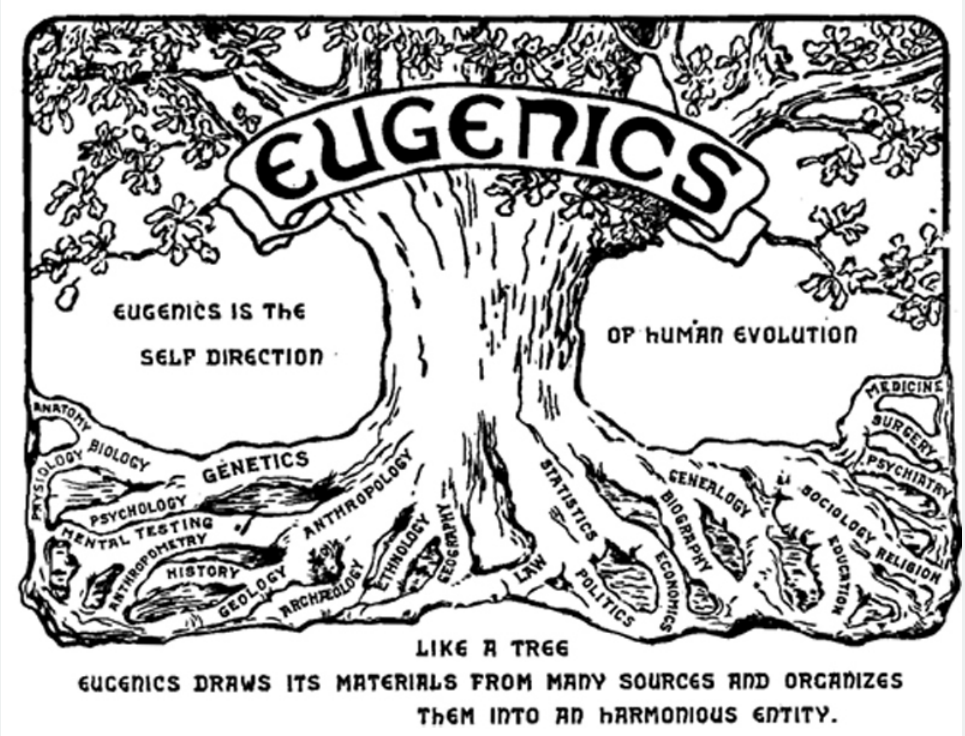


Figure 52.2.5: This logo from the Second International Eugenics Conference in New York City in September of 1921 shows how eugenics attempted to merge several fields of study with the goal of producing a genetically superior human race.

If you could prevent your child from getting a devastating genetic disease, would you do it? Would you select the sex of your child or select for their attractiveness, strength, or intelligence? How far would you go to maximize the possibility of resistance to disease? The genetic engineering of a human child, the production of "designer babies" with desirable phenotypic characteristics, was once a topic restricted to science fiction. This is the case no longer: science fiction is now overlapping into science fact. Many phenotypic choices for offspring are already available, with many more likely to be possible in the not too

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Eugenics is the use of information and technology from a variety of sources to improve the genetic makeup of the human race. The goal of creating genetically superior humans was quite prevalent (although controversial) in several countries during the early 20th century, but fell into disrepute when Nazi Germany developed an extensive eugenics program in the 1930's and 40's. As part of their program, the Nazis forcibly sterilized hundreds of thousands of the so-called "unfit" and killed tens of thousands of institutionally disabled people as part of a systematic program to develop a genetically superior race of Germans known as Aryans. Ever since, eugenic ideas have not been as publicly expressed, but there are still those who promote them.

Efforts have been made in the past to control traits in human children using donated sperm from men with desired traits. In fact, eugenicist Robert Klark Graham established a sperm bank in 1980 that included samples exclusively from donors with high IQs. The "genius" sperm bank failed to capture the public's imagination and the operation closed in 1999.

In more recent times, the procedure known as prenatal genetic diagnosis (PGD) has been developed. PGD involves the screening of human embryos as part of the process of *in vitro* fertilization, during which embryos are conceived and grown outside the mother's body for some period of time before they are implanted. The term PGD usually refers to both the diagnosis, selection, and the implantation of the selected embryos.

In the least controversial use of PGD, embryos are tested for the presence of alleles which cause genetic diseases such as sickle cell disease, muscular dystrophy, and hemophilia, in which a single disease-causing allele or pair of alleles has been identified. By excluding embryos containing these alleles from implantation into the mother, the disease is prevented, and the unused embryos are either donated to science or discarded. There are relatively few in the worldwide medical community that question the ethics of this type of procedure, which allows individuals scared to have children because of the alleles they carry to do so successfully. The major limitation to this procedure is its expense. Not usually covered by medical insurance and thus out of reach financially for most couples, only a very small percentage of all live births use such complicated methodologies. Yet, even in cases like these where the ethical issues may seem to be clear-cut, not everyone agrees with the morality of these types of procedures. For example, to those who take the position that human life begins at conception, the discarding of unused embryos, a necessary result of PGD, is unacceptable under any circumstances.

A murkier ethical situation is found in the selection of a child's sex, which is easily performed by PGD. Currently, countries such as Great Britain have banned the selection of a child's sex for reasons other than preventing sex-linked diseases. Other countries allow the procedure for "family balancing", based on the desire of some parents to have at least one child of each sex. Still others, including the United States, have taken a scattershot approach to regulating these practices, essentially leaving it to the individual practicing physician to decide which practices are acceptable and which are not.

Even murkier are rare instances of disabled parents, such as those with deafness or dwarfism, who select embryos via PGD to ensure that they share their disability. These parents usually cite many positive aspects of their disabilities and associated culture as reasons for their choice, which they see as their moral right. To others, to purposely cause a disability in a child violates the basic medical principle of *Primum non nocere*, "first, do no harm." This procedure, although not illegal in most countries, demonstrates the complexity of ethical issues associated with choosing genetic traits in offspring.

Where could this process lead? Will this technology become more affordable and how should it be used? With the ability of technology to progress rapidly and unpredictably, a lack of definitive guidelines for the use of reproductive technologies before they arise might make it difficult for legislators to keep pace once they are in fact realized, assuming the process needs any government regulation at all. Other bioethicists argue that we should only deal with technologies that exist now, and not in some uncertain future. They argue that these types of procedures will always be expensive and rare, so the fears of eugenics and "master" races are unfounded and overstated. The debate continues.

Summary

The early stages of embryonic development begin with fertilization. The process of fertilization is tightly controlled to ensure that only one sperm fuses with one egg. After fertilization, the zygote undergoes cleavage to form the blastula. The blastula, which in some species is a hollow ball of cells, undergoes a process called gastrulation, in which the three germ layers form. The ectoderm

gives rise to the nervous system and the epidermal skin cells, the mesoderm gives rise to the muscle cells and connective tissue in the body, and the endoderm gives rise to columnar cells and internal organs.

Glossary

acrosomal reaction
series of biochemical reactions that the sperm uses to break through the zona pellucida

blastocyst
structure formed when cells in the mammalian blastula separate into an inner and outer layer

gastrulation
process in which the blastula folds over itself to form the three germ layers

holoblastic
complete cleavage; takes place in cells with a small amount of yolk

inner cell mass
inner layer of cells in the blastocyst

meroblastic
partial cleavage; takes place in cells with a large amount of yolk

polyspermy
condition in which one egg is fertilized by multiple sperm

trophoblast
outer layer of cells in the blastocyst

zona pellucida
protective layer of glycoproteins on the mammalian egg

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52.3: Gastrulation

Skills to Develop

- Discuss how fertilization occurs
- Explain how the embryo forms from the zygote
- Discuss the role of cleavage and gastrulation in animal development

The process in which an organism develops from a single-celled zygote to a multi-cellular organism is complex and well-regulated. The early stages of embryonic development are also crucial for ensuring the fitness of the organism.

Fertilization

Fertilization, pictured in Figure 52.3.1a is the process in which gametes (an egg and sperm) fuse to form a zygote. The egg and sperm each contain one set of chromosomes. To ensure that the offspring has only one complete diploid set of chromosomes, only one sperm must fuse with one egg. In mammals, the egg is protected by a layer of extracellular matrix consisting mainly of glycoproteins called the zona pellucida. When a sperm binds to the zona pellucida, a series of biochemical events, called the acrosomal reactions, take place. In placental mammals, the acrosome contains digestive enzymes that initiate the degradation of the glycoprotein matrix protecting the egg and allowing the sperm plasma membrane to fuse with the egg plasma membrane, as illustrated in Figure 52.3.1b. The fusion of these two membranes creates an opening through which the sperm nucleus is transferred into the ovum. The nuclear membranes of the egg and sperm break down and the two haploid genomes condense to form a diploid genome.

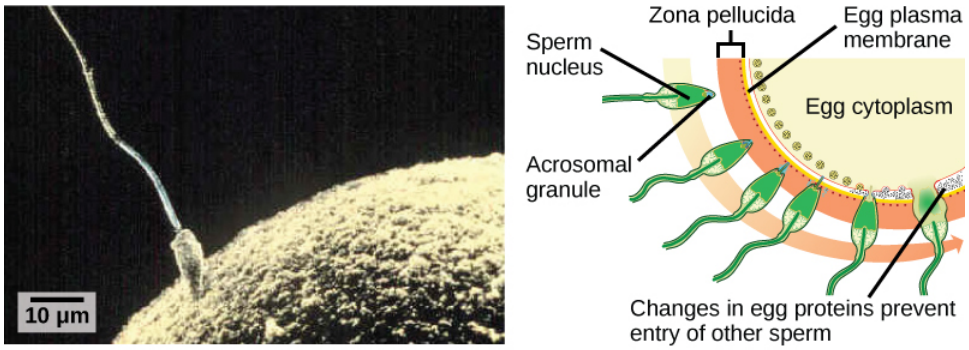


Figure 52.3.1: (a) Fertilization is the process in which sperm and egg fuse to form a zygote. (b) Acrosomal reactions help the sperm degrade the glycoprotein matrix protecting the egg and allow the sperm to transfer its nucleus. (credit: (b) modification of work by Mariana Ruiz Villareal; scale-bar data from Matt Russell)

To ensure that no more than one sperm fertilizes the egg, once the acrosomal reactions take place at one location of the egg membrane, the egg releases proteins in other locations to prevent other sperm from fusing with the egg. If this mechanism fails, multiple sperm can fuse with the egg, resulting in polyspermy. The resulting embryo is not genetically viable and dies within a few days.

Cleavage and Blastula Stage

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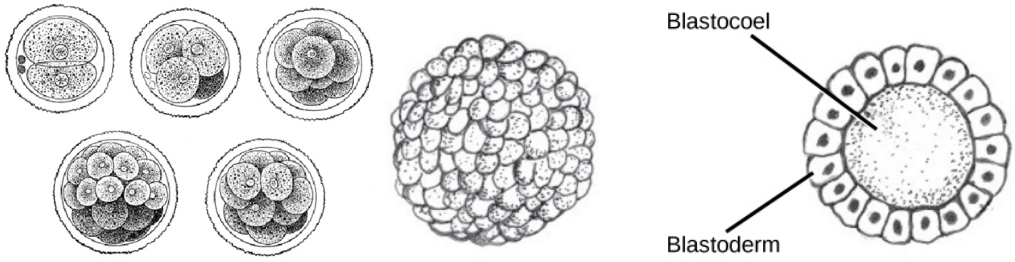


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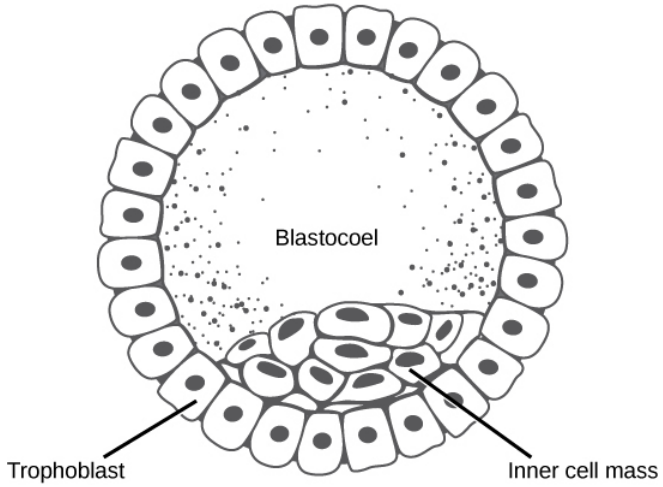


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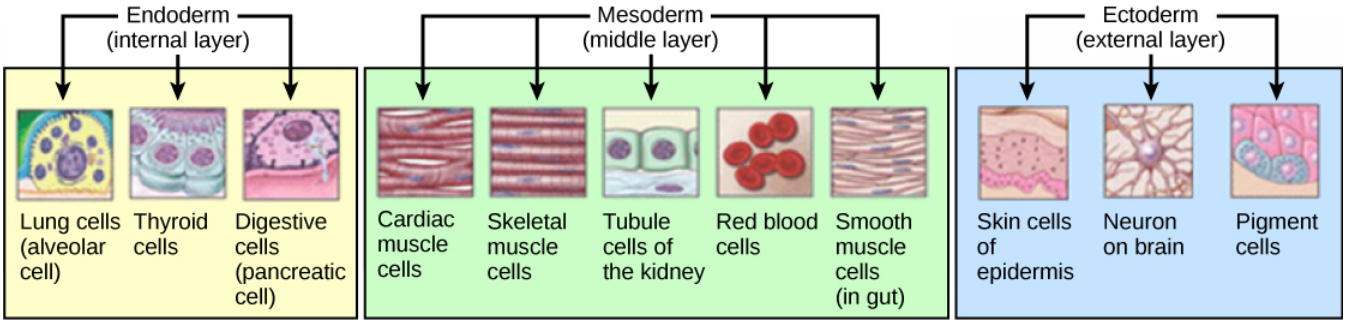


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Everyday Connection: Are Designer Babies in Our Future?

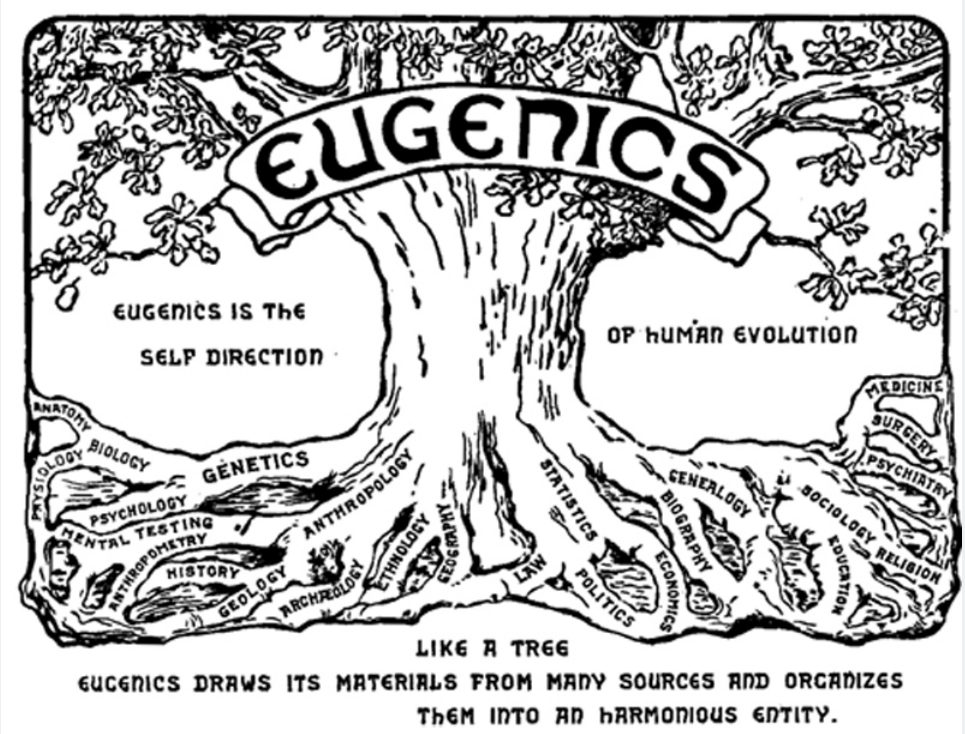


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trophoblast
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zona pellucida
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52.4: Organogenesis

Skills to Develop

- Describe the process of organogenesis
- Identify the anatomical axes formed in vertebrates

Gastrulation leads to the formation of the three germ layers that give rise, during further development, to the different organs in the animal body. This process is called organogenesis. Organogenesis is characterized by rapid and precise movements of the cells within the embryo.

Organogenesis

Organs form from the germ layers through the process of differentiation. During differentiation, the embryonic stem cells express specific sets of genes which will determine their ultimate cell type. For example, some cells in the ectoderm will express the genes specific to skin cells. As a result, these cells will differentiate into epidermal cells. The process of differentiation is regulated by cellular signaling cascades.

Scientists study organogenesis extensively in the lab in fruit flies (*Drosophila*) and the nematode *Caenorhabditis elegans*. *Drosophila* have segments along their bodies, and the patterning associated with the segment formation has allowed scientists to study which genes play important roles in organogenesis along the length of the embryo at different time points. The nematode *C.elegans* has roughly 1000 somatic cells and scientists have studied the fate of each of these cells during their development in the nematode life cycle. There is little variation in patterns of cell lineage between individuals, unlike in mammals where cell development from the embryo is dependent on cellular cues.

In vertebrates, one of the primary steps during organogenesis is the formation of the neural system. The ectoderm forms epithelial cells and tissues, and neuronal tissues. During the formation of the neural system, special signaling molecules called growth factors signal some cells at the edge of the ectoderm to become epidermis cells. The remaining cells in the center form the neural plate. If the signaling by growth factors were disrupted, then the entire ectoderm would differentiate into neural tissue.

The neural plate undergoes a series of cell movements where it rolls up and forms a tube called the neural tube, as illustrated in Figure **52.4.1**. In further development, the neural tube will give rise to the brain and the spinal cord.

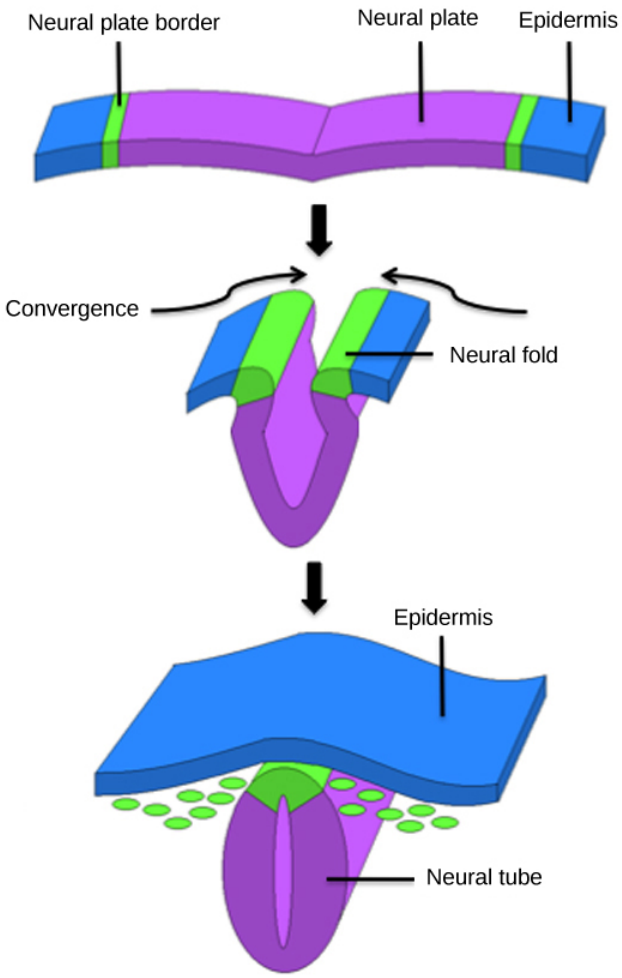


Figure 52.4.1: The central region of the ectoderm forms the neural tube, which gives rise to the brain and the spinal cord.

The mesoderm that lies on either side of the vertebrate neural tube will develop into the various connective tissues of the animal body. A spatial pattern of gene expression reorganizes the mesoderm into groups of cells called somites with spaces between them. The somites, illustrated in Figure 52.4.2 will further develop into the ribs, lungs, and segmental (spine) muscle. The mesoderm also forms a structure called the notochord, which is rod-shaped and forms the central axis of the animal body.



Figure 52.4.2: In this five-week old human embryo, somites are segments along the length of the body. (credit: modification of work by Ed Uthman)

Vertebrate Axis Formation

Even as the germ layers form, the ball of cells still retains its spherical shape. However, animal bodies have lateral-medial (left-right), dorsal-ventral (back-belly), and anterior-posterior (head-feet) axes, illustrated in Figure 52.4.3.

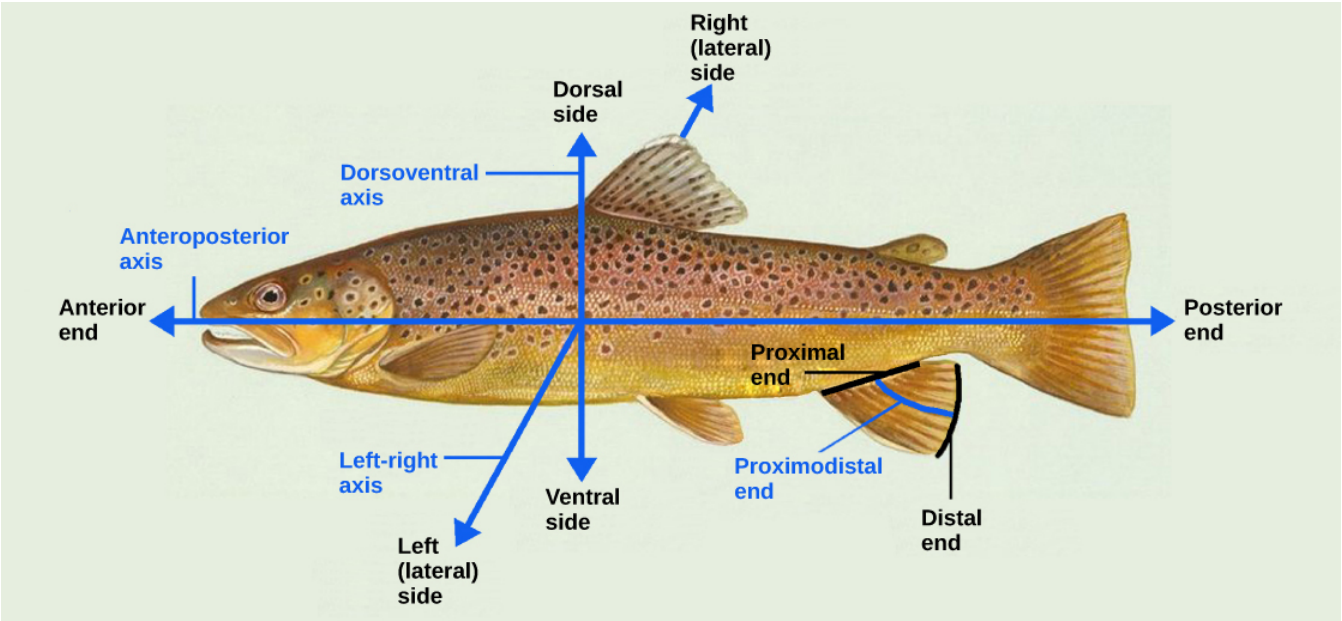


Figure 52.4.3: Animal bodies have three axes for symmetry. (credit: modification of work by NOAA)

How are these established? In one of the most seminal experiments ever to be carried out in developmental biology, Spemann and Mangold took dorsal cells from one embryo and transplanted them into the belly region of another embryo. They found that the transplanted embryo now had two notochords: one at the dorsal site from the original cells and another at the transplanted site. This suggested that the dorsal cells were genetically programmed to form the notochord and define the axis. Since then, researchers have

identified many genes that are responsible for axis formation. Mutations in these genes leads to the loss of symmetry required for organism development.

Animal bodies have externally visible symmetry. However, the internal organs are not symmetric. For example, the heart is on the left side and the liver on the right. The formation of the central left-right axis is an important process during development. This internal asymmetry is established very early during development and involves many genes. Research is still ongoing to fully understand the developmental implications of these genes.

Summary

Organogenesis is the formation of organs from the germ layers. Each germ layer gives rise to specific tissue types. The first stage is the formation of the neural system in the ectoderm. The mesoderm gives rise to somites and the notochord. Formation of vertebrate axis is another important developmental stage.

Glossary

neural tube
: tube-like structure that forms from the ectoderm and gives rise to the brain and spinal cord

organogenesis
: process of organ formation

somite
: group of cells separated by small spaces that form from the mesoderm and give rise to connective tissue

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52.5: Vertebrate Axis Pattern Formation

Skills to Develop

- Describe the process of organogenesis
- Identify the anatomical axes formed in vertebrates

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Organs form from the germ layers through the process of differentiation. During differentiation, the embryonic stem cells express specific sets of genes which will determine their ultimate cell type. For example, some cells in the ectoderm will express the genes specific to skin cells. As a result, these cells will differentiate into epidermal cells. The process of differentiation is regulated by cellular signaling cascades.

Scientists study organogenesis extensively in the lab in fruit flies (*Drosophila*) and the nematode *Caenorhabditis elegans*. *Drosophila* have segments along their bodies, and the patterning associated with the segment formation has allowed scientists to study which genes play important roles in organogenesis along the length of the embryo at different time points. The nematode *C.elegans* has roughly 1000 somatic cells and scientists have studied the fate of each of these cells during their development in the nematode life cycle. There is little variation in patterns of cell lineage between individuals, unlike in mammals where cell development from the embryo is dependent on cellular cues.

In vertebrates, one of the primary steps during organogenesis is the formation of the neural system. The ectoderm forms epithelial cells and tissues, and neuronal tissues. During the formation of the neural system, special signaling molecules called growth factors signal some cells at the edge of the ectoderm to become epidermis cells. The remaining cells in the center form the neural plate. If the signaling by growth factors were disrupted, then the entire ectoderm would differentiate into neural tissue.

The neural plate undergoes a series of cell movements where it rolls up and forms a tube called the neural tube, as illustrated in Figure **52.5.1**. In further development, the neural tube will give rise to the brain and the spinal cord.

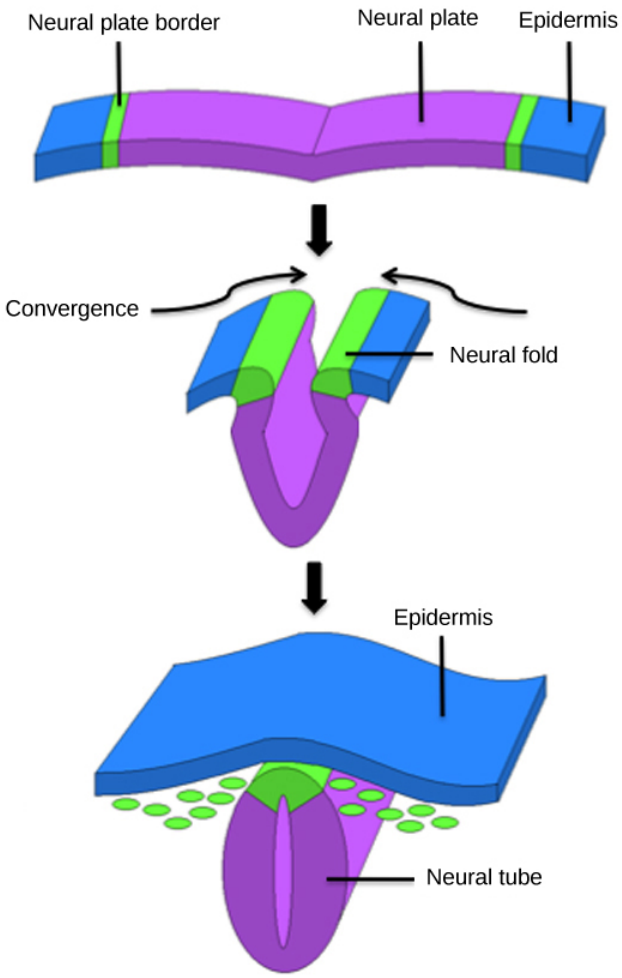


Figure 52.5.1: The central region of the ectoderm forms the neural tube, which gives rise to the brain and the spinal cord.

The mesoderm that lies on either side of the vertebrate neural tube will develop into the various connective tissues of the animal body. A spatial pattern of gene expression reorganizes the mesoderm into groups of cells called somites with spaces between them. The somites, illustrated in Figure 52.5.2 will further develop into the ribs, lungs, and segmental (spine) muscle. The mesoderm also forms a structure called the notochord, which is rod-shaped and forms the central axis of the animal body.



Figure 52.5.2: In this five-week old human embryo, somites are segments along the length of the body. (credit: modification of work by Ed Uthman)

Vertebrate Axis Formation

Even as the germ layers form, the ball of cells still retains its spherical shape. However, animal bodies have lateral-medial (left-right), dorsal-ventral (back-belly), and anterior-posterior (head-feet) axes, illustrated in Figure 52.5.3.

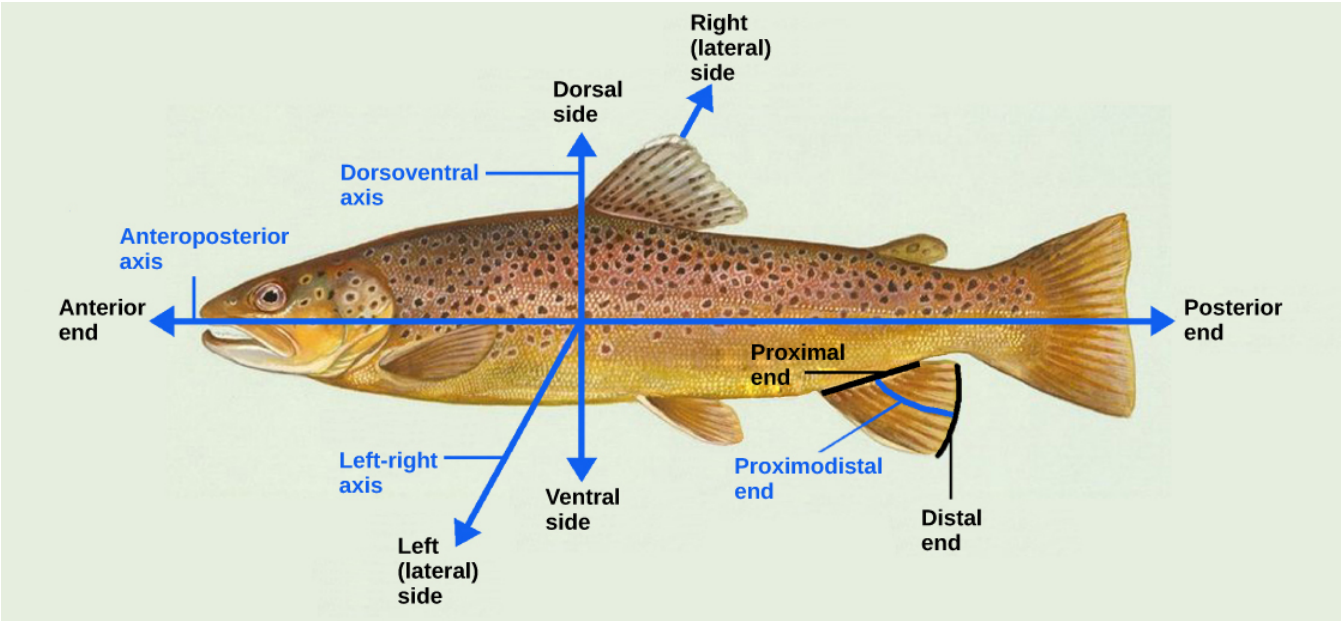


Figure 52.5.3: Animal bodies have three axes for symmetry. (credit: modification of work by NOAA)

How are these established? In one of the most seminal experiments ever to be carried out in developmental biology, Spemann and Mangold took dorsal cells from one embryo and transplanted them into the belly region of another embryo. They found that the transplanted embryo now had two notochords: one at the dorsal site from the original cells and another at the transplanted site. This suggested that the dorsal cells were genetically programmed to form the notochord and define the axis. Since then, researchers have

identified many genes that are responsible for axis formation. Mutations in these genes leads to the loss of symmetry required for organism development.

Animal bodies have externally visible symmetry. However, the internal organs are not symmetric. For example, the heart is on the left side and the liver on the right. The formation of the central left-right axis is an important process during development. This internal asymmetry is established very early during development and involves many genes. Research is still ongoing to fully understand the developmental implications of these genes.

Summary

Organogenesis is the formation of organs from the germ layers. Each germ layer gives rise to specific tissue types. The first stage is the formation of the neural system in the ectoderm. The mesoderm gives rise to somites and the notochord. Formation of vertebrate axis is another important developmental stage.

Glossary

neural tube
: tube-like structure that forms from the ectoderm and gives rise to the brain and spinal cord

organogenesis
: process of organ formation

somite
: group of cells separated by small spaces that form from the mesoderm and give rise to connective tissue

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52.6: Human Development

Skills to Develop

- Explain fetal development during the three trimesters of gestation
- Describe labor and delivery
- Compare the efficacy and duration of various types of contraception
- Discuss causes of infertility and the therapeutic options available

Pregnancy begins with the fertilization of an egg and continues through to the birth of the individual. The length of time of gestation varies among animals, but is very similar among the great apes: human gestation is 266 days, while chimpanzee gestation is 237 days, a gorilla's is 257 days, and orangutan gestation is 260 days long. The fox has a 57-day gestation. Dogs and cats have similar gestations averaging 60 days. The longest gestation for a land mammal is an African elephant at 640 days. The longest gestations among marine mammals are the beluga and sperm whales at 460 days.

Human Gestation

Twenty-four hours before fertilization, the egg has finished meiosis and becomes a mature oocyte. When fertilized (at conception) the egg becomes known as a zygote. The zygote travels through the oviduct to the uterus (Figure 52.6.1). The developing embryo must implant into the wall of the uterus within seven days, or it will deteriorate and die. The outer layers of the zygote (blastocyst) grow into the endometrium by digesting the endometrial cells, and wound healing of the endometrium closes up the blastocyst into the tissue. Another layer of the blastocyst, the chorion, begins releasing a hormone called human beta chorionic gonadotropin (β-HCG) which makes its way to the corpus luteum and keeps that structure active. This ensures adequate levels of progesterone that will maintain the endometrium of the uterus for the support of the developing embryo. Pregnancy tests determine the level of β-HCG in urine or serum. If the hormone is present, the test is positive.

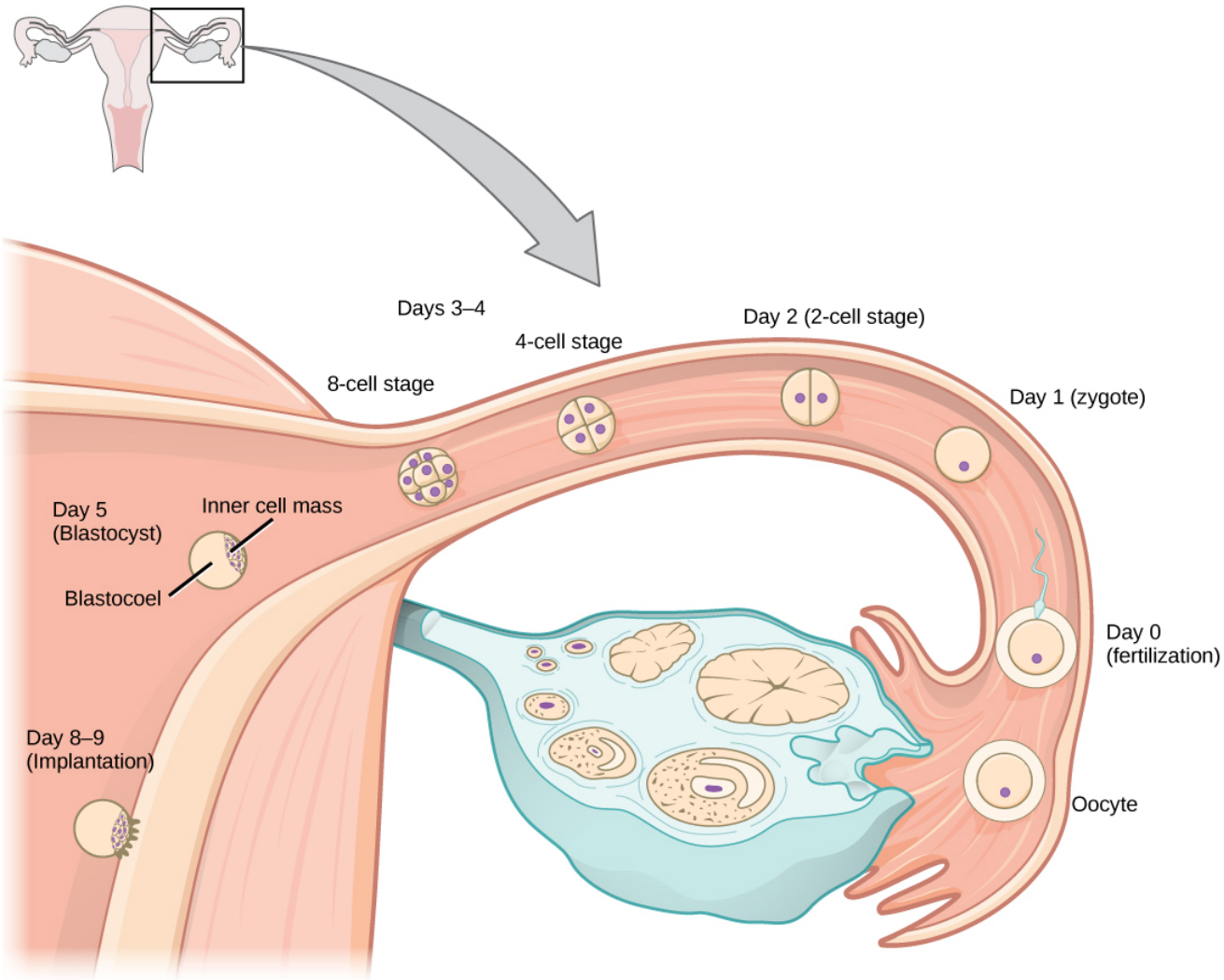


Figure 52.6.1: In humans, fertilization occurs soon after the oocyte leaves the ovary. Implantation occurs eight or nine days later. (credit: Ed Uthman)

The gestation period is divided into three equal periods or trimesters. During the first two to four weeks of the first trimester, nutrition and waste are handled by the endometrial lining through diffusion. As the trimester progresses, the outer layer of the embryo begins to merge with the endometrium, and the placenta forms. This organ takes over the nutrient and waste requirements of the embryo and fetus, with the mother's blood passing nutrients to the placenta and removing waste from it. Chemicals from the fetus, such as bilirubin, are processed by the mother's liver for elimination. Some of the mother's immunoglobulins will pass through the placenta, providing passive immunity against some potential infections.

Internal organs and body structures begin to develop during the first trimester. By five weeks, limb buds, eyes, the heart, and liver have been basically formed. By eight weeks, the term fetus applies, and the body is essentially formed, as shown in Figure 52.6.2. The individual is about five centimeters (two inches) in length and many of the organs, such as the lungs and liver, are not yet functioning. Exposure to any toxins is especially dangerous during the first trimester, as all of the body's organs and structures are going through initial development. Anything that affects that development can have a severe effect on the fetus' survival.



Figure **52.6.2**: Fetal development is shown at nine weeks gestation. (credit: Ed Uthman)

During the second trimester, the fetus grows to about 30 cm (12 inches), as shown in Figure **52.6.3**. It becomes active and the mother usually feels the first movements. All organs and structures continue to develop. The placenta has taken over the functions of nutrition and waste and the production of estrogen and progesterone from the corpus luteum, which has degenerated. The placenta will continue functioning up through the delivery of the baby.



Figure **52.6.3**: This fetus is just entering the second trimester, when the placenta takes over more of the functions performed as the baby develops. (credit: National Museum of Health and Medicine)

During the third trimester, the fetus grows to 3 to 4 kg (6 ½ -8 ½ lbs.) and about 50 cm (19-20 inches) long, as illustrated in Figure **52.6.4**. This is the period of the most rapid growth during the pregnancy. Organ development continues to birth (and some systems, such as the nervous system and liver, continue to develop after birth). The mother will be at her most uncomfortable during this trimester. She may urinate frequently due to pressure on the bladder from the fetus. There may also be intestinal blockage and circulatory problems, especially in her legs. Clots may form in her legs due to pressure from the fetus on returning veins as they enter the abdominal cavity.

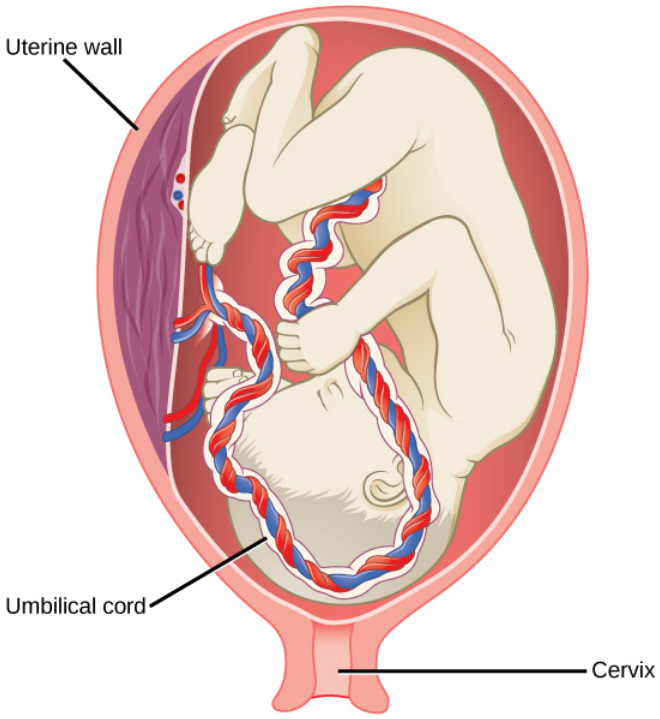


Figure 52.6.4: There is rapid fetal growth during the third trimester. (credit: modification of work by Gray's Anatomy)

Link to Learning

Visit this site to see the stages of human fetal development.

Labor and Birth

Labor is the physical efforts of expulsion of the fetus and the placenta from the uterus during birth (parturition). Toward the end of the third trimester, estrogen causes receptors on the uterine wall to develop and bind the hormone oxytocin. At this time, the baby reorients, facing forward and down with the back or crown of the head engaging the cervix (uterine opening). This causes the cervix to stretch and nerve impulses are sent to the hypothalamus, which signals for the release of oxytocin from the posterior pituitary. The oxytocin causes the smooth muscle in the uterine wall to contract. At the same time, the placenta releases prostaglandins into the uterus, increasing the contractions. A positive feedback relay occurs between the uterus, hypothalamus, and the posterior pituitary to assure an adequate supply of oxytocin. As more smooth muscle cells are recruited, the contractions increase in intensity and force.

There are three stages to labor. During stage one, the cervix thins and dilates. This is necessary for the baby and placenta to be expelled during birth. The cervix will eventually dilate to about 10 cm. During stage two, the baby is expelled from the uterus. The uterus contracts and the mother pushes as she compresses her abdominal muscles to aid the delivery. The last stage is the passage of the placenta after the baby has been born and the organ has completely disengaged from the uterine wall. If labor should stop before stage two is reached, synthetic oxytocin, known as Pitocin, can be administered to restart and maintain labor.

An alternative to labor and delivery is the surgical delivery of the baby through a procedure called a Caesarian section. This is major abdominal surgery and can lead to post-surgical complications for the mother, but in some cases it may be the only way to safely deliver the baby.

The mother's mammary glands go through changes during the third trimester to prepare for lactation and breastfeeding. When the baby begins suckling at the breast, signals are sent to the hypothalamus causing the release of prolactin from the anterior pituitary. Prolactin causes the mammary glands to produce milk. Oxytocin is also released, promoting the release of the milk. The milk contains nutrients for the baby's development and growth as well as immunoglobulins to protect the child from bacterial and viral infections.

Contraception and Birth Control

The prevention of a pregnancy comes under the terms contraception or birth control. Strictly speaking, contraception refers to preventing the sperm and egg from joining. Both terms are, however, frequently used interchangeably.

Table 52.6.1: Contraceptive Methods

Method	Examples	Failure Rate in Typical Use Over 12 Months
Barrier	male condom, female condom, sponge, cervical cap, diaphragm, spermicides	15 to 24%
Hormonal	oral, patch, vaginal ring	8%
	injection	3%
	implant	less than 1%
Other	natural family planning	12 to 25%
	withdrawal	27%
	sterilization	less than 1%

Table **52.6.1** lists common methods of contraception. The failure rates listed are not the ideal rates that could be realized, but the typical rates that occur. A failure rate is the number of pregnancies resulting from the method's use over a twelve-month period. Barrier methods, such as condoms, cervical caps, and diaphragms, block sperm from entering the uterus, preventing fertilization. Spermicides are chemicals that are placed in the vagina that kill sperm. Sponges, which are saturated with spermicides, are placed in the vagina at the cervical opening. Combinations of spermicidal chemicals and barrier methods achieve lower failure rates than do the methods when used separately.

Nearly a quarter of the couples using barrier methods, natural family planning, or withdrawal can expect a failure of the method. Natural family planning is based on the monitoring of the menstrual cycle and having intercourse only during times when the egg is not available. A woman's body temperature may rise a degree Celsius at ovulation and the cervical mucus may increase in volume and become more pliable. These changes give a general indication of when intercourse is more or less likely to result in fertilization. Withdrawal involves the removal of the penis from the vagina during intercourse, before ejaculation occurs. This is a risky method with a high failure rate due to the possible presence of sperm in the bulbourethral gland's secretion, which may enter the vagina prior to removing the penis.

Hormonal methods use synthetic progesterone (sometimes in combination with estrogen), to inhibit the hypothalamus from releasing FSH or LH, and thus prevent an egg from being available for fertilization. The method of administering the hormone affects failure rate. The most reliable method, with a failure rate of less than 1 percent, is the implantation of the hormone under the skin. The same rate can be achieved through the sterilization procedures of vasectomy in the man or of tubal ligation in the woman, or by using an intrauterine device (IUD). IUDs are inserted into the uterus and establish an inflammatory condition that prevents fertilized eggs from implanting into the uterine wall.

Compliance with the contraceptive method is a strong contributor to the success or failure rate of any particular method. The only method that is completely effective at preventing conception is abstinence. The choice of contraceptive method depends on the goals of the woman or couple. Tubal ligation and vasectomy are considered permanent prevention, while other methods are reversible and provide short-term contraception.

Termination of an existing pregnancy can be spontaneous or voluntary. Spontaneous termination is a miscarriage and usually occurs very early in the pregnancy, usually within the first few weeks. This occurs when the fetus cannot develop properly and the gestation is naturally terminated. Voluntary termination of a pregnancy is an abortion. Laws regulating abortion vary between states and tend to view fetal viability as the criteria for allowing or preventing the procedure.

Infertility

Infertility is the inability to conceive a child or carry a child to birth. About 75 percent of causes of infertility can be identified; these include diseases, such as sexually transmitted diseases that can cause scarring of the reproductive tubes in either men or women, or developmental problems frequently related to abnormal hormone levels in one of the individuals. Inadequate nutrition, especially starvation, can delay menstruation. Stress can also lead to infertility. Short-term stress can affect hormone levels, while long-term stress can delay puberty and cause less frequent menstrual cycles. Other factors that affect fertility include toxins (such as cadmium), tobacco smoking, marijuana use, gonadal injuries, and aging.

If infertility is identified, several assisted reproductive technologies (ART) are available to aid conception. A common type of ART is *in vitro* fertilization (IVF) where an egg and sperm are combined outside the body and then placed in the uterus. Eggs are obtained from the woman after extensive hormonal treatments that prepare mature eggs for fertilization and prepare the uterus for implantation of the fertilized egg. Sperm are obtained from the man and they are combined with the eggs and supported through several cell divisions to ensure viability of the zygotes. When the embryos have reached the eight-cell stage, one or more is implanted into the woman's uterus. If fertilization is not accomplished by simple IVF, a procedure that injects the sperm into an egg can be used. This is called intracytoplasmic sperm injection (ICSI) and is shown in Figure **52.6.5**. IVF procedures produce a surplus of fertilized eggs and embryos that can be frozen and stored for future use. The procedures can also result in multiple births.

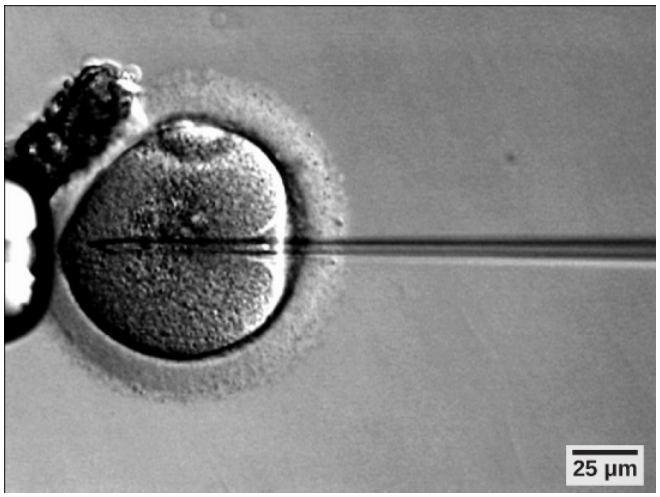


Figure **52.6.5**: A sperm is inserted into an egg for fertilization during intracytoplasmic sperm injection (ICSI). (credit: scale-bar data from Matt Russell)

Summary

Human pregnancy begins with fertilization of an egg and proceeds through the three trimesters of gestation. The labor process has three stages (contractions, delivery of the fetus, expulsion of the placenta), each propelled by hormones. The first trimester lays down the basic structures of the body, including the limb buds, heart, eyes, and the liver. The second trimester continues the development of all of the organs and systems. The third trimester exhibits the greatest growth of the fetus and culminates in labor and delivery. Prevention of a pregnancy can be accomplished through a variety of methods including barriers, hormones, or other means. Assisted reproductive technologies may help individuals who have infertility problems.

Glossary

contraception
(also, birth control) various means used to prevent pregnancy

gestation
length of time for fetal development to birth

human beta chorionic gonadotropin (*β*-HCG)
hormone produced by the chorion of the zygote that helps to maintain the corpus luteum and elevated levels of progesterone

infertility
inability to conceive, carry, and deliver children

morning sickness
condition in the mother during the first trimester; includes feelings of nausea

placenta
organ that supports the diffusion of nutrients and waste between the mother's and fetus' blood

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CHAPTER OVERVIEW

53: Behavioral Biology

53.1: Natural History of Behavior

53.2: Nerve Cells, Neurotransmitters, Hormones, and Behavior

53.2.1: Nerve Cells

53.2.2: Neurotransmitters

53.2.3: Hormones

53.2.4: Behavior and the Nervous System

53.3: Behavioral Genetics

53.3.1: Innate Behavior

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53.7: Orientation and Migratory Behavior

53.8: Animal Communication

53.8.1: Honeybee Navigation

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53.1: Natural History of Behavior

Skills to Develop

- Compare innate and learned behavior
- Discuss how movement and migration behaviors are a result of natural selection
- Discuss the different ways members of a population communicate with each other
- Give examples of how species use energy for mating displays and other courtship behaviors
- Differentiate between various mating systems
- Describe different ways that species learn

Behavior is the change in activity of an organism in response to a stimulus. Behavioral biology is the study of the biological and evolutionary bases for such changes. The idea that behaviors evolved as a result of the pressures of natural selection is not new. Animal behavior has been studied for decades, by biologists in the science of ethology, by psychologists in the science of comparative psychology, and by scientists of many disciplines in the study of neurobiology. Although there is overlap between these disciplines, scientists in these behavioral fields take different approaches. Comparative psychology is an extension of work done in human and behavioral psychology. Ethology is an extension of genetics, evolution, anatomy, physiology, and other biological disciplines. Still, one cannot study behavioral biology without touching on both comparative psychology and ethology.

One goal of behavioral biology is to dissect out the innate behaviors, which have a strong genetic component and are largely independent of environmental influences, from the learned behaviors, which result from environmental conditioning. Innate behavior, or instinct, is important because there is no risk of an incorrect behavior being learned. They are “hard wired” into the system. On the other hand, learned behaviors, although riskier, are flexible, dynamic, and can be altered according to changes in the environment.

Innate Behaviors: Movement and Migration

Innate or instinctual behaviors rely on response to stimuli. The simplest example of this is a reflex action, an involuntary and rapid response to stimulus. To test the “knee-jerk” reflex, a doctor taps the patellar tendon below the kneecap with a rubber hammer. The stimulation of the nerves there leads to the reflex of extending the leg at the knee. This is similar to the reaction of someone who touches a hot stove and instinctually pulls his or her hand away. Even humans, with our great capacity to learn, still exhibit a variety of innate behaviors.

Kinesis and Taxis

Another activity or movement of innate behavior is kinesis, or the undirected movement in response to a stimulus. Orthokinesis is the increased or decreased speed of movement of an organism in response to a stimulus. Woodlice, for example, increase their speed of movement when exposed to high or low temperatures. This movement, although random, increases the probability that the insect spends less time in the unfavorable environment. Another example is klinokinesis, an increase in turning behaviors. It is exhibited by bacteria such as *E. coli* which, in association with orthokinesis, helps the organisms randomly find a more hospitable environment.

A similar, but more directed version of kinesis is taxis: the directed movement towards or away from a stimulus. This movement can be in response to light (phototaxis), chemical signals (chemotaxis), or gravity (geotaxis) and can be directed toward (positive) or away (negative) from the source of the stimulus. An example of a positive chemotaxis is exhibited by the unicellular protozoan *Tetrahymena thermophila*. This organism swims using its cilia, at times moving in a straight line, and at other times making turns. The attracting chemotactic agent alters the frequency of turning as the organism moves directly toward the source, following the increasing concentration gradient.

Fixed Action Patterns

A fixed action pattern is a series of movements elicited by a stimulus such that even when the stimulus is removed, the pattern goes on to completion. An example of such a behavior occurs in the three-spined stickleback, a small freshwater fish (Figure **53.1.1**). Males of this species develop a red belly during breeding season and show instinctual aggressiveness to other males during this time. In laboratory experiments, researchers exposed such fish to objects that in no way resemble a fish in their shape, but which

were painted red on their lower halves. The male sticklebacks responded aggressively to the objects just as if they were real male sticklebacks.

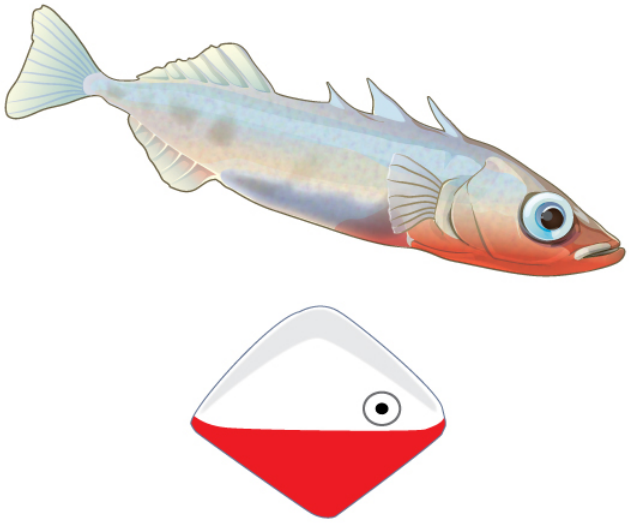


Figure **53.1.1**: Male three-spined stickleback fish exhibit a fixed action pattern. During mating season, the males, which develop a bright red belly, react strongly to red-bottomed objects that in no way resemble fish.

Migration

Migration is the long-range seasonal movement of animals. It is an evolved, adapted response to variation in resource availability, and it is a common phenomenon found in all major groups of animals. Birds fly south for the winter to get to warmer climates with sufficient food, and salmon migrate to their spawning grounds. The popular 2005 documentary *March of the Penguins* followed the 62-mile migration of emperor penguins through Antarctica to bring food back to their breeding site and to their young. Wildebeests (Figure **53.1.2**) migrate over 1800 miles each year in search of new grasslands.



Figure **53.1.2**: Wildebeests migrate in a clockwise fashion over 1800 miles each year in search of rain-ripened grass. (credit: Eric Inafuku)

Although migration is thought of as innate behavior, only some migrating species always migrate (obligate migration). Animals that exhibit facultative migration can choose to migrate or not. Additionally, in some animals, only a portion of the population

migrates, whereas the rest does not migrate (incomplete migration). For example, owls that live in the tundra may migrate in years when their food source, small rodents, is relatively scarce, but not migrate during the years when rodents are plentiful.

Foraging

Foraging is the act of searching for and exploiting food resources. Feeding behaviors that maximize energy gain and minimize energy expenditure are called optimal foraging behaviors, and these are favored by natural section. The painted stork, for example, uses its long beak to search the bottom of a freshwater marshland for crabs and other food (Figure **53.1.3**).



Figure **53.1.3**: The painted stork uses its long beak to forage. (credit: J.M. Garg)

Innate Behaviors: Living in Groups

Not all animals live in groups, but even those that live relatively solitary lives, with the exception of those that can reproduce asexually, must mate. Mating usually involves one animal signaling another so as to communicate the desire to mate. There are several types of energy-intensive behaviors or displays associated with mating, called mating rituals. Other behaviors found in populations that live in groups are described in terms of which animal benefits from the behavior. In selfish behavior, only the animal in question benefits; in altruistic behavior, one animal's actions benefit another animal; cooperative behavior describes when both animals benefit. All of these behaviors involve some sort of communication between population members.

Communication within a Species

Animals communicate with each other using stimuli known as signals. An example of this is seen in the three-spined stickleback, where the visual signal of a red region in the lower half of a fish signals males to become aggressive and signals females to mate. Other signals are chemical (pheromones), aural (sound), visual (courtship and aggressive displays), or tactile (touch). These types of communication may be instinctual or learned or a combination of both. These are not the same as the communication we associate with language, which has been observed only in humans and perhaps in some species of primates and cetaceans.

A pheromone is a secreted chemical signal used to obtain a response from another individual of the same species. The purpose of pheromones is to elicit a specific behavior from the receiving individual. Pheromones are especially common among social insects, but they are used by many species to attract the opposite sex, to sound alarms, to mark food trails, and to elicit other, more complex behaviors. Even humans are thought to respond to certain pheromones called axillary steroids. These chemicals influence human perception of other people, and in one study were responsible for a group of women synchronizing their menstrual cycles. The role of pheromones in human-to-human communication is still somewhat controversial and continues to be researched.

Songs are an example of an aural signal, one that needs to be heard by the recipient. Perhaps the best known of these are songs of birds, which identify the species and are used to attract mates. Other well-known songs are those of whales, which are of such low frequency that they can travel long distances underwater. Dolphins communicate with each other using a wide variety of vocalizations. Male crickets make chirping sounds using a specialized organ to attract a mate, repel other males, and to announce a successful mating.

Courtship displays are a series of ritualized visual behaviors (signals) designed to attract and convince a member of the opposite sex to mate. These displays are ubiquitous in the animal kingdom. Often these displays involve a series of steps, including an initial display by one member followed by a response from the other. If at any point, the display is performed incorrectly or a proper response is not given, the mating ritual is abandoned and the mating attempt will be unsuccessful. The mating display of the common stork is shown in Figure **53.1.4**.

Aggressive displays are also common in the animal kingdom. An example is when a dog bares its teeth when it wants another dog to back down. Presumably, these displays communicate not only the willingness of the animal to fight, but also its fighting ability. Although these displays do signal aggression on the part of the sender, it is thought that these displays are actually a mechanism to reduce the amount of actual fighting that occurs between members of the same species: they allow individuals to assess the fighting ability of their opponent and thus decide whether it is "worth the fight." The testing of certain hypotheses using game theory has led to the conclusion that some of these displays may overstate an animal's actual fighting ability and are used to "bluff" the opponent. This type of interaction, even if "dishonest," would be favored by natural selection if it is successful more times than not.

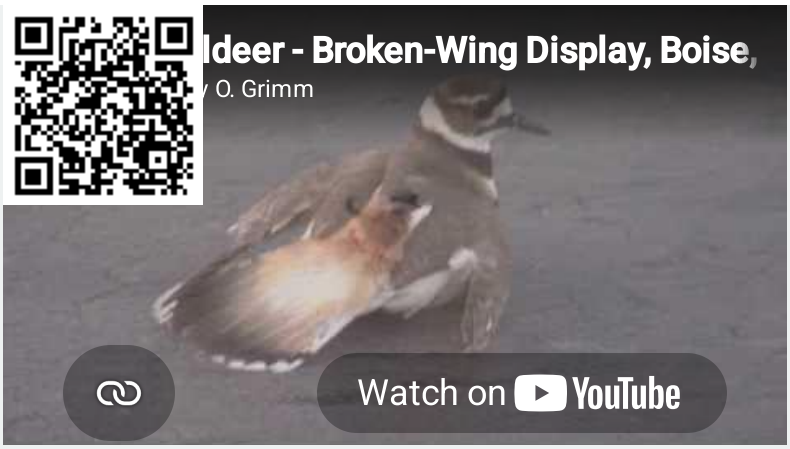


Figure **53.1.4**: This stork's courtship display is designed to attract potential mates. (credit: Linda "jinterwas"/Flickr)

Distraction displays are seen in birds and some fish. They are designed to attract a predator away from the nest that contains their young. This is an example of an altruistic behavior: it benefits the young more than the individual performing the display, which is putting itself at risk by doing so.

Many animals, especially primates, communicate with other members in the group through touch. Activities such as grooming, touching the shoulder or root of the tail, embracing, lip contact, and greeting ceremonies have all been observed in the Indian langur, an Old World monkey. Similar behaviors are found in other primates, especially in the great apes.

Link to Learning



The killdeer bird distracts predators from its eggs by faking a broken wing display in this video taken in Boise, Idaho.

Altruistic Behaviors

Behaviors that lower the fitness of the individual but increase the fitness of another individual are termed altruistic. Examples of such behaviors are seen widely across the animal kingdom. Social insects such as worker bees have no ability to reproduce, yet they maintain the queen so she can populate the hive with her offspring. Meerkats keep a sentry standing guard to warn the rest of the colony about intruders, even though the sentry is putting itself at risk. Wolves and wild dogs bring meat to pack members not present during a hunt. Lemurs take care of infants unrelated to them. Although on the surface, these behaviors appear to be altruistic, it may not be so simple.

There has been much discussion over why altruistic behaviors exist. Do these behaviors lead to overall evolutionary advantages for their species? Do they help the altruistic individual pass on its own genes? And what about such activities between unrelated individuals? One explanation for altruistic-type behaviors is found in the genetics of natural selection. In the 1976 book, *The Selfish Gene*, scientist Richard Dawkins attempted to explain many seemingly altruistic behaviors from the viewpoint of the gene itself. Although a gene obviously cannot be selfish in the human sense, it may appear that way if the sacrifice of an individual benefits related individuals that share genes that are identical by descent (present in relatives because of common lineage). Mammal parents make this sacrifice to take care of their offspring. Emperor penguins migrate miles in harsh conditions to bring food back for their young. Selfish gene theory has been controversial over the years and is still discussed among scientists in related fields.

Even less-related individuals, those with less genetic identity than that shared by parent and offspring, benefit from seemingly altruistic behavior. The activities of social insects such as bees, wasps, ants, and termites are good examples. Sterile workers in these societies take care of the queen because they are closely related to it, and as the queen has offspring, she is passing on genes from the workers indirectly. Thus, it is of fitness benefit for the worker to maintain the queen without having any direct chance of passing on its genes due to its sterility. The lowering of individual fitness to enhance the reproductive fitness of a relative and thus one's inclusive fitness evolves through kin selection. This phenomenon can explain many superficially altruistic behaviors seen in animals. However, these behaviors may not be truly defined as altruism in these cases because the actor is actually increasing its own fitness either directly (through its own offspring) or indirectly (through the inclusive fitness it gains through relatives that share genes with it).

Unrelated individuals may also act altruistically to each other, and this seems to defy the "selfish gene" explanation. An example of this observed in many monkey species where a monkey will present its back to an unrelated monkey to have that individual pick the parasites from its fur. After a certain amount of time, the roles are reversed and the first monkey now grooms the second monkey. Thus, there is reciprocity in the behavior. Both benefit from the interaction and their fitness is raised more than if neither cooperated nor if one cooperated and the other did not cooperate. This behavior is still not necessarily altruism, as the "giving" behavior of the actor is based on the expectation that it will be the "receiver" of the behavior in the future, termed reciprocal altruism. Reciprocal altruism requires that individuals repeatedly encounter each other, often the result of living in the same social group, and that cheaters (those that never "give back") are punished.

Evolutionary game theory, a modification of classical game theory in mathematics, has shown that many of these so-called "altruistic behaviors" are not altruistic at all. The definition of "pure" altruism, based on human behavior, is an action that benefits another without any direct benefit to oneself. Most of the behaviors previously described do not seem to satisfy this definition, and game theorists are good at finding "selfish" components in them. Others have argued that the terms "selfish" and "altruistic" should be dropped completely when discussing animal behavior, as they describe human behavior and may not be directly applicable to instinctual animal activity. What is clear, though, is that heritable behaviors that improve the chances of passing on one's genes or a portion of one's genes are favored by natural selection and will be retained in future generations as long as those behaviors convey a fitness advantage. These instinctual behaviors may then be applied, in special circumstances, to other species, as long as it doesn't lower the animal's fitness.

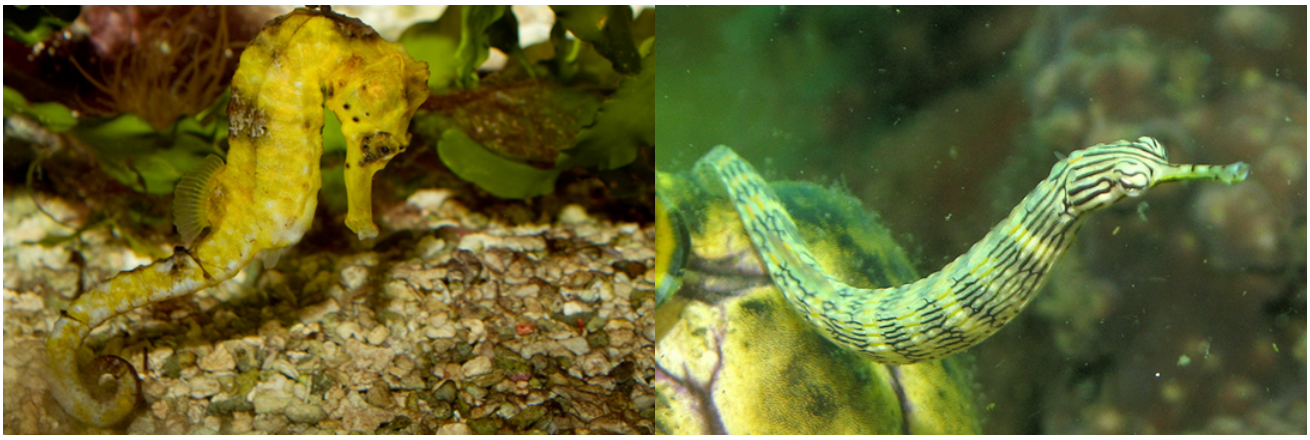
Finding Sex Partners

Not all animals reproduce sexually, but many that do have the same challenge: they need to find a suitable mate and often have to compete with other individuals to obtain one. Significant energy is spent in the process of locating, attracting, and mating with the sex partner. Two types of selection occur during this process and can lead to traits that are important to reproduction called secondary sexual characteristics: intersexual selection, the choosing of a mate where individuals of one sex choose mates of the other sex, and intrasexual selection, the competition for mates between species members of the same sex. Intersexual selection is often complex because choosing a mate may be based on a variety of visual, aural, tactile, and chemical cues. An example of intersexual selection is when female peacocks choose to mate with the male with the brightest plumage. This type of selection often leads to traits in the chosen sex that do not enhance survival, but are those traits most attractive to the opposite sex (often at the expense of survival). Intrasexual selection involves mating displays and aggressive mating rituals such as rams butting heads—the winner of these battles is the one that is able to mate. Many of these rituals use up considerable energy but result in the selection of the healthiest, strongest, and/or most dominant individuals for mating. Three general mating systems, all involving innate as opposed to learned behaviors, are seen in animal populations: monogamous, polygynous, and polyandrous.

In monogamous systems, one male and one female are paired for at least one breeding season. In some animals, such as the gray wolf, these associations can last much longer, even a lifetime. Several explanations have been proposed for this type of mating system. The "mate-guarding hypothesis" states that males stay with the female to prevent other males from mating with her. This behavior is advantageous in such situations where mates are scarce and difficult to find. Another explanation is the "male-assistance hypothesis," where males that remain with a female to help guard and rear their young will have more and healthier offspring. Monogamy is observed in many bird populations where, in addition to the parental care from the female, the male is also a major provider of parental care for the chicks. A third explanation for the evolutionary advantages of monogamy is the "female-enforcement hypothesis." In this scenario, the female ensures that the male does not have other offspring that might compete with her own, so she actively interferes with the male's signaling to attract other mates.

Polygynous mating refers to one male mating with multiple females. In these situations, the female must be responsible for most of the parental care as the single male is not capable of providing care to that many offspring. In resourced-based polygyny, males compete for territories with the best resources, and then mate with females that enter the territory, drawn to its resource richness. The female benefits by mating with a dominant, genetically fit male; however, it is at the cost of having no male help in caring for the offspring. An example is seen in the yellow-rumped honeyguide, a bird whose males defend beehives because the females feed on their wax. As the females approach, the male defending the nest will mate with them. Harem mating structures are a type of polygynous system where certain males dominate mating while controlling a territory with resources. Elephant seals, where the alpha male dominates the mating within the group are an example. A third type of polygyny is a lek system. Here there is a communal courting area where several males perform elaborate displays for females, and the females choose their mate from this group. This behavior is observed in several bird species including the sage grouse and the prairie chicken.

In polyandrous mating systems, one female mates with many males. These types of systems are much rarer than monogamous and polygynous mating systems. In pipefishes and seahorses, males receive the eggs from the female, fertilize them, protect them within a pouch, and give birth to the offspring (Figure **53.1.5**). Therefore, the female is able to provide eggs to several males without the burden of carrying the fertilized eggs.



a b

Figure 53.1.5: Polyandrous mating, in which one female mates with many males, occurs in the (a) seahorse and the (b) pipefish. (credit a: modification of work by Brian Gratwicke; credit b: modification of work by Stephen Childs)

Simple Learned Behaviors

The majority of the behaviors previously discussed were innate or at least have an innate component (variations on the innate behaviors may be learned). They are inherited and the behaviors do not change in response to signals from the environment. Conversely, learned behaviors, even though they may have instinctive components, allow an organism to adapt to changes in the environment and are modified by previous experiences. Simple learned behaviors include habituation and imprinting—both are important to the maturation process of young animals.

Habituation

Habituation is a simple form of learning in which an animal stops responding to a stimulus after a period of repeated exposure. This is a form of non-associative learning, as the stimulus is not associated with any punishment or reward. Prairie dogs typically sound an alarm call when threatened by a predator, but they become habituated to the sound of human footsteps when no harm is associated with this sound, therefore, they no longer respond to them with an alarm call. In this example, habituation is specific to the sound of human footsteps, as the animals still respond to the sounds of potential predators.

Imprinting

Imprinting is a type of learning that occurs at a particular age or a life stage that is rapid and independent of the species involved. Hatchling ducks recognize the first adult they see, their mother, and make a bond with her. A familiar sight is ducklings walking or swimming after their mothers (Figure **53.1.6**). This is another type of non-associative learning, but is very important in the maturation process of these animals as it encourages them to stay near their mother so they will be protected, greatly increasing their chances of survival. However, if newborn ducks see a human before they see their mother, they will imprint on the human and follow it in just the same manner as they would follow their real mother.



Figure **53.1.6**: The attachment of ducklings to their mother is an example of imprinting. (credit: modification of work by Mark Harkin)

Link to Learning



The International Crane Foundation has helped raise the world's population of whooping cranes from 21 individuals to about 600. Imprinting hatchlings has been a key to success: biologists wear full crane costumes so the birds never "see" humans. Watch this video to learn more.

Conditioned Behavior

Conditioned behaviors are types of associative learning, where a stimulus becomes associated with a consequence. During operant conditioning, the behavioral response is modified by its consequences, with regards to its form, strength, or frequency.

Classical Conditioning

In classical conditioning, a response called the conditioned response is associated with a stimulus that it had previously not been associated with, the conditioned stimulus. The response to the original, unconditioned stimulus is called the unconditioned response. The most cited example of classical conditioning is Ivan Pavlov's experiments with dogs (Figure **53.1.7**). In Pavlov's experiments, the unconditioned response was the salivation of dogs in response to the unconditioned stimulus of seeing or smelling their food. The conditioning stimulus that researchers associated with the unconditioned response was the ringing of a bell. During conditioning, every time the animal was given food, the bell was rung. This was repeated during several trials. After some time, the dog learned to associate the ringing of the bell with food and to respond by salivating. After the conditioning period was finished, the dog would respond by salivating when the bell was rung, even when the unconditioned stimulus, the food, was absent. Thus,

the ringing of the bell became the conditioned stimulus and the salivation became the conditioned response. Although it is thought by some scientists that the unconditioned and conditioned responses are identical, even Pavlov discovered that the saliva in the conditioned dogs had characteristic differences when compared to the unconditioned dog.

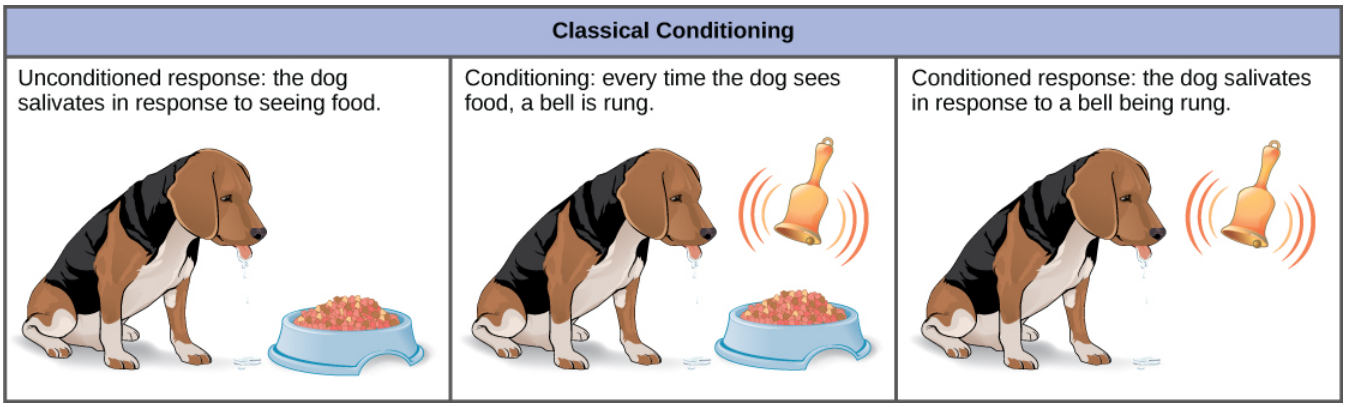


Figure **53.1.7**: In the classic Pavlovian response, the dog becomes conditioned to associate the ringing of the bell with food.

It had been thought by some scientists that this type of conditioning required multiple exposures to the paired stimulus and response, but it is now known that this is not necessary in all cases, and that some conditioning can be learned in a single pairing experiment. Classical conditioning is a major tenet of behaviorism, a branch of psychological philosophy that proposes that all actions, thoughts, and emotions of living things are behaviors that can be treated by behavior modification and changes in the environment.

Operant Conditioning

In operant conditioning, the conditioned behavior is gradually modified by its consequences as the animal responds to the stimulus. A major proponent of such conditioning was psychologist B.F. Skinner, the inventor of the Skinner box. Skinner put rats in his boxes that contained a lever that would dispense food to the rat when depressed. While initially the rat would push the lever a few times by accident, it eventually associated pushing the lever with getting the food. This type of learning is an example of operant conditioning. Operant learning is the basis of most animal training. The conditioned behavior is continually modified by positive or negative reinforcement, often a reward such as food or some type of punishment, respectively. In this way, the animal is conditioned to associate a type of behavior with the punishment or reward, and, over time, can be induced to perform behaviors that they would not have done in the wild, such as the “tricks” dolphins perform at marine amusement park shows (Figure **53.1.8**).



Figure **53.1.8**: The training of dolphins by rewarding them with food is an example of positive reinforcement operant conditioning. (credit: Roland Tanglao)

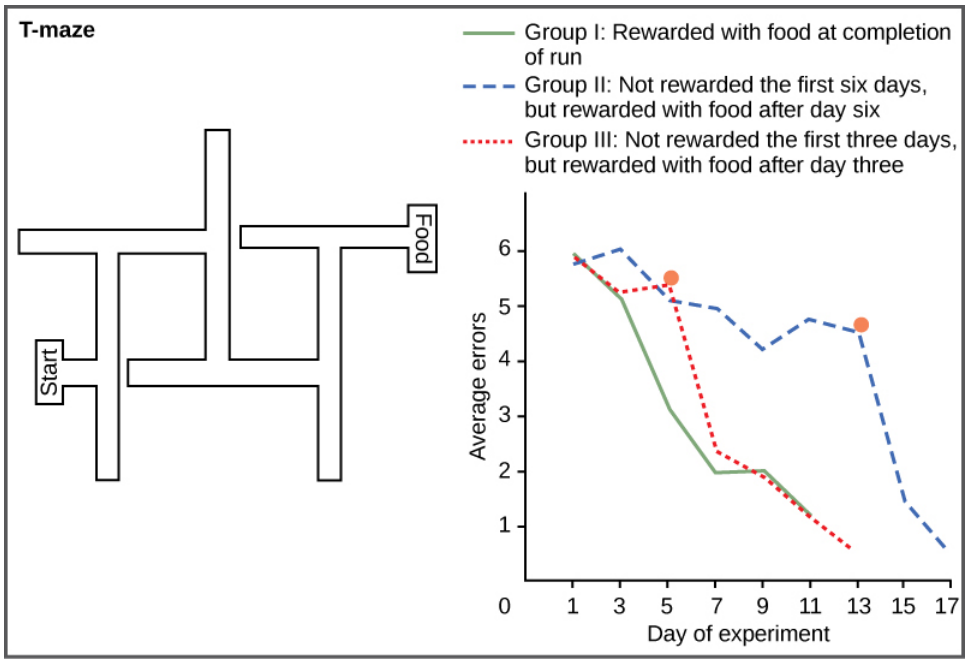
Cognitive Learning

Classical and operant conditioning are inefficient ways for humans and other intelligent animals to learn. Some primates, including humans, are able to learn by imitating the behavior of others and by taking instructions. The development of complex language by humans has made cognitive learning, the manipulation of information using the mind, the most prominent method of human

learning. In fact, that is how students are learning right now by reading this book. As students read, they can make mental images of objects or organisms and imagine changes to them, or behaviors by them, and anticipate the consequences. In addition to visual processing, cognitive learning is also enhanced by remembering past experiences, touching physical objects, hearing sounds, tasting food, and a variety of other sensory-based inputs. Cognitive learning is so powerful that it can be used to understand conditioning in detail. In the reverse scenario, conditioning cannot help someone learn about cognition.

Classic work on cognitive learning was done by Wolfgang Köhler with chimpanzees. He demonstrated that these animals were capable of abstract thought by showing that they could learn how to solve a puzzle. When a banana was hung in their cage too high for them to reach, and several boxes were placed randomly on the floor, some of the chimps were able to stack the boxes one on top of the other, climb on top of them, and get the banana. This implies that they could visualize the result of stacking the boxes even before they had performed the action. This type of learning is much more powerful and versatile than conditioning.

Cognitive learning is not limited to primates, although they are the most efficient in using it. Maze running experiments done with rats by H.C. Blodgett in the 1920s were the first to show cognitive skills in a simple mammal. The motivation for the animals to work their way through the maze was a piece of food at its end. In these studies, the animals in Group I were run in one trial per day and had food available to them each day on completion of the run (Figure **53.1.9**). Group II rats were not fed in the maze for the first six days and then subsequent runs were done with food for several days after. Group III rats had food available on the third day and every day thereafter. The results were that the control rats, Group I, learned quickly, and figured out how to run the maze in seven days. Group III did not learn much during the three days without food, but rapidly caught up to the control group when given the food reward. Group II learned very slowly for the six days with no reward to motivate them, and they did not begin to catch up to the control group until the day food was given, and then it took two days longer to learn the maze.



Redrawn after H. C. Blodgett, The effect of the introduction of reward upon the maze performance of rats. Univ. Calif. Publ. Psychol., 1929, 4, No. 8, pages 117 and 120.

Figure **53.1.9**: Group I (the green solid line) found food at the end of each trial, group II (the blue dashed line) did not find food for the first 6 days, and group III (the red dotted line) did not find food during runs on the first three days. Notice that rats given food earlier learned faster and eventually caught up to the control group. The orange dots on the group II and III lines show the days when food rewards were added to the mazes.

It may not be immediately obvious that this type of learning is different than conditioning. Although one might be tempted to believe that the rats simply learned how to find their way through a conditioned series of right and left turns, E.C. Tolman proved a decade later that the rats were making a representation of the maze in their minds, which he called a “cognitive map.” This was an early demonstration of the power of cognitive learning and how these abilities were not just limited to humans.

Sociobiology

Sociobiology is an interdisciplinary science originally popularized by social insect researcher E.O. Wilson in the 1970s. Wilson defined the science as "the extension of population biology and evolutionary theory to social organization."[1] The main thrust of sociobiology is that animal and human behavior, including aggressiveness and other social interactions, can be explained almost solely in terms of genetics and natural selection. This science is controversial; noted scientist such as the late Stephen Jay Gould criticized the approach for ignoring the environmental effects on behavior. This is another example of the "nature versus nurture" debate of the role of genetics versus the role of environment in determining an organism's characteristics.

Sociobiology also links genes with behaviors and has been associated with "biological determinism," the belief that all behaviors are hardwired into our genes. No one disputes that certain behaviors can be inherited and that natural selection plays a role retaining them. It is the application of such principles to human behavior that sparks this controversy, which remains active today.

Summary

Behaviors are responses to stimuli. They can either be instinctual/innate behaviors, which are not influenced by the environment, or learned behaviors, which are influenced by environmental changes. Instinctual behaviors include mating systems and methods of communication. Learned behaviors include imprinting and habituation, conditioning, and, most powerfully, cognitive learning. Although the connection between behavior, genetics, and evolution is well established, the explanation of human behavior as entirely genetic is controversial.

Footnotes

1. 1 Edward O. Wilson. *On Human Nature* (1978; repr., Cambridge: Harvard University Press, 2004), xx.

Glossary

aggressive display
: visual display by a species member to discourage other members of the same species or different species

behavior
: change in an organism's activities in response to a stimulus

behavioral biology
: study of the biology and evolution of behavior

classical conditioning
: association of a specific stimulus and response through conditioning

cognitive learning
: knowledge and skills acquired by the manipulation of information in the mind

conditioned behavior
: behavior that becomes associated with a specific stimulus through conditioning

courtship display
: visual display used to attract a mate

distraction display
: visual display used to distract predators away from a nesting site

ethology
: biological study of animal behavior

fixed action pattern
: series of instinctual behaviors that, once initiated, always goes to completion regardless of changes in the environment

foraging
behaviors species use to find food

habituation
ability of a species to ignore repeated stimuli that have no consequence

imprinting
identification of parents by newborns as the first organism they see after birth

innate behavior
instinctual behavior that is not altered by changes in the environment

intersexual selection
selection of a desirable mate of the opposite sex

intrasexual selection
competition between members of the same sex for a mate

kin selection
sacrificing one's own life so that one's genes will be passed on to future generations by relatives

kinesis
undirected movement of an organism in response to a stimulus

learned behavior
behavior that responds to changes in the environment

migration
long-range seasonal movement of animal species

monogamy
mating system whereby one male and one female remain coupled for at least one mating season

operant conditioning
learned behaviors in response to positive and/or negative reinforcement

polyandry
mating system where one female mates with many males

polygyny
mating system where one male mates with many females

reflex action
action in response to direct physical stimulation of a nerve

signal
method of communication between animals including those obtained by the senses of smell, hearing, sight, or touch

taxis
directed movement in response to a stimulus

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CHAPTER OVERVIEW

53.2: Nerve Cells, Neurotransmitters, Hormones, and Behavior

53.2.1: Nerve Cells

53.2.2: Neurotransmitters

53.2.3: Hormones

53.2.4: Behavior and the Nervous System

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53.2.1: Nerve Cells

Skills to Develop

- List and describe the functions of the structural components of a neuron
- List and describe the four main types of neurons
- Compare the functions of different types of glial cells

Nervous systems throughout the animal kingdom vary in structure and complexity, as illustrated by the variety of animals shown in Figure **53.2.1.1**. Some organisms, like sea sponges, lack a true nervous system. Others, like jellyfish, lack a true brain and instead have a system of separate but connected nerve cells (neurons) called a "nerve net." Echinoderms such as sea stars have nerve cells that are bundled into fibers called nerves. Flatworms of the phylum Platyhelminthes have both a central nervous system (CNS), made up of a small "brain" and two nerve cords, and a peripheral nervous system (PNS) containing a system of nerves that extend throughout the body. The insect nervous system is more complex but also fairly decentralized. It contains a brain, ventral nerve cord, and ganglia (clusters of connected neurons). These ganglia can control movements and behaviors without input from the brain. Octopi may have the most complicated of invertebrate nervous systems—they have neurons that are organized in specialized lobes and eyes that are structurally similar to vertebrate species.

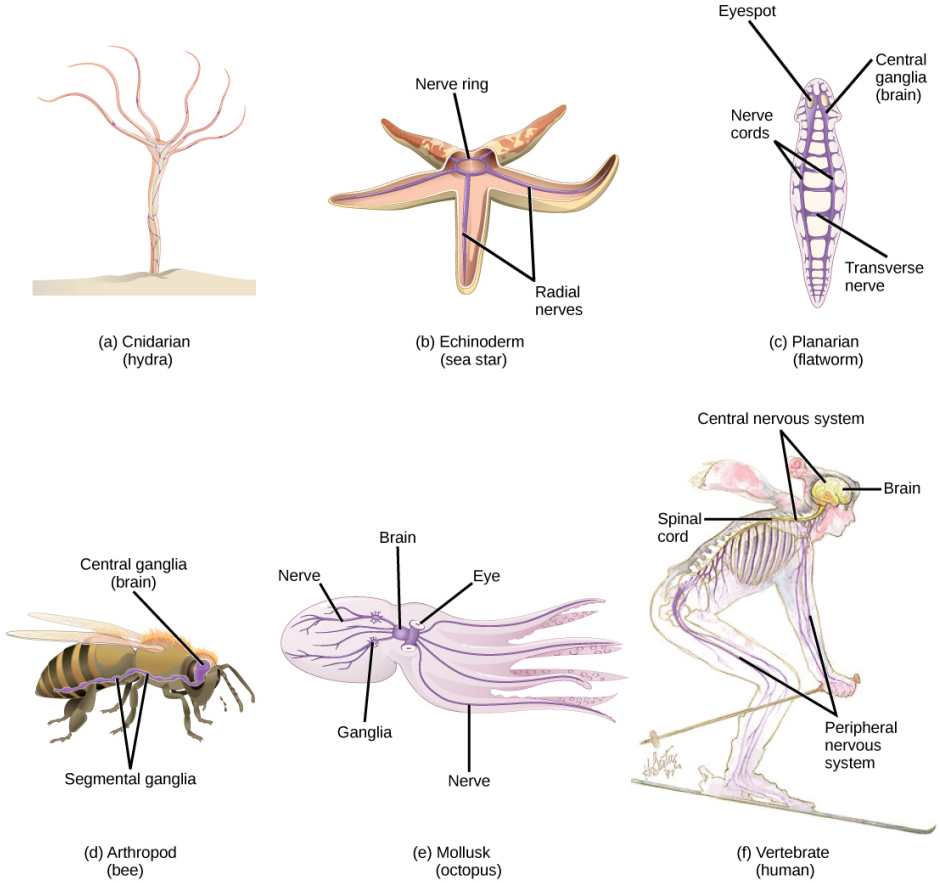


Figure **53.2.1.1**: Nervous systems vary in structure and complexity. In (a) cnidarians, nerve cells form a decentralized nerve net. In (b) echinoderms, nerve cells are bundled into fibers called nerves. In animals exhibiting bilateral symmetry such as (c) planarians, neurons cluster into an anterior brain that processes information. In addition to a brain, (d) arthropods have clusters of nerve cell bodies, called peripheral ganglia, located along the ventral nerve cord. Mollusks such as squid and (e) octopi, which must hunt to survive, have complex brains containing millions of neurons. In (f) vertebrates, the brain and spinal cord comprise the central nervous system, while neurons extending into the rest of the body comprise the peripheral nervous system. (credit e: modification of work by Michael Vecchione, Clyde F.E. Roper, and Michael J. Sweeney, NOAA; credit f: modification of work by NIH).

Compared to invertebrates, vertebrate nervous systems are more complex, centralized, and specialized. While there is great diversity among different vertebrate nervous systems, they all share a basic structure: a CNS that contains a brain and spinal cord

and a PNS made up of peripheral sensory and motor nerves. One interesting difference between the nervous systems of invertebrates and vertebrates is that the nerve cords of many invertebrates are located ventrally whereas the vertebrate spinal cords are located dorsally. There is debate among evolutionary biologists as to whether these different nervous system plans evolved separately or whether the invertebrate body plan arrangement somehow "flipped" during the evolution of vertebrates.

Link to Learning



Watch this video of biologist Mark Kirschner discussing the "flipping" phenomenon of vertebrate evolution.

The nervous system is made up of neurons, specialized cells that can receive and transmit chemical or electrical signals, and glia, cells that provide support functions for the neurons by playing an information processing role that is complementary to neurons. A neuron can be compared to an electrical wire—it transmits a signal from one place to another. Glia can be compared to the workers at the electric company who make sure wires go to the right places, maintain the wires, and take down wires that are broken. Although glia have been compared to workers, recent evidence suggests that also usurp some of the signaling functions of neurons.

There is great diversity in the types of neurons and glia that are present in different parts of the nervous system. There are four major types of neurons, and they share several important cellular components.

Neurons

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors—from basic reflexes to more complicated behaviors like finding food and courting mates. The ability of neurons to communicate with each other as well as with other types of cells underlies all of these behaviors.

Most neurons share the same cellular components. But neurons are also highly specialized—different types of neurons have different sizes and shapes that relate to their functional roles.

Parts of a Neuron

Like other cells, each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components. Neurons also contain unique structures, illustrated in Figure **53.2.1.2** for receiving and sending the electrical signals that make neuronal communication possible. Dendrites are tree-like structures that extend away from the cell body to receive messages from other neurons at specialized junctions called synapses. Although some neurons do not have any dendrites, some types of neurons have multiple dendrites. Dendrites can have small protrusions called dendritic spines, which further increase surface area for possible synaptic connections.

Once a signal is received by the dendrite, it then travels passively to the cell body. The cell body contains a specialized structure, the axon hillock that integrates signals from multiple synapses and serves as a junction between the cell body and an axon. An axon is a tube-like structure that propagates the integrated signal to specialized endings called axon terminals. These terminals in turn synapse on other neurons, muscle, or target organs. Chemicals released at axon terminals allow signals to be communicated to

these other cells. Neurons usually have one or two axons, but some neurons, like amacrine cells in the retina, do not contain any axons. Some axons are covered with myelin, which acts as an insulator to minimize dissipation of the electrical signal as it travels down the axon, greatly increasing the speed on conduction. This insulation is important as the axon from a human motor neuron can be as long as a meter—from the base of the spine to the toes. The myelin sheath is not actually part of the neuron. Myelin is produced by glial cells. Along the axon there are periodic gaps in the myelin sheath. These gaps are called nodes of Ranvier and are sites where the signal is “recharged” as it travels along the axon.

It is important to note that a single neuron does not act alone—neuronal communication depends on the connections that neurons make with one another (as well as with other cells, like muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

Art Connection

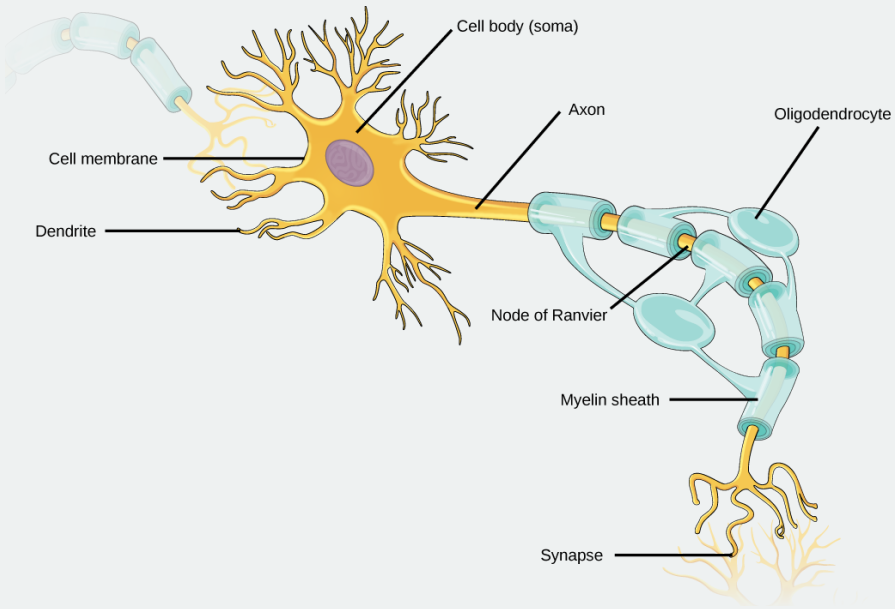


Figure 53.2.1.2: Neurons contain organelles common to many other cells, such as a nucleus and mitochondria. They also have more specialized structures, including dendrites and axons.

Which of the following statements is false?

A. The soma is the cell body of a nerve cell.
B. Myelin sheath provides an insulating layer to the dendrites.
C. Axons carry the signal from the soma to the target.
D. Dendrites carry the signal to the soma.

Types of Neurons

There are different types of neurons, and the functional role of a given neuron is intimately dependent on its structure. There is an amazing diversity of neuron shapes and sizes found in different parts of the nervous system (and across species), as illustrated by the neurons shown in Figure 53.2.1.3.

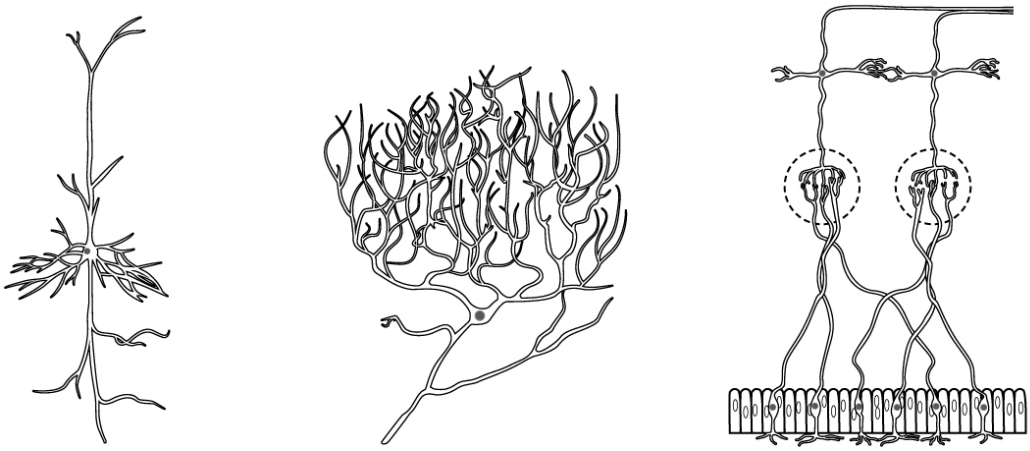


Figure 53.2.1.3: There is great diversity in the size and shape of neurons throughout the nervous system. Examples include (a) a pyramidal cell from the cerebral cortex, (b) a Purkinje cell from the cerebellar cortex, and (c) olfactory cells from the olfactory epithelium and olfactory bulb.

While there are many defined neuron cell subtypes, neurons are broadly divided into four basic types: unipolar, bipolar, multipolar, and pseudounipolar. Figure 53.2.1.4 illustrates these four basic neuron types. Unipolar neurons have only one structure that extends away from the soma. These neurons are not found in vertebrates but are found in insects where they stimulate muscles or glands. A bipolar neuron has one axon and one dendrite extending from the soma. An example of a bipolar neuron is a retinal bipolar cell, which receives signals from photoreceptor cells that are sensitive to light and transmits these signals to ganglion cells that carry the signal to the brain. Multipolar neurons are the most common type of neuron. Each multipolar neuron contains one axon and multiple dendrites. Multipolar neurons can be found in the central nervous system (brain and spinal cord). An example of a multipolar neuron is a Purkinje cell in the cerebellum, which has many branching dendrites but only one axon. Pseudounipolar cells share characteristics with both unipolar and bipolar cells. A pseudounipolar cell has a single process that extends from the soma, like a unipolar cell, but this process later branches into two distinct structures, like a bipolar cell. Most sensory neurons are pseudounipolar and have an axon that branches into two extensions: one connected to dendrites that receive sensory information and another that transmits this information to the spinal cord.

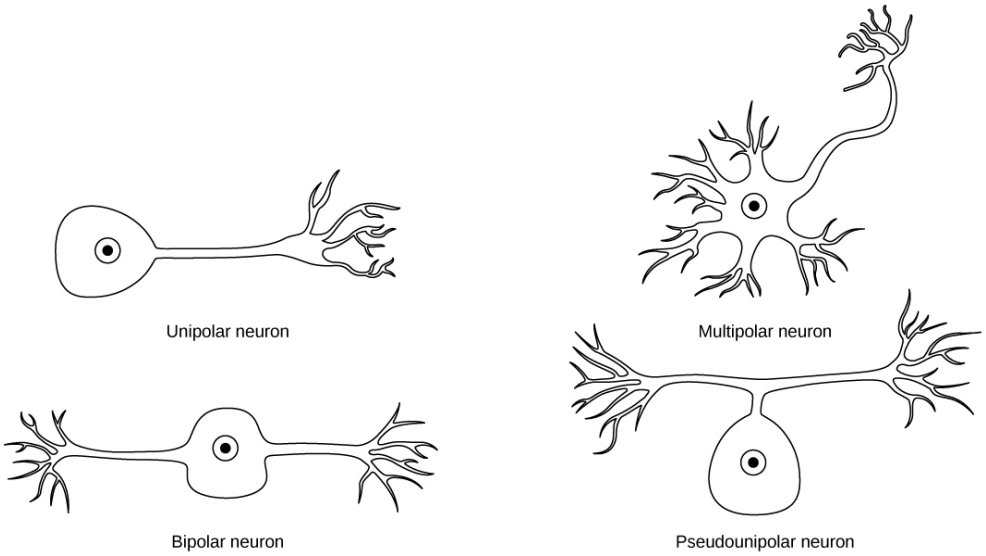


Figure 53.2.1.4: Neurons are broadly divided into four main types based on the number and placement of axons: (1) unipolar, (2) bipolar, (3) multipolar, and (4) pseudounipolar.

Everyday Connection: Neurogenesis

At one time, scientists believed that people were born with all the neurons they would ever have. Research performed during the last few decades indicates that neurogenesis, the birth of new neurons, continues into adulthood. Neurogenesis was first discovered in songbirds that produce new neurons while learning songs. For mammals, new neurons also play an important role in learning: about 1000 new neurons develop in the hippocampus (a brain structure involved in learning and memory) each day. While most of the new neurons will die, researchers found that an increase in the number of surviving new neurons in the hippocampus correlated with how well rats learned a new task. Interestingly, both exercise and some antidepressant medications also promote neurogenesis in the hippocampus. Stress has the opposite effect. While neurogenesis is quite limited compared to regeneration in other tissues, research in this area may lead to new treatments for disorders such as Alzheimer's, stroke, and epilepsy.

How do scientists identify new neurons? A researcher can inject a compound called bromodeoxyuridine (BrdU) into the brain of an animal. While all cells will be exposed to BrdU, BrdU will only be incorporated into the DNA of newly generated cells that are in S phase. A technique called immunohistochemistry can be used to attach a fluorescent label to the incorporated BrdU, and a researcher can use fluorescent microscopy to visualize the presence of BrdU, and thus new neurons, in brain tissue. Figure **53.2.1.5** is a micrograph which shows fluorescently labeled neurons in the hippocampus of a rat.

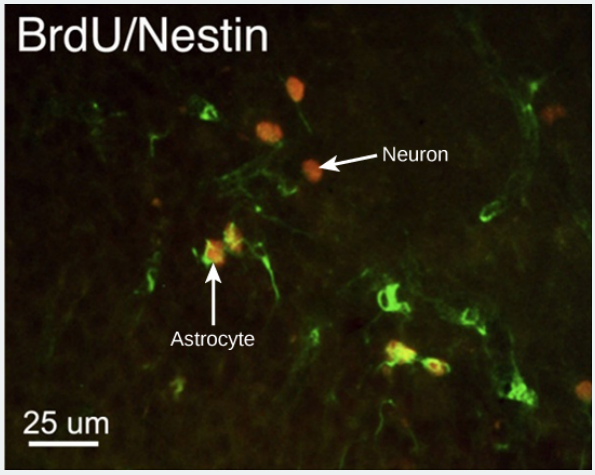


Figure **53.2.1.5**: This micrograph shows fluorescently labeled new neurons in a rat hippocampus. Cells that are actively dividing have bromodoxyuridine (BrdU) incorporated into their DNA and are labeled in red. Cells that express glial fibrillary acidic protein (GFAP) are labeled in green. Astrocytes, but not neurons, express GFAP. Thus, cells that are labeled both red and green are actively dividing astrocytes, whereas cells labeled red only are actively dividing neurons. (credit: modification of work by Dr. Maryam Faiz, et. al., University of Barcelona; scale-bar data from Matt Russell)

Link to Learning

This site contains more information about neurogenesis, including an interactive laboratory simulation and a video that explains how BrdU labels new cells.

Glia

While glia are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of ten. Neurons would be unable to function without the vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons, and provide myelin sheaths around axons. Scientists have recently discovered that they also play a role in responding to nerve activity and modulating communication between nerve cells. When glia do not function properly, the result can be disastrous—most brain tumors are caused by mutations in glia.

Types of Glia

There are several different types of glia with different functions, two of which are shown in Figure **53.2.1.6**. Astrocytes, shown in Figure **53.2.1.7** make contact with both capillaries and neurons in the CNS. They provide nutrients and other substances to neurons, regulate the concentrations of ions and chemicals in the extracellular fluid, and provide structural support for synapses. Astrocytes also form the blood-brain barrier—a structure that blocks entrance of toxic substances into the brain. Astrocytes, in particular, have been shown through calcium imaging experiments to become active in response to nerve activity, transmit calcium waves between astrocytes, and modulate the activity of surrounding synapses.

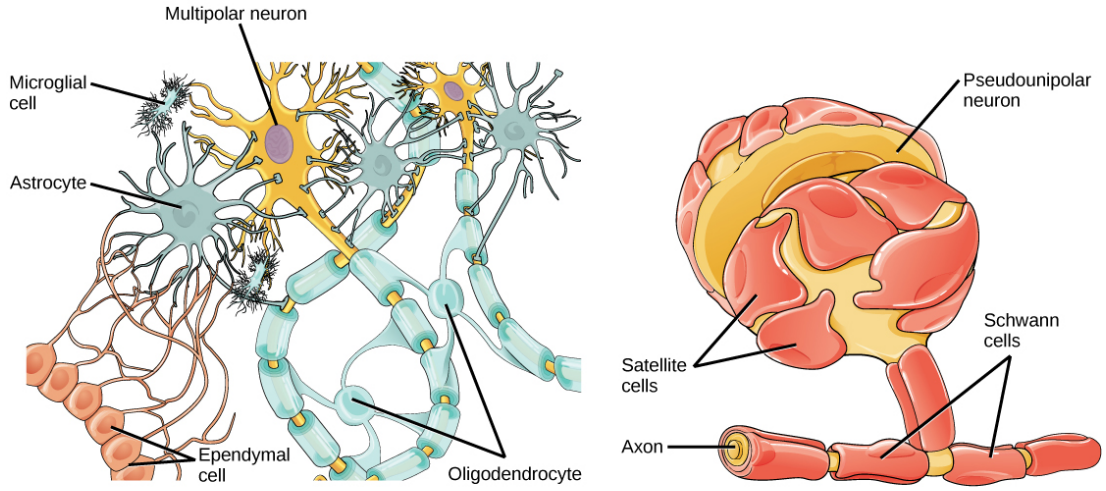
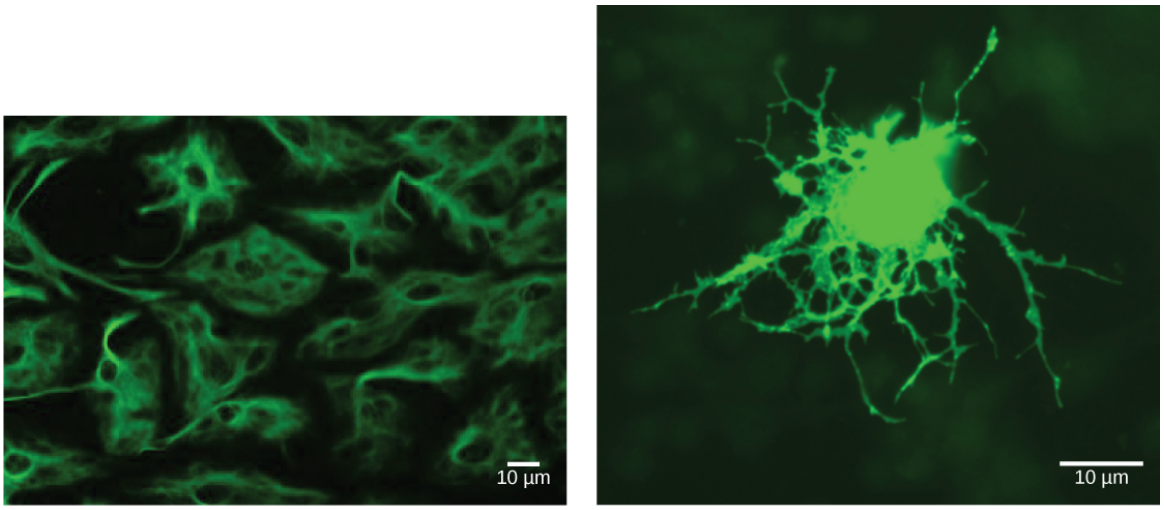


Figure **53.2.1.6**: Glial cells support neurons and maintain their environment. Glial cells of the (a) central nervous system include oligodendrocytes, astrocytes, ependymal cells, and microglial cells. Oligodendrocytes form the myelin sheath around axons. Astrocytes provide nutrients to neurons, maintain their extracellular environment, and provide structural support. Microglia scavenge pathogens and dead cells. Ependymal cells produce cerebrospinal fluid that cushions the neurons. Glial cells of the (b) peripheral nervous system include Schwann cells, which form the myelin sheath, and satellite cells, which provide nutrients and structural support to neurons.

Satellite glia provide nutrients and structural support for neurons in the PNS. Microglia scavenge and degrade dead cells and protect the brain from invading microorganisms. Oligodendrocytes, shown in Figure **53.2.1.7** form myelin sheaths around axons in the CNS. One axon can be myelinated by several oligodendrocytes, and one oligodendrocyte can provide myelin for multiple neurons. This is distinctive from the PNS where a single Schwann cell provides myelin for only one axon as the entire Schwann cell surrounds the axon. Radial glia serve as scaffolds for developing neurons as they migrate to their end destinations. Ependymal cells line fluid-filled ventricles of the brain and the central canal of the spinal cord. They are involved in the production of cerebrospinal fluid, which serves as a cushion for the brain, moves the fluid between the spinal cord and the brain, and is a component for the choroid plexus.



(a) Astrocyte (b) Oligodendrocyte

Figure **53.2.1.7**: (a) Astrocytes and (b) oligodendrocytes are glial cells of the central nervous system. (credit a: modification of work by Uniformed Services University; credit b: modification of work by Jurjen Broeke; scale-bar data from Matt Russell)

Summary

The nervous system is made up of neurons and glia. Neurons are specialized cells that are capable of sending electrical as well as chemical signals. Most neurons contain dendrites, which receive these signals, and axons that send signals to other neurons or tissues. There are four main types of neurons: unipolar, bipolar, multipolar, and pseudounipolar neurons. Glia are non-neuronal cells in the nervous system that support neuronal development and signaling. There are several types of glia that serve different functions.

Art Connections

Figure **53.2.1.2**: Which of the following statements is false?

A. The soma is the cell body of a nerve cell.
B. Myelin sheath provides an insulating layer to the dendrites.
C. Axons carry the signal from the soma to the target.
D. Dendrites carry the signal to the soma.

Answer

B

Glossary

astrocyte
glial cell in the central nervous system that provide nutrients, extracellular buffering, and structural support for neurons; also makes up the blood-brain barrier

axon
tube-like structure that propagates a signal from a neuron’s cell body to axon terminals

axon hillock
electrically sensitive structure on the cell body of a neuron that integrates signals from multiple neuronal connections

axon terminal
structure on the end of an axon that can form a synapse with another neuron

dendrite
structure that extends away from the cell body to receive messages from other neurons

ependymal
cell that lines fluid-filled ventricles of the brain and the central canal of the spinal cord; involved in production of cerebrospinal fluid

glia
(also, glial cells) cells that provide support functions for neurons

microglia
glia that scavenge and degrade dead cells and protect the brain from invading microorganisms

myelin
fatty substance produced by glia that insulates axons

neuron
specialized cell that can receive and transmit electrical and chemical signals

nodes of Ranvier
gaps in the myelin sheath where the signal is recharged

oligodendrocyte
glial cell that myelinates central nervous system neuron axons

radial glia
glia that serve as scaffolds for developing neurons as they migrate to their final destinations

satellite glia
glial cell that provides nutrients and structural support for neurons in the peripheral nervous system

Schwann cell
glial cell that creates myelin sheath around a peripheral nervous system neuron axon

synapse
junction between two neurons where neuronal signals are communicated

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53.2.2: Neurotransmitters

Learning Objectives

- Categorize the major neurotransmitters by chemical type and effect

Synapses

There are two types of connections between electrically active cells, chemical synapses and electrical synapses. In a **chemical synapse**, a chemical signal—namely, a neurotransmitter—is released from one cell and it affects the other cell. In an **electrical synapse**, there is a direct connection between the two cells so that ions can pass directly from one cell to the next. If one cell is depolarized in an electrical synapse, the joined cell also depolarizes because the ions pass between the cells. Chemical synapses involve the transmission of chemical information from one cell to the next. This section will concentrate on the chemical type of synapse.

An example of a chemical synapse is the neuromuscular junction (NMJ) described in the chapter on muscle tissue. In the nervous system, there are many more synapses that are essentially the same as the NMJ. All synapses have common characteristics, which can be summarized in this list:

- presynaptic element
- neurotransmitter (packaged in vesicles)
- synaptic cleft
- receptor proteins
- postsynaptic element
- neurotransmitter elimination or re-uptake

For the NMJ, these characteristics are as follows: the presynaptic element is the motor neuron's axon terminals, the neurotransmitter is acetylcholine, the synaptic cleft is the space between the cells where the neurotransmitter diffuses, the receptor protein is the nicotinic acetylcholine receptor, the postsynaptic element is the sarcolemma of the muscle cell, and the neurotransmitter is eliminated by acetylcholinesterase. Other synapses are similar to this, and the specifics are different, but they all contain the same characteristics.

Neurotransmitter Release

When an action potential reaches the axon terminals, voltage-gated Ca^{2+} channels in the membrane of the synaptic end bulb open. The concentration of Ca^{2+} increases inside the end bulb, and the Ca^{2+} ion associates with proteins in the outer surface of neurotransmitter vesicles. The Ca^{2+} facilitates the merging of the vesicle with the presynaptic membrane so that the neurotransmitter is released through exocytosis into the small gap between the cells, known as the **synaptic cleft**.

Once in the synaptic cleft, the neurotransmitter diffuses the short distance to the postsynaptic membrane and can interact with neurotransmitter receptors. Receptors are specific for the neurotransmitter, and the two fit together like a key and lock. One neurotransmitter binds to its receptor and will not bind to receptors for other neurotransmitters, making the binding a specific chemical event (Figure 3).

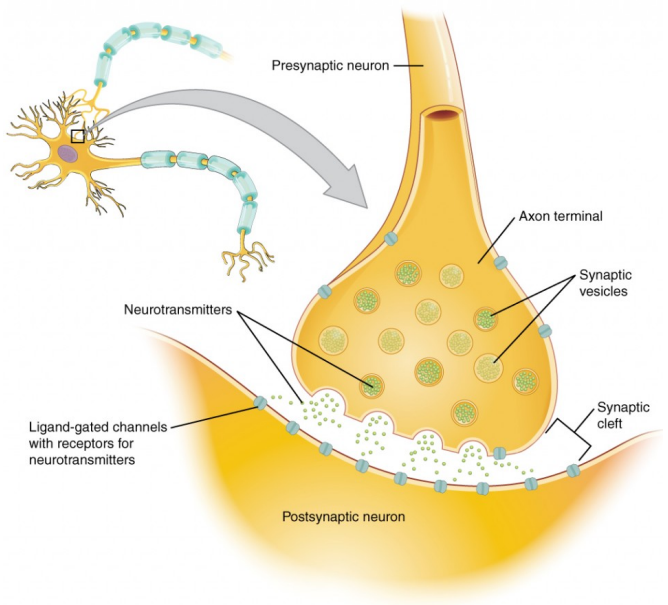


Figure 3. **The Synapse.** The synapse is a connection between a neuron and its target cell (which is not necessarily a neuron). The presynaptic element is the synaptic end bulb of the axon where Ca^{2+} enters the bulb to cause vesicle fusion and neurotransmitter release. The neurotransmitter diffuses across the synaptic cleft to bind to its receptor. The neurotransmitter is cleared from the synapse either by enzymatic degradation, neuronal reuptake, or glial reuptake.

Neurotransmitter Systems

There are several systems of neurotransmitters that are found at various synapses in the nervous system. These groups refer to the chemicals that are the neurotransmitters, and within the groups are specific systems.

The first group, which is a neurotransmitter system of its own, is the **cholinergic system**. It is the system based on acetylcholine. This includes the NMJ as an example of a cholinergic synapse, but cholinergic synapses are found in other parts of the nervous system. They are in the autonomic nervous system, as well as distributed throughout the brain.

The cholinergic system has two types of receptors, the **nicotinic receptor** is found in the NMJ as well as other synapses. There is also an acetylcholine receptor known as the **muscarinic receptor**. Both of these receptors are named for drugs that interact with the receptor in addition to acetylcholine. Nicotine will bind to the nicotinic receptor and activate it similar to acetylcholine. Muscarine, a product of certain mushrooms, will bind to the muscarinic receptor. However, nicotine will not bind to the muscarinic receptor and muscarine will not bind to the nicotinic receptor.

Another group of neurotransmitters are amino acids. This includes glutamate (Glu), GABA (gamma-aminobutyric acid, a derivative of glutamate), and glycine (Gly). These amino acids have an amino group and a carboxyl group in their chemical structures. Glutamate is one of the 20 amino acids that are used to make proteins. Each amino acid neurotransmitter would be part of its own system, namely the glutamatergic, GABAergic, and glycinergic systems. They each have their own receptors and do not interact with each other. Amino acid neurotransmitters are eliminated from the synapse by reuptake. A pump in the cell membrane of the presynaptic element, or sometimes a neighboring glial cell, will clear the amino acid from the synaptic cleft so that it can be recycled, repackaged in vesicles, and released again.

Another class of neurotransmitter is the **biogenic amine**, a group of neurotransmitters that are enzymatically made from amino acids. They have amino groups in them, but no longer have carboxyl groups and are therefore no longer classified as amino acids. Serotonin is made from tryptophan. It is the basis of the serotonergic system, which has its own specific receptors. Serotonin is transported back into the presynaptic cell for repackaging.

Other biogenic amines are made from tyrosine, and include dopamine, norepinephrine, and epinephrine. Dopamine is part of its own system, the dopaminergic system, which has dopamine receptors. Dopamine is removed from the synapse by transport proteins in the presynaptic cell membrane. Norepinephrine and epinephrine belong to the adrenergic neurotransmitter system. The two molecules are very similar and bind to the same receptors, which are referred to as alpha and beta receptors. Norepinephrine and epinephrine are also transported back into the presynaptic cell. The chemical epinephrine (*epi–* = “on”; “*-nephrine*” = kidney)

is also known as adrenaline (*renal* = “kidney”), and norepinephrine is sometimes referred to as noradrenaline. The adrenal gland produces epinephrine and norepinephrine to be released into the blood stream as hormones.

A **neuropeptide** is a neurotransmitter molecule made up of chains of amino acids connected by peptide bonds. This is what a protein is, but the term protein implies a certain length to the molecule. Some neuropeptides are quite short, such as met-enkephalin, which is five amino acids long. Others are long, such as beta-endorphin, which is 31 amino acids long. Neuropeptides are often released at synapses in combination with another neurotransmitter, and they often act as hormones in other systems of the body, such as vasoactive intestinal peptide (VIP) or substance P.

The effect of a neurotransmitter on the postsynaptic element is entirely dependent on the receptor protein. First, if there is no receptor protein in the membrane of the postsynaptic element, then the neurotransmitter has no effect. The depolarizing or hyperpolarizing effect is also dependent on the receptor. When acetylcholine binds to the nicotinic receptor, the postsynaptic cell is depolarized. This is because the receptor is a cation channel and positively charged Na^+ will rush into the cell. However, when acetylcholine binds to the muscarinic receptor, of which there are several variants, it might cause depolarization or hyperpolarization of the target cell.

The amino acid neurotransmitters, glutamate, glycine, and GABA, are almost exclusively associated with just one effect. Glutamate is considered an excitatory amino acid, but only because Glu receptors in the adult cause depolarization of the postsynaptic cell. Glycine and GABA are considered inhibitory amino acids, again because their receptors cause hyperpolarization.

The biogenic amines have mixed effects. For example, the dopamine receptors that are classified as D1 receptors are excitatory whereas D2-type receptors are inhibitory. Biogenic amine receptors and neuropeptide receptors can have even more complex effects because some may not directly affect the membrane potential, but rather have an effect on gene transcription or other metabolic processes in the neuron. The characteristics of the various neurotransmitter systems presented in this section are organized in Table 1.

Table 1. Characteristics of Neurotransmitter Systems

System	Chlolinergic	Amino acids	Biogenic amines	Neuropeptides
Neurotransmitters	Acetylchlonie	Glutamate, glycine, GABA	Serotonin (5-HT)	met-enkaphalin, beta-endorphin, VIP, Substance P, etc.
Receptors	Nicotonic and muscarinic receptors	Glu receptors, gly receptors, GABA receptors	5-HT receptors, D1 and D2 receptors, a-adrenergic and B-adrenergetic receptors	Receptors are too numerous to list, but are specific to the peptides
Elimination	Degredation by acetylcholinesterase	Reuptake by neurons of glia	Reuptake by neurons	Degredation by enzymes called peptidases
Postsynaptic effect	Nicotonic receptor causes depolarization. Muscarinic receptors can cause both depolarization of hyperpolarization depending on the subtype	Glu receptors cause depolarization. Gly and GABA receptors cause hyperpolarization	Depolarization or hyperpolarization depends on the specific receptor. For example, D1 receptors cause depolarization and D2 receptors cause hyperpolarization	Depolarization or hyperpolarization depends on the specific receptor

The important thing to remember about neurotransmitters, and signaling chemicals in general, is that the effect is entirely dependent on the receptor. Neurotransmitters bind to one of two classes of receptors at the cell surface, ionotropic or metabotropic (Figure 4). Ionotropic receptors are ligand-gated ion channels, such as the nicotinic receptor for acetylcholine or the glycine receptor. A **metabotropic receptor** involves a complex of proteins that result in metabolic changes within the cell. The receptor complex includes the transmembrane receptor protein, a G protein, and an effector protein. The neurotransmitter, referred to as the

first messenger, binds to the receptor protein on the extracellular surface of the cell, and the intracellular side of the protein initiates activity of the G protein. The **G protein** is a guanosine triphosphate (GTP) hydrolase that physically moves from the receptor protein to the effector protein to activate the latter. An **effector protein** is an enzyme that catalyzes the generation of a new molecule, which acts as the intracellular mediator of the signal that binds to the receptor. This intracellular mediator is called the second messenger.

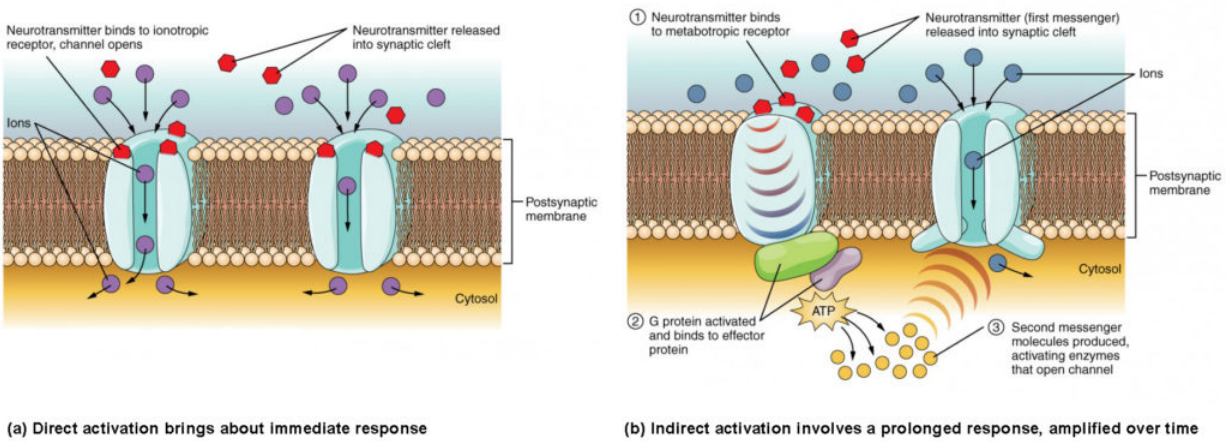
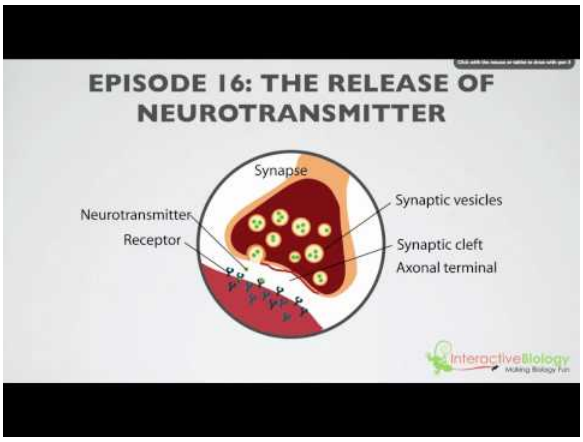


Figure 4. Receptor Types. (a) An ionotropic receptor is a channel that opens when the neurotransmitter binds to it. (b) A metabotropic receptor is a complex that causes metabolic changes in the cell when the neurotransmitter binds to it (1). After binding, the G protein hydrolyzes GTP and moves to the effector protein (2). When the G protein contacts the effector protein, a second messenger is generated, such as cAMP (3). The second messenger can then go on to cause changes in the neuron, such as opening or closing ion channels, metabolic changes, and changes in gene transcription.

Different receptors use different second messengers. Two common examples of second messengers are cyclic adenosine monophosphate (cAMP) and inositol triphosphate (IP_3). The enzyme adenylate cyclase (an example of an effector protein) makes cAMP, and phospholipase C is the enzyme that makes IP_3. Second messengers, after they are produced by the effector protein, cause metabolic changes within the cell. These changes are most likely the activation of other enzymes in the cell. In neurons, they often modify ion channels, either opening or closing them. These enzymes can also cause changes in the cell, such as the activation of genes in the nucleus, and therefore the increased synthesis of proteins. In neurons, these kinds of changes are often the basis of stronger connections between cells at the synapse and may be the basis of learning and memory.

Watch this video to learn about the release of a neurotransmitter.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/aapi/?p=362

The action potential reaches the end of the axon, called the axon terminal, and a chemical signal is released to tell the target cell to do something—either to initiate a new action potential, or to suppress that activity. In a very short space, the electrical signal of the action potential is changed into the chemical signal of a neurotransmitter and then back to electrical changes in the target cell membrane. What is the importance of voltage-gated calcium channels in the release of neurotransmitters?

Try It

The underlying cause of some neurodegenerative diseases, such as Alzheimer's and Parkinson's, appears to be related to proteins—specifically, to proteins behaving badly. One of the strongest theories of what causes Alzheimer's disease is based on the accumulation of beta-amyloid plaques, dense conglomerations of a protein that is not functioning correctly. Parkinson's disease is linked to an increase in a protein known as alpha-synuclein that is toxic to the cells of the substantia nigra nucleus in the midbrain.

For proteins to function correctly, they are dependent on their three-dimensional shape. The linear sequence of amino acids folds into a three-dimensional shape that is based on the interactions between and among those amino acids. When the folding is disturbed, and proteins take on a different shape, they stop functioning correctly. But the disease is not necessarily the result of functional loss of these proteins; rather, these altered proteins start to accumulate and may become toxic. For example, in Alzheimer's, the hallmark of the disease is the accumulation of these amyloid plaques in the cerebral cortex. The term coined to describe this sort of disease is "proteopathy" and it includes other diseases. Creutzfeld-Jacob disease, the human variant of the prion disease known as mad cow disease in the bovine, also involves the accumulation of amyloid plaques, similar to Alzheimer's. Diseases of other organ systems can fall into this group as well, such as cystic fibrosis or type 2 diabetes. Recognizing the relationship between these diseases has suggested new therapeutic possibilities. Interfering with the accumulation of the proteins, and possibly as early as their original production within the cell, may unlock new ways to alleviate these devastating diseases.

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53.2.3: Hormones

Skills to Develop

- List the different types of hormones
- Explain their role in maintaining homeostasis

Maintaining homeostasis within the body requires the coordination of many different systems and organs. Communication between neighboring cells, and between cells and tissues in distant parts of the body, occurs through the release of chemicals called hormones. Hormones are released into body fluids (usually blood) that carry these chemicals to their target cells. At the target cells, which are cells that have a receptor for a signal or ligand from a signal cell, the hormones elicit a response. The cells, tissues, and organs that secrete hormones make up the endocrine system. Examples of glands of the endocrine system include the adrenal glands, which produce hormones such as epinephrine and norepinephrine that regulate responses to stress, and the thyroid gland, which produces thyroid hormones that regulate metabolic rates.

Although there are many different hormones in the human body, they can be divided into three classes based on their chemical structure: lipid-derived, amino acid-derived, and peptide (peptide and proteins) hormones. One of the key distinguishing features of lipid-derived hormones is that they can diffuse across plasma membranes whereas the amino acid-derived and peptide hormones cannot.

Lipid-Derived Hormones (or Lipid-soluble Hormones)

Most lipid hormones are derived from cholesterol and thus are structurally similar to it, as illustrated in Figure **53.2.3.1**. The primary class of lipid hormones in humans is the steroid hormones. Chemically, these hormones are usually ketones or alcohols; their chemical names will end in “-ol” for alcohols or “-one” for ketones. Examples of steroid hormones include estradiol, which is an estrogen, or female sex hormone, and testosterone, which is an androgen, or male sex hormone. These two hormones are released by the female and male reproductive organs, respectively. Other steroid hormones include aldosterone and cortisol, which are released by the adrenal glands along with some other types of androgens. Steroid hormones are insoluble in water, and they are transported by transport proteins in blood. As a result, they remain in circulation longer than peptide hormones. For example, cortisol has a half-life of 60 to 90 minutes, while epinephrine, an amino acid derived-hormone, has a half-life of approximately one minute.

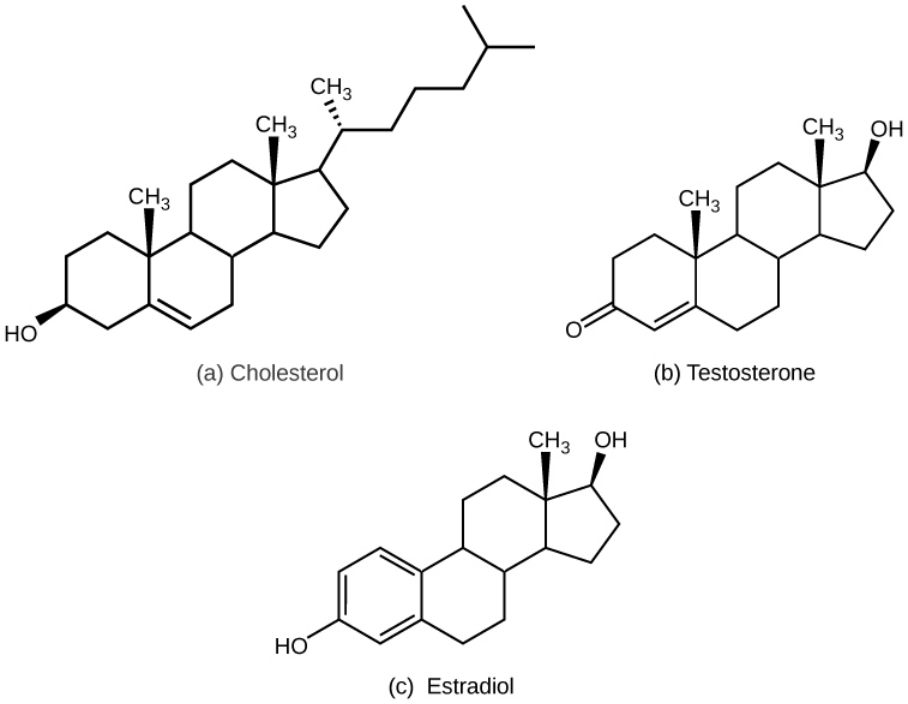


Figure **53.2.3.1**: The structures shown here represent (a) cholesterol, plus the steroid hormones (b) testosterone and (c) estradiol.

Amino Acid-Derived Hormones

The amino acid-derived hormones are relatively small molecules that are derived from the amino acids tyrosine and tryptophan, shown in Figure **53.2.3.2**. If a hormone is amino acid-derived, its chemical name will end in "-ine". Examples of amino acid-derived hormones include epinephrine and norepinephrine, which are synthesized in the medulla of the adrenal glands, and thyroxine, which is produced by the thyroid gland. The pineal gland in the brain makes and secretes melatonin which regulates sleep cycles.

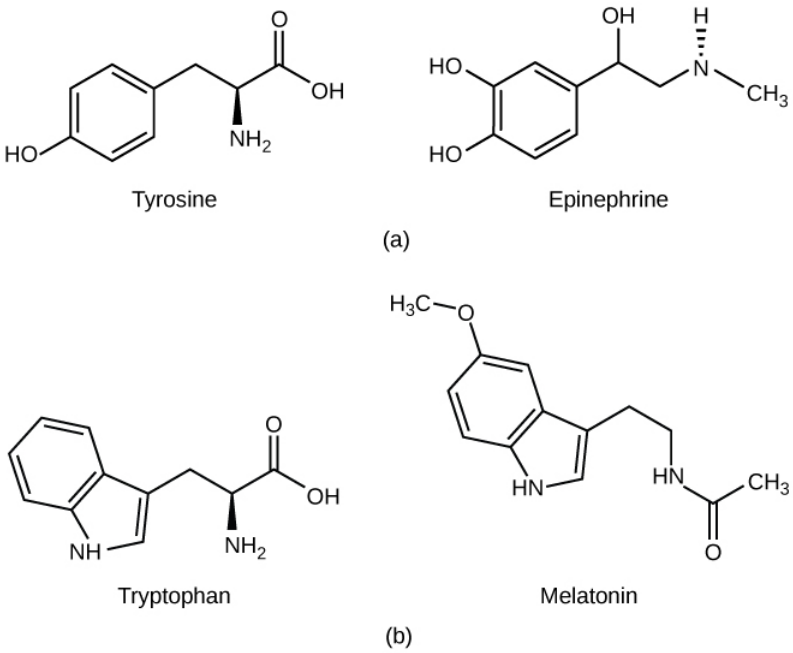
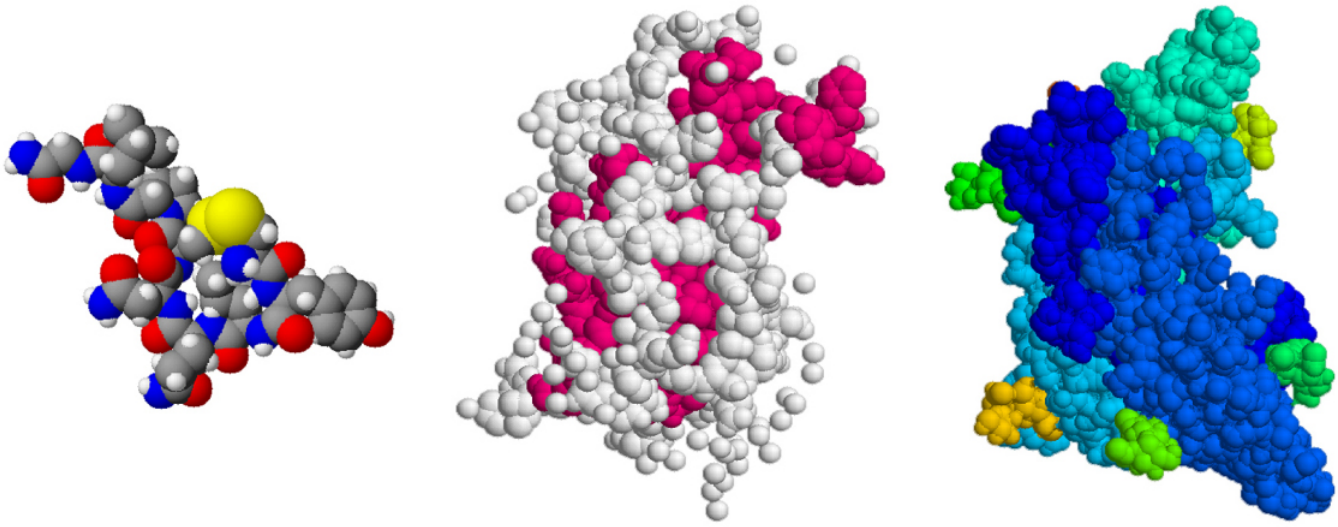


Figure **53.2.3.2**: (a) The hormone epinephrine, which triggers the fight-or-flight response, is derived from the amino acid tyrosine. (b) The hormone melatonin, which regulates circadian rhythms, is derived from the amino acid tryptophan.

Peptide Hormones

The structure of peptide hormones is that of a polypeptide chain (chain of amino acids). The peptide hormones include molecules that are short polypeptide chains, such as antidiuretic hormone and oxytocin produced in the brain and released into the blood in the posterior pituitary gland. This class also includes small proteins, like growth hormones produced by the pituitary, and large glycoproteins such as follicle-stimulating hormone produced by the pituitary. Figure **53.2.3.3** illustrates these peptide hormones.

Secreted peptides like insulin are stored within vesicles in the cells that synthesize them. They are then released in response to stimuli such as high blood glucose levels in the case of insulin. Amino acid-derived and polypeptide hormones are water-soluble and insoluble in lipids. These hormones cannot pass through plasma membranes of cells; therefore, their receptors are found on the surface of the target cells.



(a) (b) (c)

Figure 53.2.3.3: The structures of peptide hormones (a) oxytocin, (b) growth hormone, and (c) follicle-stimulating hormone are shown. These peptide hormones are much larger than those derived from cholesterol or amino acids.

Career Connection: Endocrinologist

An endocrinologist is a medical doctor who specializes in treating disorders of the endocrine glands, hormone systems, and glucose and lipid metabolic pathways. An endocrine surgeon specializes in the surgical treatment of endocrine diseases and glands. Some of the diseases that are managed by endocrinologists: disorders of the pancreas (diabetes mellitus), disorders of the pituitary (gigantism, acromegaly, and pituitary dwarfism), disorders of the thyroid gland (goiter and Graves' disease), and disorders of the adrenal glands (Cushing's disease and Addison's disease).

Endocrinologists are required to assess patients and diagnose endocrine disorders through extensive use of laboratory tests. Many endocrine diseases are diagnosed using tests that stimulate or suppress endocrine organ functioning. Blood samples are then drawn to determine the effect of stimulating or suppressing an endocrine organ on the production of hormones. For example, to diagnose diabetes mellitus, patients are required to fast for 12 to 24 hours. They are then given a sugary drink, which stimulates the pancreas to produce insulin to decrease blood glucose levels. A blood sample is taken one to two hours after the sugar drink is consumed. If the pancreas is functioning properly, the blood glucose level will be within a normal range. Another example is the A1C test, which can be performed during blood screening. The A1C test measures average blood glucose levels over the past two to three months by examining how well the blood glucose is being managed over a long time.

Once a disease has been diagnosed, endocrinologists can prescribe lifestyle changes and/or medications to treat the disease. Some cases of diabetes mellitus can be managed by exercise, weight loss, and a healthy diet; in other cases, medications may be required to enhance insulin release. If the disease cannot be controlled by these means, the endocrinologist may prescribe insulin injections.

In addition to clinical practice, endocrinologists may also be involved in primary research and development activities. For example, ongoing islet transplant research is investigating how healthy pancreas islet cells may be transplanted into diabetic patients. Successful islet transplants may allow patients to stop taking insulin injections.

Summary

There are three basic types of hormones: lipid-derived, amino acid-derived, and peptide. Lipid-derived hormones are structurally similar to cholesterol and include steroid hormones such as estradiol and testosterone. Amino acid-derived hormones are relatively small molecules and include the adrenal hormones epinephrine and norepinephrine. Peptide hormones are polypeptide chains or proteins and include the pituitary hormones, antidiuretic hormone (vasopressin), and oxytocin.

Glossary

amino acid-derived hormone
hormone derived from amino acids

lipid-derived hormone
hormone derived mostly from cholesterol

peptide hormone
hormone composed of a polypeptide chain

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53.2.4: Behavior and the Nervous System

Learning Objectives

1. Summarize the primary functions of the CNS and of the subsystems of the PNS.
2. Explain how the electrical components of the nervous system and the chemical components of the endocrine system work together to influence behavior.

Now that we have considered how individual neurons operate and the roles of the different brain areas, it is time to ask how the body manages to "put it all together." How do the complex activities in the various parts of the brain, the simple all-or-nothing firings of billions of interconnected neurons, and the various chemical systems within the body, work together to allow the body to respond to the social environment and engage in everyday behaviors? In this section we will see that the complexities of human behavior are accomplished through the joint actions of electrical and chemical processes in the nervous system and the endocrine system.

Electrical Control of Behavior: The Nervous System

The nervous system (Figure **53.2.4.17**), the electrical information highway of the body, is made up of nerves—*bundles of interconnected neurons that fire in synchrony to carry messages*. The *central nervous system (CNS)*, made up of the brain and spinal cord, is the major controller of the body's functions, charged with interpreting sensory information and responding to it with its own directives. The CNS interprets information coming in from the senses, formulates an appropriate reaction, and sends responses to the appropriate system to respond accordingly. Everything that we see, hear, smell, touch, and taste is conveyed to us from our sensory organs as neural impulses, and each of the commands that the brain sends to the body, both consciously and unconsciously, travels through this system as well.

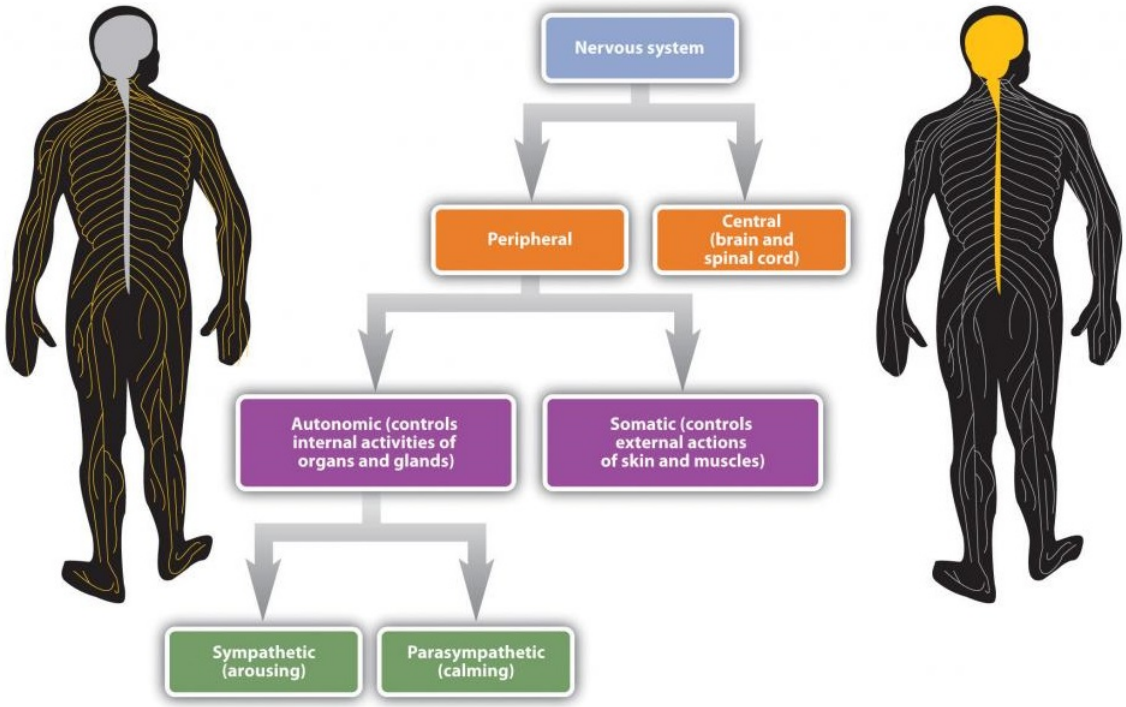


Figure **53.2.4.17**: The Functional Divisions of the Nervous System

Nerves are differentiated according to their function. A sensory (or afferent) neuron*carries information from the sensory receptors*, whereas a motor (or efferent) neuron*transmits information to the muscles and glands*. An interneuron, which is by far the most common type of neuron, is located primarily within the CNS and is *responsible for communicating among the neurons*.

Interneurons allow the brain to combine the multiple sources of available information to create a coherent picture of the sensory information being conveyed.

The spinal cord is *the long, thin, tubular bundle of nerves and supporting cells that extends down from the brain*. It is the central throughway of information for the body. Within the spinal cord, ascending tracts of sensory neurons relay sensory information from the sense organs to the brain while descending tracts of motor neurons relay motor commands back to the body. When a quicker-than-usual response is required, the spinal cord can do its own processing, bypassing the brain altogether. A reflex is *an involuntary and nearly instantaneous movement in response to a stimulus*. Reflexes are triggered when sensory information is powerful enough to reach a given threshold and the interneurons in the spinal cord act to send a message back through the motor neurons without relaying the information to the brain (Figure **53.2.4.18**). When you touch a hot stove and immediately pull your hand back, or when you fumble your cell phone and instinctively reach to catch it before it falls, reflexes in your spinal cord order the appropriate responses before your brain even knows what is happening.

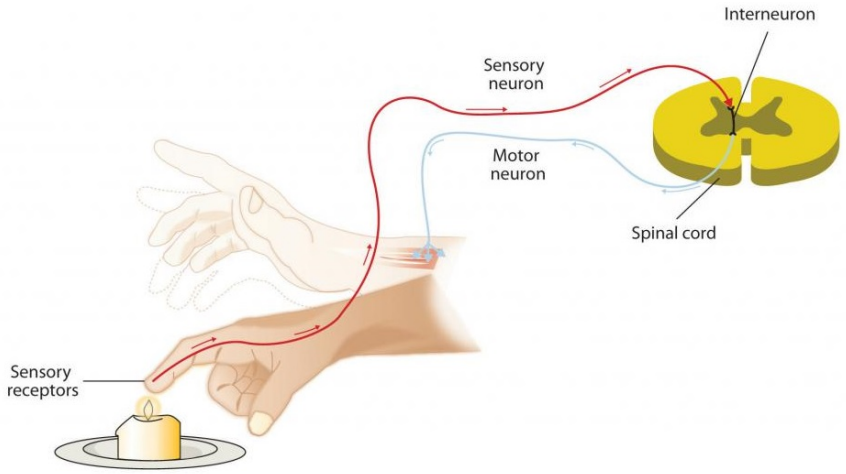


Figure **53.2.4.18** The Reflex. The central nervous system can interpret signals from sensory neurons and respond to them extremely quickly via the motor neurons without any need for the brain to be involved. These quick responses, known as reflexes, can reduce the damage that we might experience as a result of, for instance, touching a hot stove.

If the central nervous system is the command center of the body, the *peripheral nervous system (PNS)* represents the front line. The PNS links the CNS to the body's sense receptors, muscles, and glands. As you can see in Figure **53.2.4.19**, the peripheral nervous system is itself divided into two subsystems, one controlling internal responses and one controlling external responses.

The autonomic nervous system (ANS) is *the division of the PNS that governs the internal activities of the human body, including heart rate, breathing, digestion, salivation, perspiration, urination, and sexual arousal*. Many of the actions of the ANS, such as heart rate and digestion, are automatic and out of our conscious control, but others, such as breathing and sexual activity, can be controlled and influenced by conscious processes.

The somatic nervous system (SNS) is *the division of the PNS that controls the external aspects of the body*, including the skeletal muscles, skin, and sense organs. The somatic nervous system consists primarily of motor nerves responsible for sending brain signals for muscle contraction.

The autonomic nervous system itself can be further subdivided into the *sympathetic* and *parasympathetic* systems (Figure **53.2.4.19**). The sympathetic division of the ANS is *involved in preparing the body for behavior, particularly in response to stress, by activating the organs and the glands in the endocrine system*. The parasympathetic division of the ANS*tends to calm the body by slowing the heart and breathing and by allowing the body to recover from the activities that the sympathetic system causes*. The sympathetic and the parasympathetic divisions normally function in opposition to each other, such that the sympathetic division acts a bit like the accelerator pedal on a car and the parasympathetic division acts like the brake.

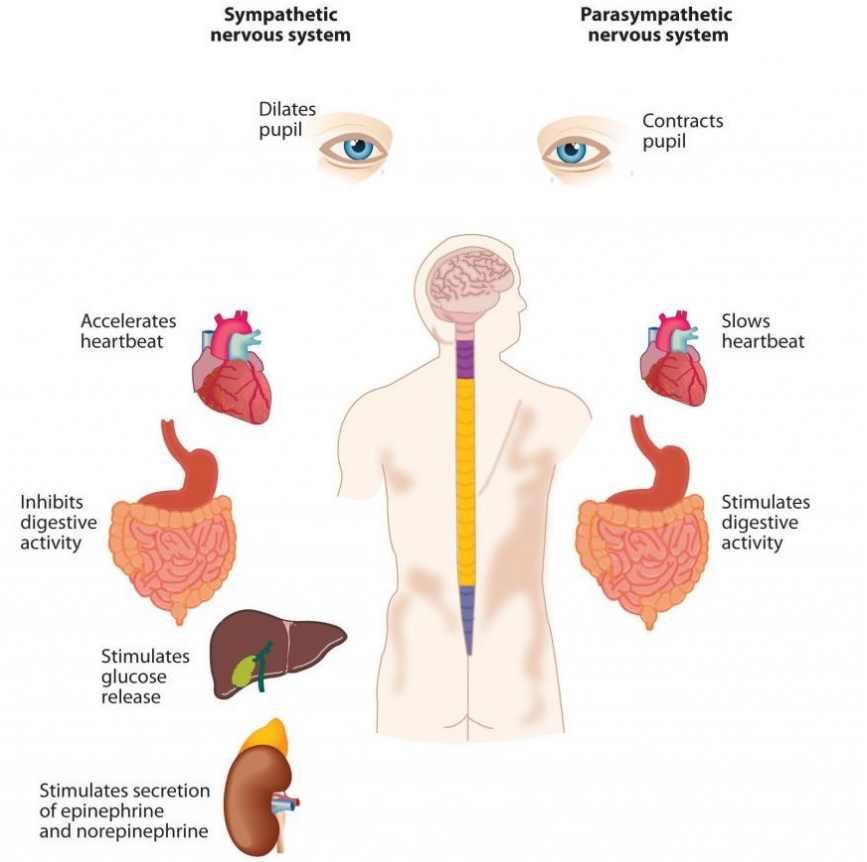


Figure **53.2.4.19**: The Autonomic Nervous System. The autonomic nervous system has two divisions: The sympathetic division acts to energize the body, preparing it for action. The parasympathetic division acts to calm the body, allowing it to rest.

Our everyday activities are controlled by the interaction between the sympathetic and parasympathetic nervous systems. For example, when we get out of bed in the morning, we would experience a sharp drop in blood pressure if it were not for the action of the sympathetic system, which automatically increases blood flow through the body. Similarly, after we eat a big meal, the parasympathetic system automatically sends more blood to the stomach and intestines, allowing us to efficiently digest the food. And perhaps you've had the experience of not being at all hungry before a stressful event, such as a sports game or an exam (when the sympathetic division was primarily in action), but suddenly finding yourself starved afterward, as the parasympathetic takes over. The two systems work together to maintain vital bodily functions, resulting in homeostasis, *the natural balance in the body's systems*.

The Body's Chemicals Help Control Behavior: The Endocrine System

The nervous system is designed to protect us from danger through its interpretation of and reactions to stimuli. But a primary function of the sympathetic and parasympathetic nervous systems is to interact with the *endocrine system* to elicit chemicals that provide another system for influencing our feelings and behaviors.

A gland in the endocrine system is made up of *groups of cells that function to secrete hormones*. A hormone is *a chemical that moves throughout the body to help regulate emotions and behaviors*. When the hormones released by one gland arrive at receptor tissues or other glands, these receiving receptors may trigger the release of other hormones, resulting in a series of complex chemical chain reactions. The endocrine system works together with the nervous system to influence many aspects of human behavior, including growth, reproduction, and metabolism. And the endocrine system plays a vital role in emotions. Because the glands in men and women differ, hormones also help explain some of the observed behavioral differences between men and women. The major glands in the endocrine system are shown in Figure **53.2.4.20**.

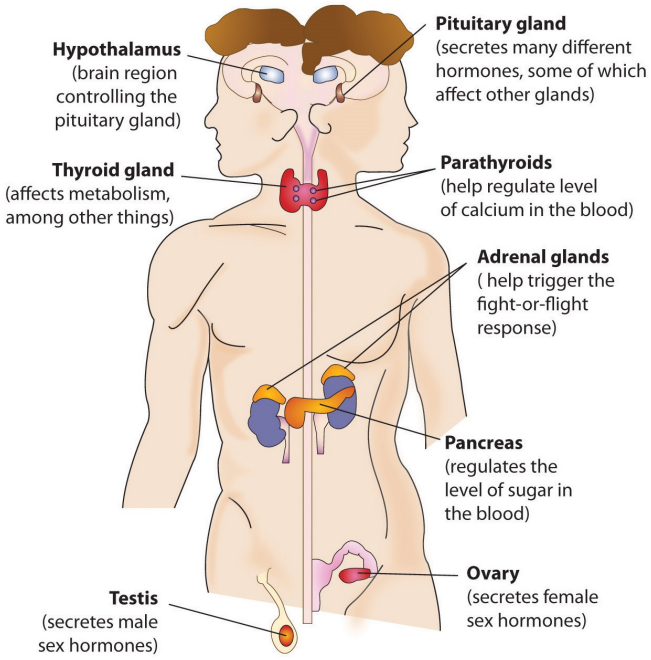


Figure 53.2.4.20: The Major Glands of the Endocrine System.

The male is shown on the left and the female on the right.

The pituitary gland, *a small pea-sized gland located near the center of the brain, is responsible for controlling the body's growth*, but it also has many other influences that make it of primary importance to regulating behavior. The pituitary secretes hormones that influence our responses to pain as well as hormones that signal the ovaries and testes to make sex hormones. The pituitary gland also controls ovulation and the menstrual cycle in women. Because the pituitary has such an important influence on other glands, it is sometimes known as the "master gland."

Other glands in the endocrine system include the *pancreas*, which secretes hormones designed to keep the body supplied with fuel to produce and maintain stores of energy; the *pineal gland*, located in the middle of the brain, which secretes melatonin, a hormone that helps regulate the wake-sleep cycle; and the *thyroid* and *parathyroid glands*, which are responsible for determining how quickly the body uses energy and hormones, and controlling the amount of calcium in the blood and bones.

The body has two triangular *adrenal glands*, one atop each kidney. The adrenal glands*produce hormones that regulate salt and water balance in the body, and they are involved in metabolism, the immune system, and sexual development and function*. The most important function of the adrenal glands is to secrete the hormones *epinephrine* (also known as *adrenaline*) and *norepinephrine* (also known as *noradrenaline*) when we are excited, threatened, or stressed. Epinephrine and norepinephrine stimulate the sympathetic division of the ANS, causing increased heart and lung activity, dilation of the pupils, and increases in blood sugar, which give the body a surge of energy to respond to a threat. The activity and role of the adrenal glands in response to stress provides an excellent example of the close relationship and interdependency of the nervous and endocrine systems. A quick-acting nervous system is essential for immediate activation of the adrenal glands, while the endocrine system mobilizes the body for action.

The male sex glands, known as the testes, secrete a number of hormones, the most important of which is testosterone, *the male sex hormone*. Testosterone regulates body changes associated with sexual development, including enlargement of the penis, deepening of the voice, growth of facial and pubic hair, and the increase in muscle growth and strength. The ovaries, *the female sex glands*, are located in the pelvis. They produce eggs and secrete the female hormones *estrogen* and *progesterone*. Estrogen is involved in the development of female sexual features, including breast growth, the accumulation of body fat around the hips and thighs, and the growth spurt that occurs during puberty. Both estrogen and progesterone are also involved in pregnancy and the regulation of the menstrual cycle.

Recent research has pinpointed some of the important roles of the sex hormones in social behavior. Dabbs, Hargrove, and Heusel (1996) measured the testosterone levels of 240 men who were members of 12 fraternities at two universities. They also obtained descriptions of the fraternities from university officials, fraternity officers, yearbook and chapter house photographs, and researcher

field notes. The researchers correlated the testosterone levels and the descriptions of each fraternity. They found that the fraternities with the highest average testosterone levels were also more wild and unruly, and one of these fraternities was known across campus for the crudeness of its behavior. On the other hand, the fraternities with the lowest average testosterone levels were more well behaved, friendly and pleasant, academically successful, and socially responsible. Banks and Dabbs (1996) found that juvenile delinquents and prisoners who had high levels of testosterone also acted more violently, and Tremblay et al. (1998) found that testosterone was related to toughness and leadership behaviors in adolescent boys. Although testosterone levels are higher in men than in women, the relationship between testosterone and aggression is not limited to males. Studies have also shown a positive relationship between testosterone and aggression and related behaviors (such as competitiveness) in women (Cashdan, 2003).

It must be kept in mind that the observed relationships between testosterone levels and aggressive behavior that have been found in these studies do not prove that testosterone causes aggression—the relationships are only correlational. In fact, there is evidence that the relationship between violence and testosterone also goes in the other direction: Playing an aggressive game, such as tennis or even chess, increases the testosterone levels of the winners and decreases the testosterone levels of losers (Gladue, Boechler, & McCaul, 1989; Mazur, Booth, & Dabbs, 1992), and perhaps this is why excited soccer fans sometimes riot when their team wins.

Recent research has also begun to document the role that female sex hormones may play in reactions to others. A study about hormonal influences on social-cognitive functioning (Macrae, Alnwick, Milne, & Schloerscheidt, 2002) found that women were more easily able to perceive and categorize male faces during the more fertile phases of their menstrual cycles. Although researchers did not directly measure the presence of hormones, it is likely that phase-specific hormonal differences influenced the women's perceptions.

At this point you can begin to see the important role the hormones play in behavior. But the hormones we have reviewed in this section represent only a subset of the many influences that hormones have on our behaviors. In the chapters to come we will consider the important roles that hormones play in many other behaviors, including sleeping, sexual activity, and helping and harming others.

Key Takeaways

- The body uses both electrical and chemical systems to create homeostasis.
- The CNS is made up of bundles of nerves that carry messages to and from the PNS
- The peripheral nervous system is composed of the autonomic nervous system (ANS) and the peripheral nervous system (PNS). The ANS is further divided into the sympathetic (activating) and parasympathetic (calming) nervous systems. These divisions are activated by glands and organs in the endocrine system.
- Specific nerves, including sensory neurons, motor neurons, and interneurons, each have specific functions.
- The spinal cord may bypass the brain by responding rapidly using reflexes.
- The pituitary gland is a master gland, affecting many other glands.
- Hormones produced by the pituitary and adrenal glands regulate growth, stress, sexual functions, and chemical balance in the body.
- The adrenal glands produce epinephrine and norepinephrine, the hormones responsible for our reactions to stress.
- The sex hormones, testosterone, estrogen, and progesterone, play an important role in sex differences.

Exercises and Critical Thinking

1. Recall a time when you were threatened or stressed. What physiological reactions did you experience in the situation, and what aspects of the endocrine system do you think created those reactions?
2. Consider the emotions that you have experienced over the past several weeks. What hormones do you think might have been involved in creating those emotions?

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53.3: Behavioral Genetics

Skills to Develop

- Compare innate and learned behavior
- Discuss how movement and migration behaviors are a result of natural selection
- Discuss the different ways members of a population communicate with each other
- Give examples of how species use energy for mating displays and other courtship behaviors
- Differentiate between various mating systems
- Describe different ways that species learn

Behavior is the change in activity of an organism in response to a stimulus. Behavioral biology is the study of the biological and evolutionary bases for such changes. The idea that behaviors evolved as a result of the pressures of natural selection is not new. Animal behavior has been studied for decades, by biologists in the science of ethology, by psychologists in the science of comparative psychology, and by scientists of many disciplines in the study of neurobiology. Although there is overlap between these disciplines, scientists in these behavioral fields take different approaches. Comparative psychology is an extension of work done in human and behavioral psychology. Ethology is an extension of genetics, evolution, anatomy, physiology, and other biological disciplines. Still, one cannot study behavioral biology without touching on both comparative psychology and ethology.

One goal of behavioral biology is to dissect out the innate behaviors, which have a strong genetic component and are largely independent of environmental influences, from the learned behaviors, which result from environmental conditioning. Innate behavior, or instinct, is important because there is no risk of an incorrect behavior being learned. They are “hard wired” into the system. On the other hand, learned behaviors, although riskier, are flexible, dynamic, and can be altered according to changes in the environment.

Innate Behaviors: Movement and Migration

Innate or instinctual behaviors rely on response to stimuli. The simplest example of this is a reflex action, an involuntary and rapid response to stimulus. To test the “knee-jerk” reflex, a doctor taps the patellar tendon below the kneecap with a rubber hammer. The stimulation of the nerves there leads to the reflex of extending the leg at the knee. This is similar to the reaction of someone who touches a hot stove and instinctually pulls his or her hand away. Even humans, with our great capacity to learn, still exhibit a variety of innate behaviors.

Kinesis and Taxis

Another activity or movement of innate behavior is kinesis, or the undirected movement in response to a stimulus. Orthokinesis is the increased or decreased speed of movement of an organism in response to a stimulus. Woodlice, for example, increase their speed of movement when exposed to high or low temperatures. This movement, although random, increases the probability that the insect spends less time in the unfavorable environment. Another example is klinokinesis, an increase in turning behaviors. It is exhibited by bacteria such as *E. coli* which, in association with orthokinesis, helps the organisms randomly find a more hospitable environment.

A similar, but more directed version of kinesis is taxis: the directed movement towards or away from a stimulus. This movement can be in response to light (phototaxis), chemical signals (chemotaxis), or gravity (geotaxis) and can be directed toward (positive) or away (negative) from the source of the stimulus. An example of a positive chemotaxis is exhibited by the unicellular protozoan *Tetrahymena thermophila*. This organism swims using its cilia, at times moving in a straight line, and at other times making turns. The attracting chemotactic agent alters the frequency of turning as the organism moves directly toward the source, following the increasing concentration gradient.

Fixed Action Patterns

A fixed action pattern is a series of movements elicited by a stimulus such that even when the stimulus is removed, the pattern goes on to completion. An example of such a behavior occurs in the three-spined stickleback, a small freshwater fish (Figure **53.3.1**). Males of this species develop a red belly during breeding season and show instinctual aggressiveness to other males during this time. In laboratory experiments, researchers exposed such fish to objects that in no way resemble a fish in their shape, but which

were painted red on their lower halves. The male sticklebacks responded aggressively to the objects just as if they were real male sticklebacks.

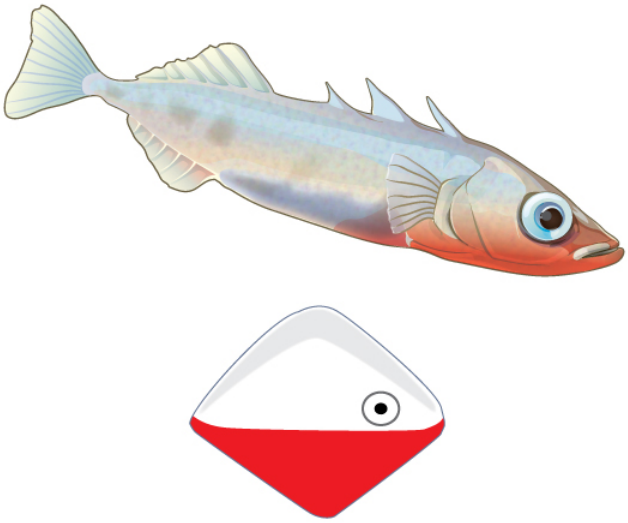


Figure **53.3.1**: Male three-spined stickleback fish exhibit a fixed action pattern. During mating season, the males, which develop a bright red belly, react strongly to red-bottomed objects that in no way resemble fish.

Migration

Migration is the long-range seasonal movement of animals. It is an evolved, adapted response to variation in resource availability, and it is a common phenomenon found in all major groups of animals. Birds fly south for the winter to get to warmer climates with sufficient food, and salmon migrate to their spawning grounds. The popular 2005 documentary *March of the Penguins* followed the 62-mile migration of emperor penguins through Antarctica to bring food back to their breeding site and to their young. Wildebeests (Figure **53.3.2**) migrate over 1800 miles each year in search of new grasslands.



Figure **53.3.2**: Wildebeests migrate in a clockwise fashion over 1800 miles each year in search of rain-ripened grass. (credit: Eric Inafuku)

Although migration is thought of as innate behavior, only some migrating species always migrate (obligate migration). Animals that exhibit facultative migration can choose to migrate or not. Additionally, in some animals, only a portion of the population

migrates, whereas the rest does not migrate (incomplete migration). For example, owls that live in the tundra may migrate in years when their food source, small rodents, is relatively scarce, but not migrate during the years when rodents are plentiful.

Foraging

Foraging is the act of searching for and exploiting food resources. Feeding behaviors that maximize energy gain and minimize energy expenditure are called optimal foraging behaviors, and these are favored by natural section. The painted stork, for example, uses its long beak to search the bottom of a freshwater marshland for crabs and other food (Figure **53.3.3**).



Figure **53.3.3**: The painted stork uses its long beak to forage. (credit: J.M. Garg)

Innate Behaviors: Living in Groups

Not all animals live in groups, but even those that live relatively solitary lives, with the exception of those that can reproduce asexually, must mate. Mating usually involves one animal signaling another so as to communicate the desire to mate. There are several types of energy-intensive behaviors or displays associated with mating, called mating rituals. Other behaviors found in populations that live in groups are described in terms of which animal benefits from the behavior. In selfish behavior, only the animal in question benefits; in altruistic behavior, one animal's actions benefit another animal; cooperative behavior describes when both animals benefit. All of these behaviors involve some sort of communication between population members.

Communication within a Species

Animals communicate with each other using stimuli known as signals. An example of this is seen in the three-spined stickleback, where the visual signal of a red region in the lower half of a fish signals males to become aggressive and signals females to mate. Other signals are chemical (pheromones), aural (sound), visual (courtship and aggressive displays), or tactile (touch). These types of communication may be instinctual or learned or a combination of both. These are not the same as the communication we associate with language, which has been observed only in humans and perhaps in some species of primates and cetaceans.

A pheromone is a secreted chemical signal used to obtain a response from another individual of the same species. The purpose of pheromones is to elicit a specific behavior from the receiving individual. Pheromones are especially common among social insects, but they are used by many species to attract the opposite sex, to sound alarms, to mark food trails, and to elicit other, more complex behaviors. Even humans are thought to respond to certain pheromones called axillary steroids. These chemicals influence human perception of other people, and in one study were responsible for a group of women synchronizing their menstrual cycles. The role of pheromones in human-to-human communication is still somewhat controversial and continues to be researched.

Songs are an example of an aural signal, one that needs to be heard by the recipient. Perhaps the best known of these are songs of birds, which identify the species and are used to attract mates. Other well-known songs are those of whales, which are of such low frequency that they can travel long distances underwater. Dolphins communicate with each other using a wide variety of vocalizations. Male crickets make chirping sounds using a specialized organ to attract a mate, repel other males, and to announce a successful mating.

Courtship displays are a series of ritualized visual behaviors (signals) designed to attract and convince a member of the opposite sex to mate. These displays are ubiquitous in the animal kingdom. Often these displays involve a series of steps, including an initial display by one member followed by a response from the other. If at any point, the display is performed incorrectly or a proper response is not given, the mating ritual is abandoned and the mating attempt will be unsuccessful. The mating display of the common stork is shown in Figure **53.3.4**.

Aggressive displays are also common in the animal kingdom. An example is when a dog bares its teeth when it wants another dog to back down. Presumably, these displays communicate not only the willingness of the animal to fight, but also its fighting ability. Although these displays do signal aggression on the part of the sender, it is thought that these displays are actually a mechanism to reduce the amount of actual fighting that occurs between members of the same species: they allow individuals to assess the fighting ability of their opponent and thus decide whether it is "worth the fight." The testing of certain hypotheses using game theory has led to the conclusion that some of these displays may overstate an animal's actual fighting ability and are used to "bluff" the opponent. This type of interaction, even if "dishonest," would be favored by natural selection if it is successful more times than not.

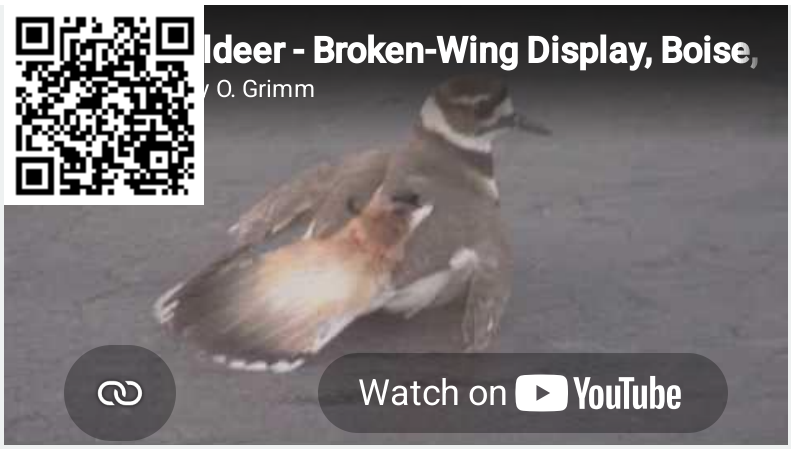


Figure **53.3.4**: This stork's courtship display is designed to attract potential mates. (credit: Linda "jinterwas"/Flickr)

Distraction displays are seen in birds and some fish. They are designed to attract a predator away from the nest that contains their young. This is an example of an altruistic behavior: it benefits the young more than the individual performing the display, which is putting itself at risk by doing so.

Many animals, especially primates, communicate with other members in the group through touch. Activities such as grooming, touching the shoulder or root of the tail, embracing, lip contact, and greeting ceremonies have all been observed in the Indian langur, an Old World monkey. Similar behaviors are found in other primates, especially in the great apes.

Link to Learning



The killdeer bird distracts predators from its eggs by faking a broken wing display in this video taken in Boise, Idaho.

Altruistic Behaviors

Behaviors that lower the fitness of the individual but increase the fitness of another individual are termed altruistic. Examples of such behaviors are seen widely across the animal kingdom. Social insects such as worker bees have no ability to reproduce, yet they maintain the queen so she can populate the hive with her offspring. Meerkats keep a sentry standing guard to warn the rest of the colony about intruders, even though the sentry is putting itself at risk. Wolves and wild dogs bring meat to pack members not present during a hunt. Lemurs take care of infants unrelated to them. Although on the surface, these behaviors appear to be altruistic, it may not be so simple.

There has been much discussion over why altruistic behaviors exist. Do these behaviors lead to overall evolutionary advantages for their species? Do they help the altruistic individual pass on its own genes? And what about such activities between unrelated individuals? One explanation for altruistic-type behaviors is found in the genetics of natural selection. In the 1976 book, *The Selfish Gene*, scientist Richard Dawkins attempted to explain many seemingly altruistic behaviors from the viewpoint of the gene itself. Although a gene obviously cannot be selfish in the human sense, it may appear that way if the sacrifice of an individual benefits related individuals that share genes that are identical by descent (present in relatives because of common lineage). Mammal parents make this sacrifice to take care of their offspring. Emperor penguins migrate miles in harsh conditions to bring food back for their young. Selfish gene theory has been controversial over the years and is still discussed among scientists in related fields.

Even less-related individuals, those with less genetic identity than that shared by parent and offspring, benefit from seemingly altruistic behavior. The activities of social insects such as bees, wasps, ants, and termites are good examples. Sterile workers in these societies take care of the queen because they are closely related to it, and as the queen has offspring, she is passing on genes from the workers indirectly. Thus, it is of fitness benefit for the worker to maintain the queen without having any direct chance of passing on its genes due to its sterility. The lowering of individual fitness to enhance the reproductive fitness of a relative and thus one's inclusive fitness evolves through kin selection. This phenomenon can explain many superficially altruistic behaviors seen in animals. However, these behaviors may not be truly defined as altruism in these cases because the actor is actually increasing its own fitness either directly (through its own offspring) or indirectly (through the inclusive fitness it gains through relatives that share genes with it).

Unrelated individuals may also act altruistically to each other, and this seems to defy the "selfish gene" explanation. An example of this observed in many monkey species where a monkey will present its back to an unrelated monkey to have that individual pick the parasites from its fur. After a certain amount of time, the roles are reversed and the first monkey now grooms the second monkey. Thus, there is reciprocity in the behavior. Both benefit from the interaction and their fitness is raised more than if neither cooperated nor if one cooperated and the other did not cooperate. This behavior is still not necessarily altruism, as the "giving" behavior of the actor is based on the expectation that it will be the "receiver" of the behavior in the future, termed reciprocal altruism. Reciprocal altruism requires that individuals repeatedly encounter each other, often the result of living in the same social group, and that cheaters (those that never "give back") are punished.

Evolutionary game theory, a modification of classical game theory in mathematics, has shown that many of these so-called "altruistic behaviors" are not altruistic at all. The definition of "pure" altruism, based on human behavior, is an action that benefits another without any direct benefit to oneself. Most of the behaviors previously described do not seem to satisfy this definition, and game theorists are good at finding "selfish" components in them. Others have argued that the terms "selfish" and "altruistic" should be dropped completely when discussing animal behavior, as they describe human behavior and may not be directly applicable to instinctual animal activity. What is clear, though, is that heritable behaviors that improve the chances of passing on one's genes or a portion of one's genes are favored by natural selection and will be retained in future generations as long as those behaviors convey a fitness advantage. These instinctual behaviors may then be applied, in special circumstances, to other species, as long as it doesn't lower the animal's fitness.

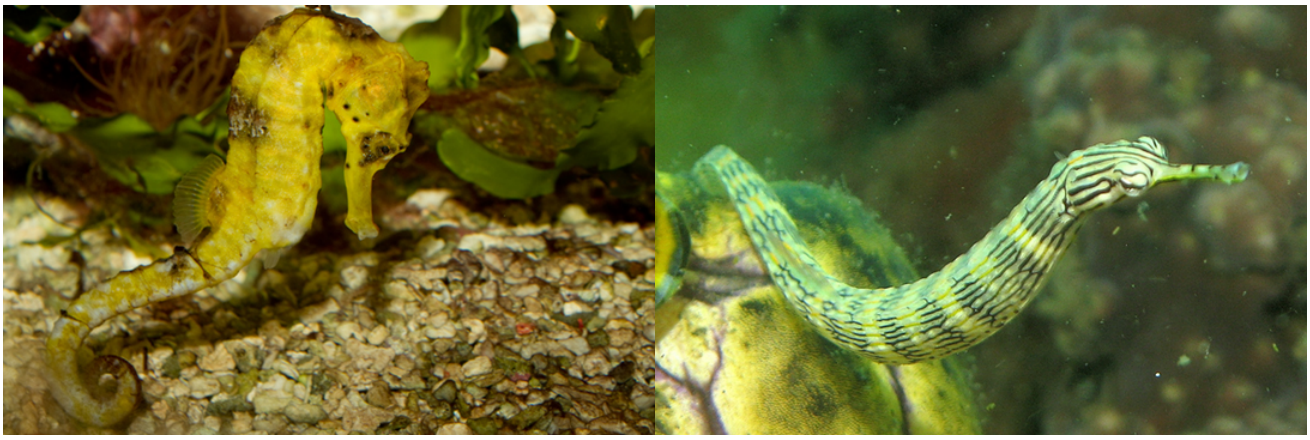
Finding Sex Partners

Not all animals reproduce sexually, but many that do have the same challenge: they need to find a suitable mate and often have to compete with other individuals to obtain one. Significant energy is spent in the process of locating, attracting, and mating with the sex partner. Two types of selection occur during this process and can lead to traits that are important to reproduction called secondary sexual characteristics: intersexual selection, the choosing of a mate where individuals of one sex choose mates of the other sex, and intrasexual selection, the competition for mates between species members of the same sex. Intersexual selection is often complex because choosing a mate may be based on a variety of visual, aural, tactile, and chemical cues. An example of intersexual selection is when female peacocks choose to mate with the male with the brightest plumage. This type of selection often leads to traits in the chosen sex that do not enhance survival, but are those traits most attractive to the opposite sex (often at the expense of survival). Intrasexual selection involves mating displays and aggressive mating rituals such as rams butting heads—the winner of these battles is the one that is able to mate. Many of these rituals use up considerable energy but result in the selection of the healthiest, strongest, and/or most dominant individuals for mating. Three general mating systems, all involving innate as opposed to learned behaviors, are seen in animal populations: monogamous, polygynous, and polyandrous.

In monogamous systems, one male and one female are paired for at least one breeding season. In some animals, such as the gray wolf, these associations can last much longer, even a lifetime. Several explanations have been proposed for this type of mating system. The "mate-guarding hypothesis" states that males stay with the female to prevent other males from mating with her. This behavior is advantageous in such situations where mates are scarce and difficult to find. Another explanation is the "male-assistance hypothesis," where males that remain with a female to help guard and rear their young will have more and healthier offspring. Monogamy is observed in many bird populations where, in addition to the parental care from the female, the male is also a major provider of parental care for the chicks. A third explanation for the evolutionary advantages of monogamy is the "female-enforcement hypothesis." In this scenario, the female ensures that the male does not have other offspring that might compete with her own, so she actively interferes with the male's signaling to attract other mates.

Polygynous mating refers to one male mating with multiple females. In these situations, the female must be responsible for most of the parental care as the single male is not capable of providing care to that many offspring. In resourced-based polygyny, males compete for territories with the best resources, and then mate with females that enter the territory, drawn to its resource richness. The female benefits by mating with a dominant, genetically fit male; however, it is at the cost of having no male help in caring for the offspring. An example is seen in the yellow-rumped honeyguide, a bird whose males defend beehives because the females feed on their wax. As the females approach, the male defending the nest will mate with them. Harem mating structures are a type of polygynous system where certain males dominate mating while controlling a territory with resources. Elephant seals, where the alpha male dominates the mating within the group are an example. A third type of polygyny is a lek system. Here there is a communal courting area where several males perform elaborate displays for females, and the females choose their mate from this group. This behavior is observed in several bird species including the sage grouse and the prairie chicken.

In polyandrous mating systems, one female mates with many males. These types of systems are much rarer than monogamous and polygynous mating systems. In pipefishes and seahorses, males receive the eggs from the female, fertilize them, protect them within a pouch, and give birth to the offspring (Figure **53.3.5**). Therefore, the female is able to provide eggs to several males without the burden of carrying the fertilized eggs.



a b

Figure 53.3.5: Polyandrous mating, in which one female mates with many males, occurs in the (a) seahorse and the (b) pipefish. (credit a: modification of work by Brian Gratwicke; credit b: modification of work by Stephen Childs)

Simple Learned Behaviors

The majority of the behaviors previously discussed were innate or at least have an innate component (variations on the innate behaviors may be learned). They are inherited and the behaviors do not change in response to signals from the environment. Conversely, learned behaviors, even though they may have instinctive components, allow an organism to adapt to changes in the environment and are modified by previous experiences. Simple learned behaviors include habituation and imprinting—both are important to the maturation process of young animals.

Habituation

Habituation is a simple form of learning in which an animal stops responding to a stimulus after a period of repeated exposure. This is a form of non-associative learning, as the stimulus is not associated with any punishment or reward. Prairie dogs typically sound an alarm call when threatened by a predator, but they become habituated to the sound of human footsteps when no harm is associated with this sound, therefore, they no longer respond to them with an alarm call. In this example, habituation is specific to the sound of human footsteps, as the animals still respond to the sounds of potential predators.

Imprinting

Imprinting is a type of learning that occurs at a particular age or a life stage that is rapid and independent of the species involved. Hatchling ducks recognize the first adult they see, their mother, and make a bond with her. A familiar sight is ducklings walking or swimming after their mothers (Figure **53.3.6**). This is another type of non-associative learning, but is very important in the maturation process of these animals as it encourages them to stay near their mother so they will be protected, greatly increasing their chances of survival. However, if newborn ducks see a human before they see their mother, they will imprint on the human and follow it in just the same manner as they would follow their real mother.



Figure **53.3.6**: The attachment of ducklings to their mother is an example of imprinting. (credit: modification of work by Mark Harkin)

Link to Learning



The International Crane Foundation has helped raise the world's population of whooping cranes from 21 individuals to about 600. Imprinting hatchlings has been a key to success: biologists wear full crane costumes so the birds never "see" humans. Watch this video to learn more.

Conditioned Behavior

Conditioned behaviors are types of associative learning, where a stimulus becomes associated with a consequence. During operant conditioning, the behavioral response is modified by its consequences, with regards to its form, strength, or frequency.

Classical Conditioning

In classical conditioning, a response called the conditioned response is associated with a stimulus that it had previously not been associated with, the conditioned stimulus. The response to the original, unconditioned stimulus is called the unconditioned response. The most cited example of classical conditioning is Ivan Pavlov's experiments with dogs (Figure **53.3.7**). In Pavlov's experiments, the unconditioned response was the salivation of dogs in response to the unconditioned stimulus of seeing or smelling their food. The conditioning stimulus that researchers associated with the unconditioned response was the ringing of a bell. During conditioning, every time the animal was given food, the bell was rung. This was repeated during several trials. After some time, the dog learned to associate the ringing of the bell with food and to respond by salivating. After the conditioning period was finished, the dog would respond by salivating when the bell was rung, even when the unconditioned stimulus, the food, was absent. Thus,

the ringing of the bell became the conditioned stimulus and the salivation became the conditioned response. Although it is thought by some scientists that the unconditioned and conditioned responses are identical, even Pavlov discovered that the saliva in the conditioned dogs had characteristic differences when compared to the unconditioned dog.

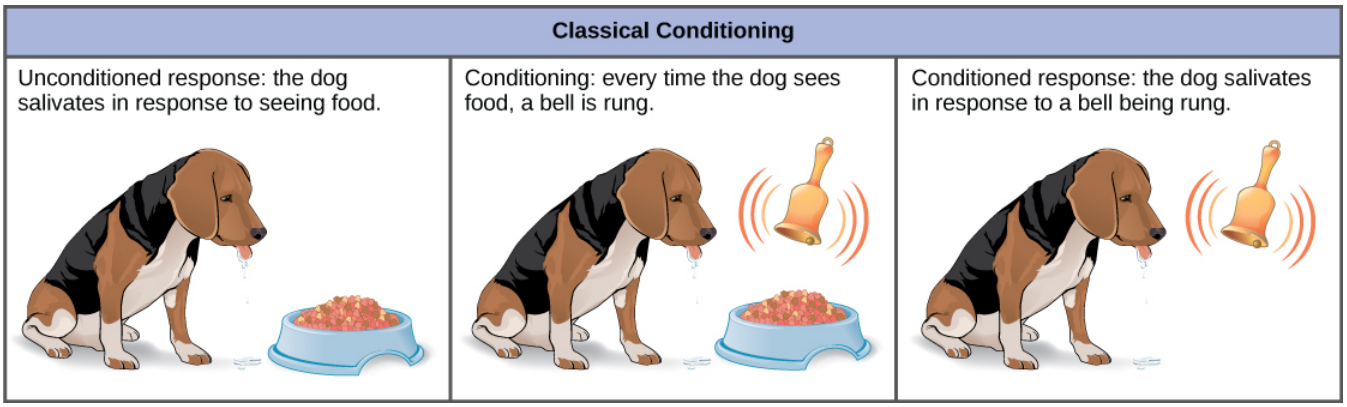


Figure **53.3.7**: In the classic Pavlovian response, the dog becomes conditioned to associate the ringing of the bell with food.

It had been thought by some scientists that this type of conditioning required multiple exposures to the paired stimulus and response, but it is now known that this is not necessary in all cases, and that some conditioning can be learned in a single pairing experiment. Classical conditioning is a major tenet of behaviorism, a branch of psychological philosophy that proposes that all actions, thoughts, and emotions of living things are behaviors that can be treated by behavior modification and changes in the environment.

Operant Conditioning

In operant conditioning, the conditioned behavior is gradually modified by its consequences as the animal responds to the stimulus. A major proponent of such conditioning was psychologist B.F. Skinner, the inventor of the Skinner box. Skinner put rats in his boxes that contained a lever that would dispense food to the rat when depressed. While initially the rat would push the lever a few times by accident, it eventually associated pushing the lever with getting the food. This type of learning is an example of operant conditioning. Operant learning is the basis of most animal training. The conditioned behavior is continually modified by positive or negative reinforcement, often a reward such as food or some type of punishment, respectively. In this way, the animal is conditioned to associate a type of behavior with the punishment or reward, and, over time, can be induced to perform behaviors that they would not have done in the wild, such as the “tricks” dolphins perform at marine amusement park shows (Figure **53.3.8**).



Figure **53.3.8**: The training of dolphins by rewarding them with food is an example of positive reinforcement operant conditioning. (credit: Roland Tanglao)

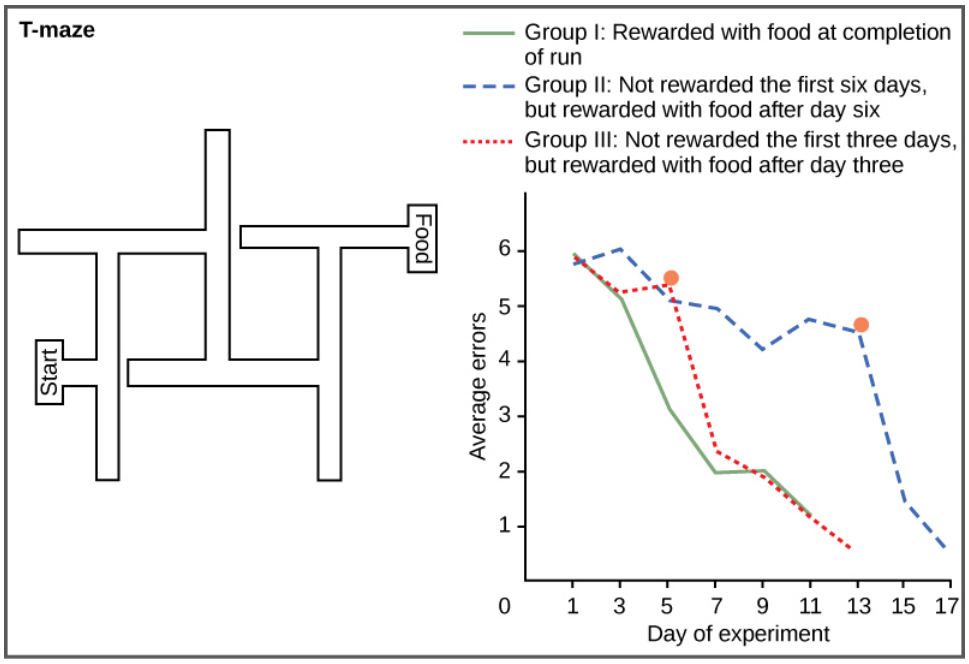
Cognitive Learning

Classical and operant conditioning are inefficient ways for humans and other intelligent animals to learn. Some primates, including humans, are able to learn by imitating the behavior of others and by taking instructions. The development of complex language by humans has made cognitive learning, the manipulation of information using the mind, the most prominent method of human

learning. In fact, that is how students are learning right now by reading this book. As students read, they can make mental images of objects or organisms and imagine changes to them, or behaviors by them, and anticipate the consequences. In addition to visual processing, cognitive learning is also enhanced by remembering past experiences, touching physical objects, hearing sounds, tasting food, and a variety of other sensory-based inputs. Cognitive learning is so powerful that it can be used to understand conditioning in detail. In the reverse scenario, conditioning cannot help someone learn about cognition.

Classic work on cognitive learning was done by Wolfgang Köhler with chimpanzees. He demonstrated that these animals were capable of abstract thought by showing that they could learn how to solve a puzzle. When a banana was hung in their cage too high for them to reach, and several boxes were placed randomly on the floor, some of the chimps were able to stack the boxes one on top of the other, climb on top of them, and get the banana. This implies that they could visualize the result of stacking the boxes even before they had performed the action. This type of learning is much more powerful and versatile than conditioning.

Cognitive learning is not limited to primates, although they are the most efficient in using it. Maze running experiments done with rats by H.C. Blodgett in the 1920s were the first to show cognitive skills in a simple mammal. The motivation for the animals to work their way through the maze was a piece of food at its end. In these studies, the animals in Group I were run in one trial per day and had food available to them each day on completion of the run (Figure **53.3.9**). Group II rats were not fed in the maze for the first six days and then subsequent runs were done with food for several days after. Group III rats had food available on the third day and every day thereafter. The results were that the control rats, Group I, learned quickly, and figured out how to run the maze in seven days. Group III did not learn much during the three days without food, but rapidly caught up to the control group when given the food reward. Group II learned very slowly for the six days with no reward to motivate them, and they did not begin to catch up to the control group until the day food was given, and then it took two days longer to learn the maze.



Redrawn after H. C. Blodgett, The effect of the introduction of reward upon the maze performance of rats. Univ. Calif. Publ. Psychol., 1929, 4, No. 8, pages 117 and 120.

Figure **53.3.9**: Group I (the green solid line) found food at the end of each trial, group II (the blue dashed line) did not find food for the first 6 days, and group III (the red dotted line) did not find food during runs on the first three days. Notice that rats given food earlier learned faster and eventually caught up to the control group. The orange dots on the group II and III lines show the days when food rewards were added to the mazes.

It may not be immediately obvious that this type of learning is different than conditioning. Although one might be tempted to believe that the rats simply learned how to find their way through a conditioned series of right and left turns, E.C. Tolman proved a decade later that the rats were making a representation of the maze in their minds, which he called a “cognitive map.” This was an early demonstration of the power of cognitive learning and how these abilities were not just limited to humans.

Sociobiology

Sociobiology is an interdisciplinary science originally popularized by social insect researcher E.O. Wilson in the 1970s. Wilson defined the science as "the extension of population biology and evolutionary theory to social organization."[1] The main thrust of sociobiology is that animal and human behavior, including aggressiveness and other social interactions, can be explained almost solely in terms of genetics and natural selection. This science is controversial; noted scientist such as the late Stephen Jay Gould criticized the approach for ignoring the environmental effects on behavior. This is another example of the "nature versus nurture" debate of the role of genetics versus the role of environment in determining an organism's characteristics.

Sociobiology also links genes with behaviors and has been associated with "biological determinism," the belief that all behaviors are hardwired into our genes. No one disputes that certain behaviors can be inherited and that natural selection plays a role retaining them. It is the application of such principles to human behavior that sparks this controversy, which remains active today.

Summary

Behaviors are responses to stimuli. They can either be instinctual/innate behaviors, which are not influenced by the environment, or learned behaviors, which are influenced by environmental changes. Instinctual behaviors include mating systems and methods of communication. Learned behaviors include imprinting and habituation, conditioning, and, most powerfully, cognitive learning. Although the connection between behavior, genetics, and evolution is well established, the explanation of human behavior as entirely genetic is controversial.

Footnotes

1. 1 Edward O. Wilson. *On Human Nature* (1978; repr., Cambridge: Harvard University Press, 2004), xx.

Glossary

aggressive display
: visual display by a species member to discourage other members of the same species or different species

behavior
: change in an organism's activities in response to a stimulus

behavioral biology
: study of the biology and evolution of behavior

classical conditioning
: association of a specific stimulus and response through conditioning

cognitive learning
: knowledge and skills acquired by the manipulation of information in the mind

conditioned behavior
: behavior that becomes associated with a specific stimulus through conditioning

courtship display
: visual display used to attract a mate

distraction display
: visual display used to distract predators away from a nesting site

ethology
: biological study of animal behavior

fixed action pattern
: series of instinctual behaviors that, once initiated, always goes to completion regardless of changes in the environment

foraging
behaviors species use to find food

habituation
ability of a species to ignore repeated stimuli that have no consequence

imprinting
identification of parents by newborns as the first organism they see after birth

innate behavior
instinctual behavior that is not altered by changes in the environment

intersexual selection
selection of a desirable mate of the opposite sex

intrasexual selection
competition between members of the same sex for a mate

kin selection
sacrificing one's own life so that one's genes will be passed on to future generations by relatives

kinesis
undirected movement of an organism in response to a stimulus

learned behavior
behavior that responds to changes in the environment

migration
long-range seasonal movement of animal species

monogamy
mating system whereby one male and one female remain coupled for at least one mating season

operant conditioning
learned behaviors in response to positive and/or negative reinforcement

polyandry
mating system where one female mates with many males

polygyny
mating system where one male mates with many females

reflex action
action in response to direct physical stimulation of a nerve

signal
method of communication between animals including those obtained by the senses of smell, hearing, sight, or touch

taxis
directed movement in response to a stimulus

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53.3.1: Innate Behavior

Behavior is action that alters the relationship between an organism and its environment. Behavior may occur as a result of

- an external stimulus (e.g., sight of a predator)
- internal stimulus (e.g., hunger)
- or, more often, a mixture of the two (e.g., mating behavior)

It is often useful to distinguish between

- **innate behavior** = behavior determined by the "hard-wiring" of the nervous system. It is usually inflexible, a given stimulus triggering a given response. A salamander raised away from water until long after its siblings begin swimming successfully will swim every bit as well as they the very first time it is placed in the water. Clearly this rather elaborate response is "built in" in the species and not something that must be acquired by practice.
- **learned behavior** = behavior that is more or less permanently altered as a result of the experience of the individual organism (e.g., learning to play baseball well).
- However, careful analysis often reveals that any particular behavior is a combination of innate and learned components.

Examples of innate behavior:

- **taxes**
- **reflexes**
- **instincts**

Taxes

Some organisms respond to a stimulus by automatically moving directly toward or away from or at some defined angle to it. These responses are called taxes. They are similar to tropisms in plants except that actual locomotion of the entire organism is involved. Link to a detailed discussion.

Reflexes

The Withdrawal Reflex

When you touch a hot object, you quickly pull you hand away using the withdrawal reflex.

These are the steps:

- The stimulus is detected by **receptors** in the skin.
- These initiate nerve impulses in **sensory neurons** leading from the receptors to the spinal cord.
- The impulses travel into the spinal cord where the sensory nerve terminals synapse with **interneurons**.
    - Some of these synapse with **motor neurons** that travel out from the spinal cord entering mixed nerves that lead to the flexors that withdraw your hand.
    - Others synapse with inhibitory interneurons that suppress any motor output to extensors whose contraction would interfere with the withdrawal reflex.

The Stretch Reflex

The **stretch reflex** is examined (with a diagram) on a separate page. Link to it.

Instincts

Instincts are complex behavior patterns which, like reflexes, are inborn, rather inflexible, and valuable at adapting the animal to its environment. They differ from reflexes in their complexity. The entire body participates in instinctive behavior, and an elaborate series of actions may be involved.



Figure 15.11.1.1 Instincts in animals and birds

The scratching behavior of a dog and a European bullfinch, shown here, is part of their genetic heritage. The widespread behavior of scratching with a hind limb crossed over a forelimb in common to most birds, reptiles, and mammals. (Picture courtesy of Rudolf Freund and Scientific American, 1958.) So instincts are inherited just as the structure of tissues and organs is. Another example.

- The African peach-faced lovebird carries nesting materials to the nesting site by tucking them in its feathers.
- Its close relative, the Fischer's lovebird, uses its beak to transport nesting materials.
- The two species can hybridize. When they do so, the offspring succeed only in carrying nesting material in their beaks. Nevertheless, they invariably go through the motions of trying to tuck the materials in their feathers first.

Foraging Behavior

Foraging for food is a crucial behavior for animals. Like all behavior, it requires the interaction of many components. Nonetheless, it turns out that in some animals, at least, foraging behavior can be altered by a single gene.

Drosophila melanogaster

The discovery of the genetic control of foraging in Drosophila began with the observations of Marla Sokolowski when she was an undergraduate biology student at the University of Toronto.

She noticed that Drosophila larvae, feeding in her culture vessels, displayed one of two distinct feeding patterns:

- "**rovers**" who moved rapidly over the surface of the culture medium
- "**sitters** who fed at a much more leisurely pace

She went on to find that this "bimodal" pattern of behavior

- continued when the larvae became adults
- was present in populations of wild fruit flies, not just in her laboratory colonies

After further years of research, she has shown that the behavior is under the control of a single gene, named *for* ("foraging"). Two alleles are present, at almost equal frequencies, that is, *for* is polymorphic.

- for^R, which is dominant
- for^S, the recessive
- About 70% of natural populations are rovers being either homozygous for for^R or heterozygous (for^R/for^S).
- Sitters are homozygous for for^S

Both alleles encode a **PKG**, a protein kinase (an enzyme that attaches phosphate groups to target proteins) that is activated by the "second messenger" cyclic GMP (cGMP). The enzyme encoded by the for^R allele is more active than that encoded by for^S. She and her colleagues have succeeded in inserting for^R DNA into sitters who promptly become rovers.

Why this polymorphism? Why should alleles for two such different behaviors be maintained at such high frequency in the population?

One possible answer: it permits the population to thrive under varying food conditions:

- sitters are favored when food is abundant
- rovers are favored when competition for food is strong, such as in crowded cultures

Honeybees

Honeybees have their version of the *for* gene, called *Amfor* ("*Apis mellifera for*"). It, too, encodes a cGMP-dependent protein kinase (**PKG**). When worker bees first hatch, they remain in the hive tending to various housekeeping chores, such as feeding the

larvae. But when they are 2–3 weeks old, they leave the hive and begin foraging for nectar and pollen. This change in behavior coincides with the increased expression of *Amfor*. When newly-hatched workers are treated with **cGMP**, the amount of PKG in their brains goes up and they quickly begin foraging instead of doing housekeeping.

Interaction of Internal and External Stimuli

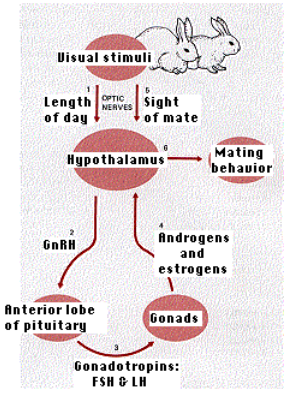


Figure 15.11.1.2 Mating rabbits

Instinctive behavior often depends on conditions in the internal environment. In many vertebrates courtship and mating behavior will not occur unless sex hormones (estrogens in females, androgens in males) are present in the blood. The target organ is a small region of the hypothalamus. When stimulated by sex hormones in its blood supply, the hypothalamus initiates the activities leading to mating. The level of sex hormones is, in turn, regulated by the activity of the anterior lobe of the pituitary gland.

The above figure outlines the interactions of external and internal stimuli that lead an animal, such as a rabbit, to see a sexual partner and mate with it.

Releasers of Instinctive Behavior

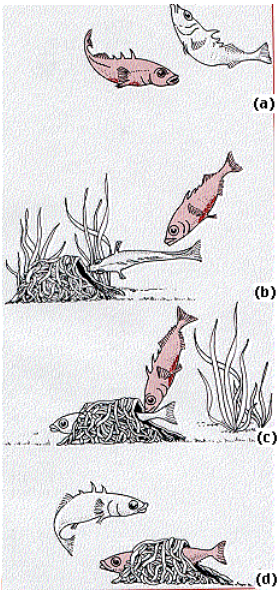


Figure 15.11.1.3 Breeding in a three-spined stickleback

Once the body is prepared for certain types of instinctive behavior, an external stimulus may be needed to initiate the response. N. Tinbergen (who shared the 1973 Nobel Prize with Konrad Lorenz and Karl von Frisch) showed that the stimulus need not necessarily be appropriate to be effective.

- During the breeding season, the female **three-spined stickleback** normally follows the red-bellied male (**a** in the figure) to the nest that he has prepared.
- He guides her into the nest (**b**) and then
- prods the base of her tail (**c**).

- She then lays eggs in the nest.
- After doing so, the male drives her from the nest, enters it himself, and fertilizes the eggs (**d**).
- Although this is the normal pattern, the female will follow almost any small red object to the nest, and once within the nest, neither the male nor any other red object need be present.
- Any object touching her near the base of her tail will cause her to release her eggs.

It is as though she were primed internally for each item of behavior and needed only one specific signal to release the behavior pattern. For this reason, signals that trigger instinctive acts are called **releasers**. Once a particular response is released, it usually runs to completion even though the stimulus has been removed. One or two prods at the base of her tail will release the entire sequence of muscular actions involved in liberating her eggs.

Chemical signals (e.g., pheromones) serve as important releasers for the social insects: ants, bees, and termites. Many of these animals emit several different pheromones which elicit, for example, alarm behavior, mating behavior, and foraging behavior in other members of their species.

The mammary glands of domestic rabbit mothers emit a pheromone that releases immediate nursing behavior by their babies (pups). A good thing, too, as mothers devote only 5–7 minutes a day to feeding their pups so they had better be quick about it.

The studies of Tinbergen and others have shown that animals can often be induced to respond to inappropriate releasers. For example, a male robin defending its territory will repeatedly attack a simple clump of red feathers instead of a stuffed robin that lacks the red breast of the males.

Although such behavior seems inappropriate to our eyes, it reveals a crucial feature of all animal behavior: animals **respond selectively** to certain aspects of the total sensory input they receive. Animals spend their lives bombarded by myriad sights, sounds, odors, etc. But their nervous system **filters** this mass of sensory data, and they respond only to those aspects that the evolutionary history of the species has proved to be significant for survival.

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53.4: Learning

Habituation

Habituation is a reduction in a previously-displayed response when no reward or punishment follows. If you make an unusual sound in the presence of the family dog, it will respond usually by turning its head toward the sound. If the stimulus is given repeatedly and nothing either pleasant or unpleasant happens to the dog, it will soon cease to respond. This lack of response is not a result of fatigue or sensory adaptation and is long-lasting; when fully habituated, the dog will not respond to the stimulus even though weeks or months have elapsed since it was last presented.

Sensitization

Sensitization is an **increase** in the response to an innocuous stimulus when that stimulus occurs after a punishing stimulus.

Sensitization in sea slugs

When the siphon of the sea slug **Aplysia** is gently touched, the animal withdraws its gill for a brief period. However, if preceded by an electrical shock to its **tail**, the same gentle touch to the siphon will elicit a longer period of withdrawal. The sensitization response to a single shock (blue bar) dies out after about an hour, and returns to baseline after a day (yellow). So it is an example of short-term memory.

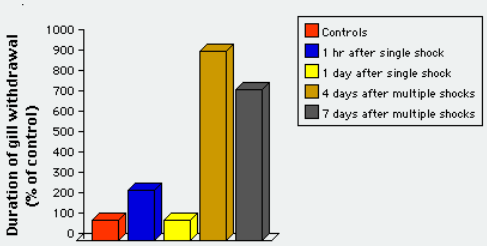


Figure 15.11.3.1 Sensitization in a sea slug

However, if the animal is sensitized with multiple shocks given over several days, its **subsequent** response to a gentle touch on the siphon is much larger and is retained longer (tan and gray bars). This is an example of long-term memory and requires protein synthesis. (These findings are the work of Eric R. Kandel, who was awarded a Nobel Prize in 2000.)

Imprinting

If newly-hatched geese are exposed to a moving object of reasonable size and emitting reasonable sounds, they will begin to follow it just as they would normally follow their mother. This is called **imprinting**. The time of exposure is quite critical. A few days after hatching, imprinting no longer occurs. Prior to this time, though, the results can be quite remarkable. A gosling imprinted to a moving box or clucking person will try to follow this object for the rest of its life. In fact, when the gosling reaches sexual maturity, it will make the imprinted object - rather than a member of its own species - the goal of its sexual drive.

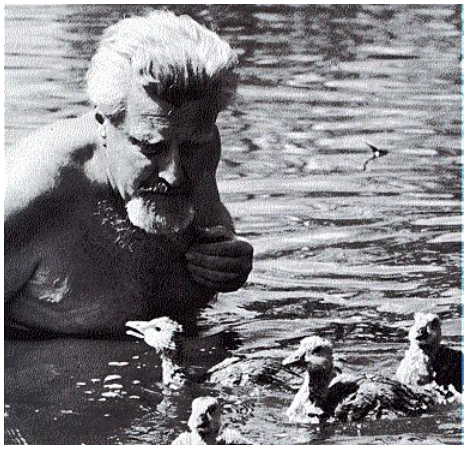


Figure 15.11.3.2 Konrad Lorenz and his imprinted goslings

Much of our knowledge of imprinting was learned from the research of Konrad Lorenz, shown here with some of his imprinted goslings. Lorenz shared a Nobel Prize in 1973 for his discoveries. (Photo by Tom McAvoy; courtesy of LIFE Magazine, ©1955, Time, Inc.)

Male **mice** become imprinted with the odor of littermates during the first three weeks of life. When they reach sexual maturity, they avoid mating with close relatives. The odor is controlled by the major histocompatibility complex (MHC).

The Conditioned Response (CR)

The conditioned response is probably the simplest form of learned behavior. It is a response that as a result of experience comes to be caused by a stimulus different from the one that originally triggered it. The Russian physiologist Ivan Pavlov found that placing meat powder in a dog's mouth would cause it to salivate.

The meat powder, an **unconditioned stimulus** (**US**), triggers a simple inborn reflex involving taste receptors, sensory neurons, networks of interneurons in the brain, and autonomic motor neurons running to the salivary glands thus producing an **unconditioned response** (**UR**).

Pavlov found that if he rang a bell every time he put the meat powder in the dog's mouth, the dog eventually salivated upon hearing the bell alone. This is the **conditioned response** (**CR**). The dog has learned to respond to a substitute stimulus, the **conditioned stimulus** (**CS**).

We assume that the physiological basis of the conditioned response is the transfer, by appropriate neurons, of nervous activity in the auditory areas of the brain to the motor neurons controlling salivation. This involves the development and/or strengthening of neural circuits, which - we may also assume - is characteristic of all forms of learning.

The conditioned response has proved to be an excellent tool for determining the sensory capabilities of other animals. For example, honeybees can be conditioned to seek food on a piece of blue cardboard. By offering other colors to a blue-conditioned bee, Karl von Frisch (who shared the 1973 Nobel Prize with Lorenz) found that honeybees can discriminate between yellow-green, blue-green, blue-violet, and ultraviolet.

Instrumental Conditioning

Pavlov's dogs were restrained and the response being conditioned (salivation) was innate. But the principles of conditioning can also be used to train animals to perform tasks that are not innate. In these cases, the animal is placed in a setting where it can move about and engage in different activities. The experimenter chooses to reward only one, e.g., turning to the left. By first rewarding (e.g., with a pellet of food) even the slightest movement to the left and then only more complete turns, a skilled experimenter can in about 2 minutes train a naive pigeon to make a complete turn. A little more work and the pigeon will pace out a figure eight.

In the example shown here, the pigeon - presented with two spots of light - pecks at the brighter and reaches down to pick up the grain of food that is its reward.

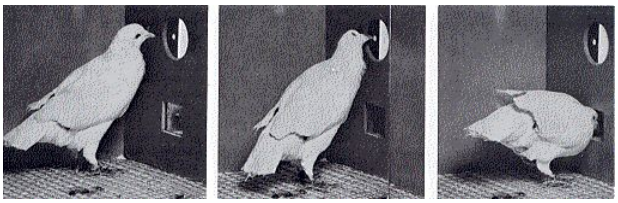


Figure 15.11.3.3 Instrumental conditioning on pigeons. (Photos courtesy of Roy DeCarava and **Scientific American**.)

Such training is known as **instrumental conditioning** or **operant conditioning**. The latter term was coined by B. F. Skinner, whose skill with the technique enabled him to train pigeons to play ping-pong and even a toy piano! It is also called **trial-and-error** learning because the animal is free to try various responses before finding the one that is rewarded.

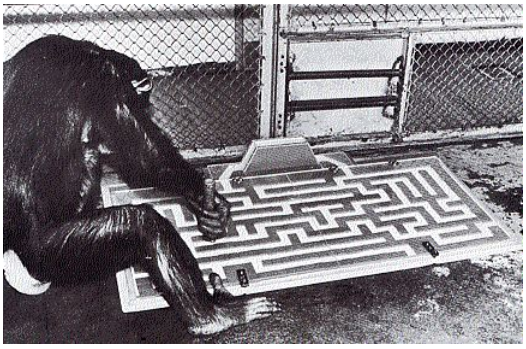


Figure 15.11.3.4 Chimpanzee solving a maze with a magnet

Maze problems are a form of instrumental conditioning in which the animal is faced with a sequence of alternatives.

In this photo (Courtesy of B. Rensch), Julia, a chimpanzee, uses a magnet to move an iron ring through a maze. Julia is able to solve mazes like this on her first attempt most (86%) of the time and sometimes faster than biology students can!

Concepts

Although most animals solve mazes and other problems by trial and error, Julia (and biology students) usually make only one or two random attempts at solving a problem and then, all of a sudden, "get it". They have made an abstract generalization about the specific problem; that is, have formed a **concept**. **Oddity problems** are an example. This young rhesus monkey has learned that food will be found - not under any particular object - but under whichever object is different from the others.

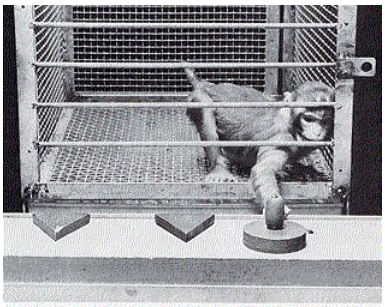


Figure 15.11.3.5 Oddity problems (Photo courtesy of H. F. Harlow, University of Wisconsin Primate Laboratory.)

In monkeys (and probably humans as well), concept formation depends on activity in the prefrontal cortex of the brain. Recent research suggests that honeybees can also solve simple oddity problems!

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53.5: The Development of Behavior

Skills to Develop

- Compare innate and learned behavior
- Discuss how movement and migration behaviors are a result of natural selection
- Discuss the different ways members of a population communicate with each other
- Give examples of how species use energy for mating displays and other courtship behaviors
- Differentiate between various mating systems
- Describe different ways that species learn

Behavior is the change in activity of an organism in response to a stimulus. Behavioral biology is the study of the biological and evolutionary bases for such changes. The idea that behaviors evolved as a result of the pressures of natural selection is not new. Animal behavior has been studied for decades, by biologists in the science of ethology, by psychologists in the science of comparative psychology, and by scientists of many disciplines in the study of neurobiology. Although there is overlap between these disciplines, scientists in these behavioral fields take different approaches. Comparative psychology is an extension of work done in human and behavioral psychology. Ethology is an extension of genetics, evolution, anatomy, physiology, and other biological disciplines. Still, one cannot study behavioral biology without touching on both comparative psychology and ethology.

One goal of behavioral biology is to dissect out the innate behaviors, which have a strong genetic component and are largely independent of environmental influences, from the learned behaviors, which result from environmental conditioning. Innate behavior, or instinct, is important because there is no risk of an incorrect behavior being learned. They are “hard wired” into the system. On the other hand, learned behaviors, although riskier, are flexible, dynamic, and can be altered according to changes in the environment.

Innate Behaviors: Movement and Migration

Innate or instinctual behaviors rely on response to stimuli. The simplest example of this is a reflex action, an involuntary and rapid response to stimulus. To test the “knee-jerk” reflex, a doctor taps the patellar tendon below the kneecap with a rubber hammer. The stimulation of the nerves there leads to the reflex of extending the leg at the knee. This is similar to the reaction of someone who touches a hot stove and instinctually pulls his or her hand away. Even humans, with our great capacity to learn, still exhibit a variety of innate behaviors.

Kinesis and Taxis

Another activity or movement of innate behavior is kinesis, or the undirected movement in response to a stimulus. Orthokinesis is the increased or decreased speed of movement of an organism in response to a stimulus. Woodlice, for example, increase their speed of movement when exposed to high or low temperatures. This movement, although random, increases the probability that the insect spends less time in the unfavorable environment. Another example is klinokinesis, an increase in turning behaviors. It is exhibited by bacteria such as *E. coli* which, in association with orthokinesis, helps the organisms randomly find a more hospitable environment.

A similar, but more directed version of kinesis is taxis: the directed movement towards or away from a stimulus. This movement can be in response to light (phototaxis), chemical signals (chemotaxis), or gravity (geotaxis) and can be directed toward (positive) or away (negative) from the source of the stimulus. An example of a positive chemotaxis is exhibited by the unicellular protozoan *Tetrahymena thermophila*. This organism swims using its cilia, at times moving in a straight line, and at other times making turns. The attracting chemotactic agent alters the frequency of turning as the organism moves directly toward the source, following the increasing concentration gradient.

Fixed Action Patterns

A fixed action pattern is a series of movements elicited by a stimulus such that even when the stimulus is removed, the pattern goes on to completion. An example of such a behavior occurs in the three-spined stickleback, a small freshwater fish (Figure **53.5.1**). Males of this species develop a red belly during breeding season and show instinctual aggressiveness to other males during this time. In laboratory experiments, researchers exposed such fish to objects that in no way resemble a fish in their shape, but which

were painted red on their lower halves. The male sticklebacks responded aggressively to the objects just as if they were real male sticklebacks.

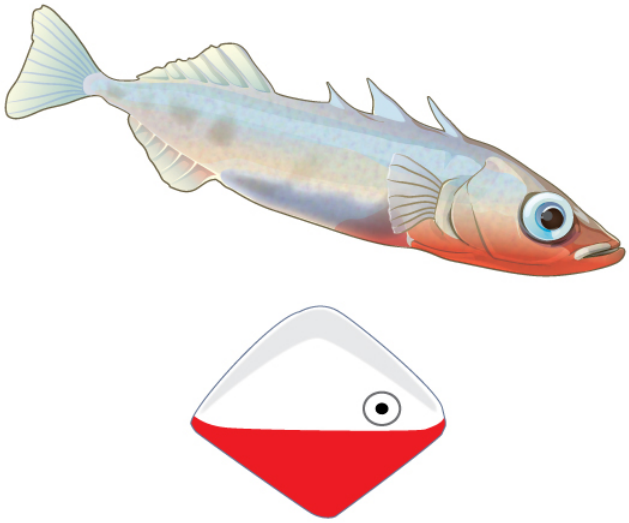


Figure **53.5.1**: Male three-spined stickleback fish exhibit a fixed action pattern. During mating season, the males, which develop a bright red belly, react strongly to red-bottomed objects that in no way resemble fish.

Migration

Migration is the long-range seasonal movement of animals. It is an evolved, adapted response to variation in resource availability, and it is a common phenomenon found in all major groups of animals. Birds fly south for the winter to get to warmer climates with sufficient food, and salmon migrate to their spawning grounds. The popular 2005 documentary *March of the Penguins* followed the 62-mile migration of emperor penguins through Antarctica to bring food back to their breeding site and to their young. Wildebeests (Figure **53.5.2**) migrate over 1800 miles each year in search of new grasslands.



Figure **53.5.2**: Wildebeests migrate in a clockwise fashion over 1800 miles each year in search of rain-ripened grass. (credit: Eric Inafuku)

Although migration is thought of as innate behavior, only some migrating species always migrate (obligate migration). Animals that exhibit facultative migration can choose to migrate or not. Additionally, in some animals, only a portion of the population

migrates, whereas the rest does not migrate (incomplete migration). For example, owls that live in the tundra may migrate in years when their food source, small rodents, is relatively scarce, but not migrate during the years when rodents are plentiful.

Foraging

Foraging is the act of searching for and exploiting food resources. Feeding behaviors that maximize energy gain and minimize energy expenditure are called optimal foraging behaviors, and these are favored by natural section. The painted stork, for example, uses its long beak to search the bottom of a freshwater marshland for crabs and other food (Figure **53.5.3**).



Figure **53.5.3**: The painted stork uses its long beak to forage. (credit: J.M. Garg)

Innate Behaviors: Living in Groups

Not all animals live in groups, but even those that live relatively solitary lives, with the exception of those that can reproduce asexually, must mate. Mating usually involves one animal signaling another so as to communicate the desire to mate. There are several types of energy-intensive behaviors or displays associated with mating, called mating rituals. Other behaviors found in populations that live in groups are described in terms of which animal benefits from the behavior. In selfish behavior, only the animal in question benefits; in altruistic behavior, one animal's actions benefit another animal; cooperative behavior describes when both animals benefit. All of these behaviors involve some sort of communication between population members.

Altruistic Behaviors

Behaviors that lower the fitness of the individual but increase the fitness of another individual are termed altruistic. Examples of such behaviors are seen widely across the animal kingdom. Social insects such as worker bees have no ability to reproduce, yet they maintain the queen so she can populate the hive with her offspring. Meerkats keep a sentry standing guard to warn the rest of the colony about intruders, even though the sentry is putting itself at risk. Wolves and wild dogs bring meat to pack members not present during a hunt. Lemurs take care of infants unrelated to them. Although on the surface, these behaviors appear to be altruistic, it may not be so simple.

There has been much discussion over why altruistic behaviors exist. Do these behaviors lead to overall evolutionary advantages for their species? Do they help the altruistic individual pass on its own genes? And what about such activities between unrelated individuals? One explanation for altruistic-type behaviors is found in the genetics of natural selection. In the 1976 book, *The Selfish Gene*, scientist Richard Dawkins attempted to explain many seemingly altruistic behaviors from the viewpoint of the gene itself. Although a gene obviously cannot be selfish in the human sense, it may appear that way if the sacrifice of an individual benefits related individuals that share genes that are identical by descent (present in relatives because of common lineage). Mammal parents

make this sacrifice to take care of their offspring. Emperor penguins migrate miles in harsh conditions to bring food back for their young. Selfish gene theory has been controversial over the years and is still discussed among scientists in related fields.

Even less-related individuals, those with less genetic identity than that shared by parent and offspring, benefit from seemingly altruistic behavior. The activities of social insects such as bees, wasps, ants, and termites are good examples. Sterile workers in these societies take care of the queen because they are closely related to it, and as the queen has offspring, she is passing on genes from the workers indirectly. Thus, it is of fitness benefit for the worker to maintain the queen without having any direct chance of passing on its genes due to its sterility. The lowering of individual fitness to enhance the reproductive fitness of a relative and thus one's inclusive fitness evolves through kin selection. This phenomenon can explain many superficially altruistic behaviors seen in animals. However, these behaviors may not be truly defined as altruism in these cases because the actor is actually increasing its own fitness either directly (through its own offspring) or indirectly (through the inclusive fitness it gains through relatives that share genes with it).

Unrelated individuals may also act altruistically to each other, and this seems to defy the "selfish gene" explanation. An example of this observed in many monkey species where a monkey will present its back to an unrelated monkey to have that individual pick the parasites from its fur. After a certain amount of time, the roles are reversed and the first monkey now grooms the second monkey. Thus, there is reciprocity in the behavior. Both benefit from the interaction and their fitness is raised more than if neither cooperated nor if one cooperated and the other did not cooperate. This behavior is still not necessarily altruism, as the "giving" behavior of the actor is based on the expectation that it will be the "receiver" of the behavior in the future, termed reciprocal altruism. Reciprocal altruism requires that individuals repeatedly encounter each other, often the result of living in the same social group, and that cheaters (those that never "give back") are punished.

Evolutionary game theory, a modification of classical game theory in mathematics, has shown that many of these so-called "altruistic behaviors" are not altruistic at all. The definition of "pure" altruism, based on human behavior, is an action that benefits another without any direct benefit to oneself. Most of the behaviors previously described do not seem to satisfy this definition, and game theorists are good at finding "selfish" components in them. Others have argued that the terms "selfish" and "altruistic" should be dropped completely when discussing animal behavior, as they describe human behavior and may not be directly applicable to instinctual animal activity. What is clear, though, is that heritable behaviors that improve the chances of passing on one's genes or a portion of one's genes are favored by natural selection and will be retained in future generations as long as those behaviors convey a fitness advantage. These instinctual behaviors may then be applied, in special circumstances, to other species, as long as it doesn't lower the animal's fitness.

Finding Sex Partners

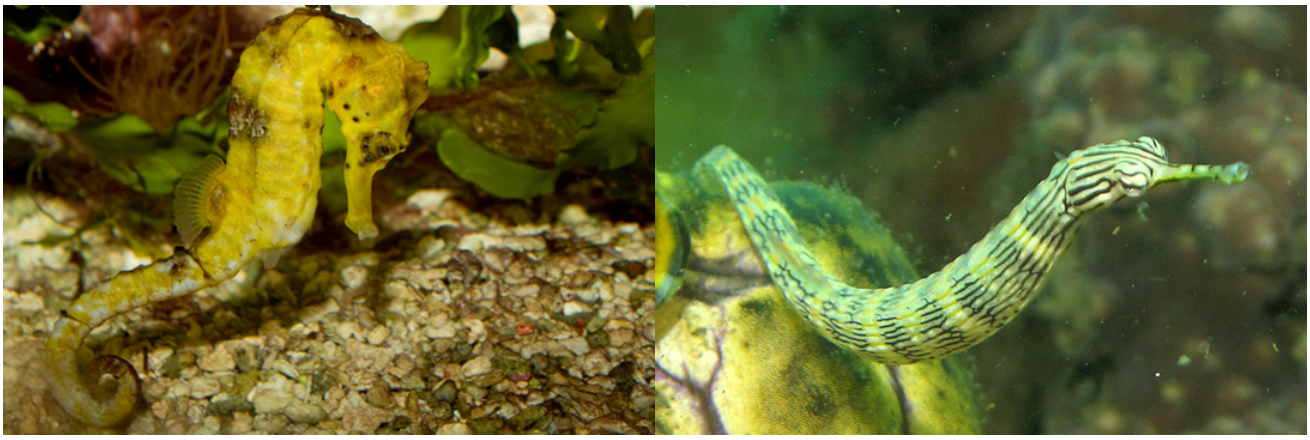
Not all animals reproduce sexually, but many that do have the same challenge: they need to find a suitable mate and often have to compete with other individuals to obtain one. Significant energy is spent in the process of locating, attracting, and mating with the sex partner. Two types of selection occur during this process and can lead to traits that are important to reproduction called secondary sexual characteristics: intersexual selection, the choosing of a mate where individuals of one sex choose mates of the other sex, and intrasexual selection, the competition for mates between species members of the same sex. Intersexual selection is often complex because choosing a mate may be based on a variety of visual, aural, tactile, and chemical cues. An example of intersexual selection is when female peacocks choose to mate with the male with the brightest plumage. This type of selection often leads to traits in the chosen sex that do not enhance survival, but are those traits most attractive to the opposite sex (often at the expense of survival). Intrasexual selection involves mating displays and aggressive mating rituals such as rams butting heads—the winner of these battles is the one that is able to mate. Many of these rituals use up considerable energy but result in the selection of the healthiest, strongest, and/or most dominant individuals for mating. Three general mating systems, all involving innate as opposed to learned behaviors, are seen in animal populations: monogamous, polygynous, and polyandrous.

In monogamous systems, one male and one female are paired for at least one breeding season. In some animals, such as the gray wolf, these associations can last much longer, even a lifetime. Several explanations have been proposed for this type of mating system. The "mate-guarding hypothesis" states that males stay with the female to prevent other males from mating with her. This behavior is advantageous in such situations where mates are scarce and difficult to find. Another explanation is the "male-assistance hypothesis," where males that remain with a female to help guard and rear their young will have more and healthier offspring. Monogamy is observed in many bird populations where, in addition to the parental care from the female, the male is also

a major provider of parental care for the chicks. A third explanation for the evolutionary advantages of monogamy is the "female-enforcement hypothesis." In this scenario, the female ensures that the male does not have other offspring that might compete with her own, so she actively interferes with the male's signaling to attract other mates.

Polygynous mating refers to one male mating with multiple females. In these situations, the female must be responsible for most of the parental care as the single male is not capable of providing care to that many offspring. In resourced-based polygyny, males compete for territories with the best resources, and then mate with females that enter the territory, drawn to its resource richness. The female benefits by mating with a dominant, genetically fit male; however, it is at the cost of having no male help in caring for the offspring. An example is seen in the yellow-rumped honeyguide, a bird whose males defend beehives because the females feed on their wax. As the females approach, the male defending the nest will mate with them. Harem mating structures are a type of polygynous system where certain males dominate mating while controlling a territory with resources. Elephant seals, where the alpha male dominates the mating within the group are an example. A third type of polygyny is a lek system. Here there is a communal courting area where several males perform elaborate displays for females, and the females choose their mate from this group. This behavior is observed in several bird species including the sage grouse and the prairie chicken.

In polyandrous mating systems, one female mates with many males. These types of systems are much rarer than monogamous and polygynous mating systems. In pipefishes and seahorses, males receive the eggs from the female, fertilize them, protect them within a pouch, and give birth to the offspring (Figure **53.5.4**). Therefore, the female is able to provide eggs to several males without the burden of carrying the fertilized eggs.



a b

Figure 53.5.4: Polyandrous mating, in which one female mates with many males, occurs in the (a) seahorse and the (b) pipefish. (credit a: modification of work by Brian Gratwicke; credit b: modification of work by Stephen Childs)

Simple Learned Behaviors

The majority of the behaviors previously discussed were innate or at least have an innate component (variations on the innate behaviors may be learned). They are inherited and the behaviors do not change in response to signals from the environment. Conversely, learned behaviors, even though they may have instinctive components, allow an organism to adapt to changes in the environment and are modified by previous experiences. Simple learned behaviors include habituation and imprinting—both are important to the maturation process of young animals.

Habituation

Habituation is a simple form of learning in which an animal stops responding to a stimulus after a period of repeated exposure. This is a form of non-associative learning, as the stimulus is not associated with any punishment or reward. Prairie dogs typically sound an alarm call when threatened by a predator, but they become habituated to the sound of human footsteps when no harm is associated with this sound, therefore, they no longer respond to them with an alarm call. In this example, habituation is specific to the sound of human footsteps, as the animals still respond to the sounds of potential predators.

Imprinting

Imprinting is a type of learning that occurs at a particular age or a life stage that is rapid and independent of the species involved. Hatchling ducks recognize the first adult they see, their mother, and make a bond with her. A familiar sight is ducklings walking or swimming after their mothers (Figure 53.5.5). This is another type of non-associative learning, but is very important in the maturation process of these animals as it encourages them to stay near their mother so they will be protected, greatly increasing their chances of survival. However, if newborn ducks see a human before they see their mother, they will imprint on the human and follow it in just the same manner as they would follow their real mother.

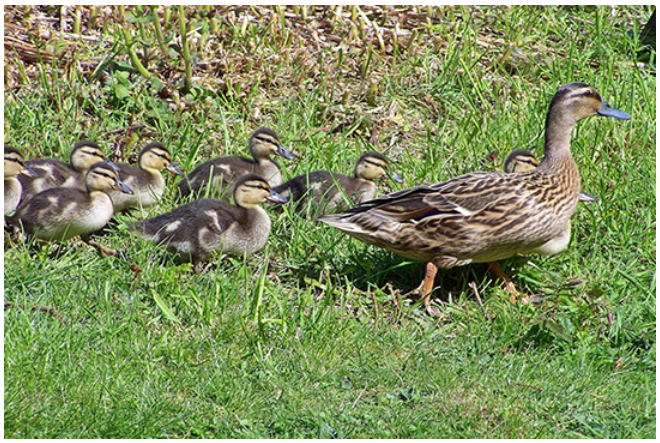


Figure 53.5.5: The attachment of ducklings to their mother is an example of imprinting. (credit: modification of work by Mark Harkin)

Link to Learning



The International Crane Foundation has helped raise the world's population of whooping cranes from 21 individuals to about 600. Imprinting hatchlings has been a key to success: biologists wear full crane costumes so the birds never "see" humans. Watch this video to learn more.

Conditioned Behavior

Conditioned behaviors are types of associative learning, where a stimulus becomes associated with a consequence. During operant conditioning, the behavioral response is modified by its consequences, with regards to its form, strength, or frequency.

Classical Conditioning

In classical conditioning, a response called the conditioned response is associated with a stimulus that it had previously not been associated with, the conditioned stimulus. The response to the original, unconditioned stimulus is called the unconditioned response. The most cited example of classical conditioning is Ivan Pavlov's experiments with dogs (Figure **53.5.6**). In Pavlov's experiments, the unconditioned response was the salivation of dogs in response to the unconditioned stimulus of seeing or smelling their food. The conditioning stimulus that researchers associated with the unconditioned response was the ringing of a bell. During conditioning, every time the animal was given food, the bell was rung. This was repeated during several trials. After some time, the dog learned to associate the ringing of the bell with food and to respond by salivating. After the conditioning period was finished, the dog would respond by salivating when the bell was rung, even when the unconditioned stimulus, the food, was absent. Thus, the ringing of the bell became the conditioned stimulus and the salivation became the conditioned response. Although it is thought by some scientists that the unconditioned and conditioned responses are identical, even Pavlov discovered that the saliva in the conditioned dogs had characteristic differences when compared to the unconditioned dog.

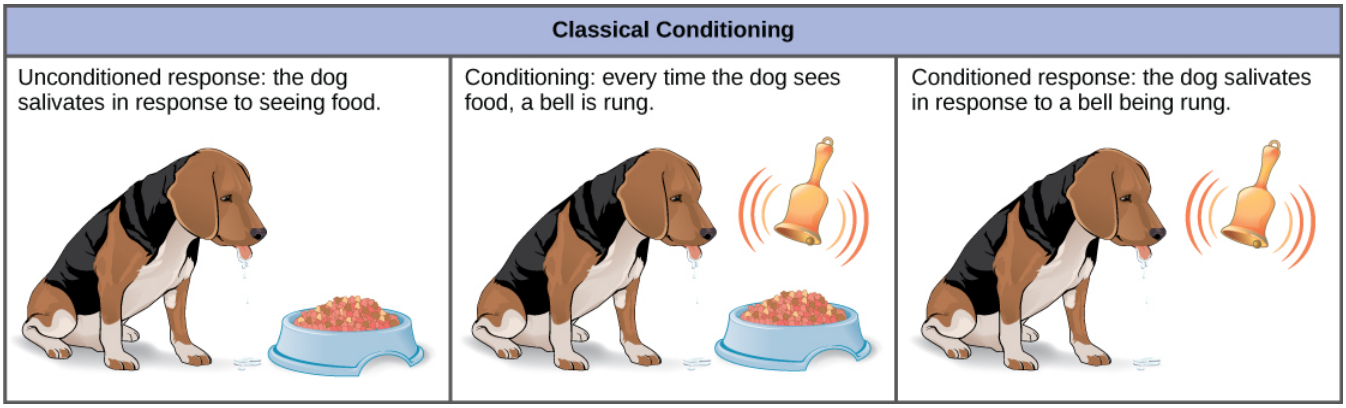


Figure **53.5.6**: In the classic Pavlovian response, the dog becomes conditioned to associate the ringing of the bell with food.

It had been thought by some scientists that this type of conditioning required multiple exposures to the paired stimulus and response, but it is now known that this is not necessary in all cases, and that some conditioning can be learned in a single pairing experiment. Classical conditioning is a major tenet of behaviorism, a branch of psychological philosophy that proposes that all actions, thoughts, and emotions of living things are behaviors that can be treated by behavior modification and changes in the environment.

Operant Conditioning

In operant conditioning, the conditioned behavior is gradually modified by its consequences as the animal responds to the stimulus. A major proponent of such conditioning was psychologist B.F. Skinner, the inventor of the Skinner box. Skinner put rats in his boxes that contained a lever that would dispense food to the rat when depressed. While initially the rat would push the lever a few times by accident, it eventually associated pushing the lever with getting the food. This type of learning is an example of operant conditioning. Operant learning is the basis of most animal training. The conditioned behavior is continually modified by positive or negative reinforcement, often a reward such as food or some type of punishment, respectively. In this way, the animal is conditioned to associate a type of behavior with the punishment or reward, and, over time, can be induced to perform behaviors that they would not have done in the wild, such as the "tricks" dolphins perform at marine amusement park shows (Figure **53.5.7**).

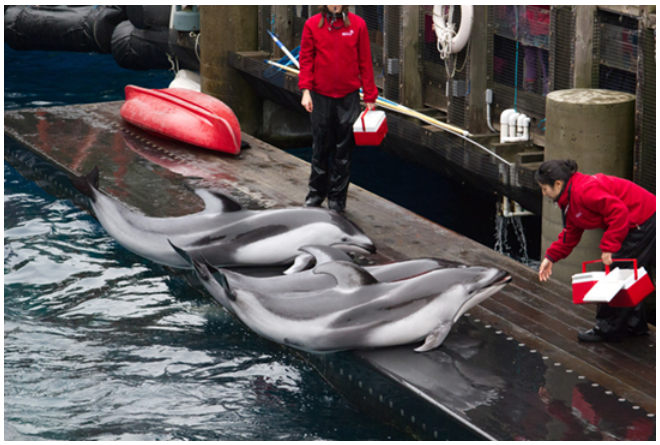


Figure 53.5.7: The training of dolphins by rewarding them with food is an example of positive reinforcement operant conditioning. (credit: Roland Tanglao)

Summary

Behaviors are responses to stimuli. They can either be instinctual/innate behaviors, which are not influenced by the environment, or learned behaviors, which are influenced by environmental changes. Instinctual behaviors include mating systems and methods of communication. Learned behaviors include imprinting and habituation, conditioning, and, most powerfully, cognitive learning. Although the connection between behavior, genetics, and evolution is well established, the explanation of human behavior as entirely genetic is controversial.

Footnotes

1. 1 Edward O. Wilson. *On Human Nature* (1978; repr., Cambridge: Harvard University Press, 2004), xx.

Glossary

aggressive display
visual display by a species member to discourage other members of the same species or different species

behavior
change in an organism's activities in response to a stimulus

behavioral biology
study of the biology and evolution of behavior

classical conditioning
association of a specific stimulus and response through conditioning

cognitive learning
knowledge and skills acquired by the manipulation of information in the mind

conditioned behavior
behavior that becomes associated with a specific stimulus through conditioning

courtship display
visual display used to attract a mate

distraction display
visual display used to distract predators away from a nesting site

ethology

biological study of animal behavior

fixed action pattern
series of instinctual behaviors that, once initiated, always goes to completion regardless of changes in the environment

foraging
behaviors species use to find food

habituation
ability of a species to ignore repeated stimuli that have no consequence

imprinting
identification of parents by newborns as the first organism they see after birth

innate behavior
instinctual behavior that is not altered by changes in the environment

intersexual selection
selection of a desirable mate of the opposite sex

intrasexual selection
competition between members of the same sex for a mate

kin selection
sacrificing one's own life so that one's genes will be passed on to future generations by relatives

kinesis
undirected movement of an organism in response to a stimulus

learned behavior
behavior that responds to changes in the environment

migration
long-range seasonal movement of animal species

monogamy
mating system whereby one male and one female remain coupled for at least one mating season

operant conditioning
learned behaviors in response to positive and/or negative reinforcement

polyandry
mating system where one female mates with many males

polygyny
mating system where one male mates with many females

reflex action
action in response to direct physical stimulation of a nerve

signal
method of communication between animals including those obtained by the senses of smell, hearing, sight, or touch

taxis

directed movement in response to a stimulus

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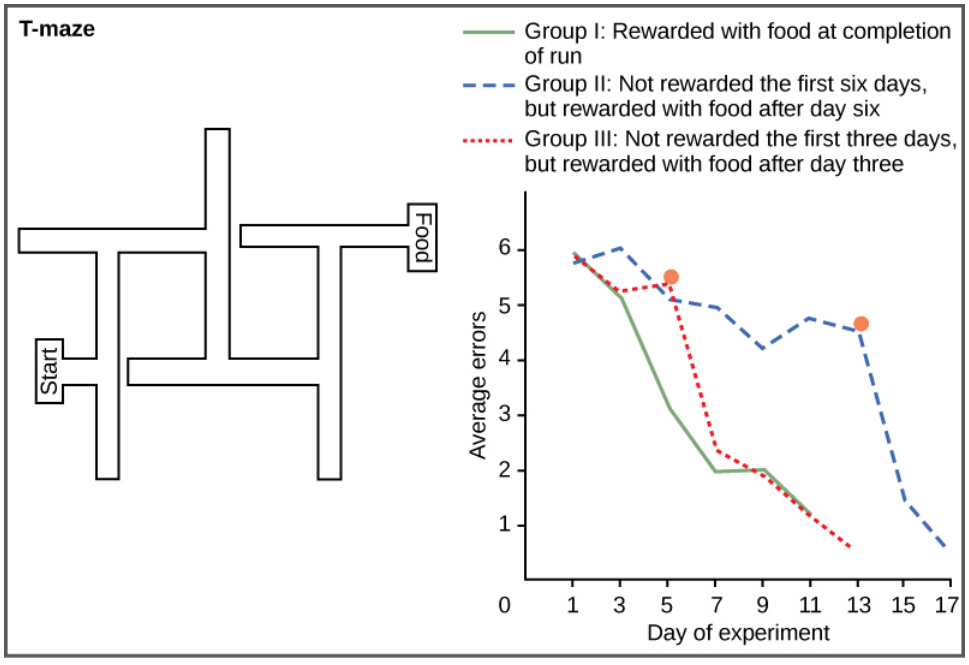
53.6: Animal Cognition

Cognitive Learning

Classical and operant conditioning are inefficient ways for humans and other intelligent animals to learn. Some primates, including humans, are able to learn by imitating the behavior of others and by taking instructions. The development of complex language by humans has made cognitive learning, the manipulation of information using the mind, the most prominent method of human learning. In fact, that is how students are learning right now by reading this book. As students read, they can make mental images of objects or organisms and imagine changes to them, or behaviors by them, and anticipate the consequences. In addition to visual processing, cognitive learning is also enhanced by remembering past experiences, touching physical objects, hearing sounds, tasting food, and a variety of other sensory-based inputs. Cognitive learning is so powerful that it can be used to understand conditioning in detail. In the reverse scenario, conditioning cannot help someone learn about cognition.

Classic work on cognitive learning was done by Wolfgang Köhler with chimpanzees. He demonstrated that these animals were capable of abstract thought by showing that they could learn how to solve a puzzle. When a banana was hung in their cage too high for them to reach, and several boxes were placed randomly on the floor, some of the chimps were able to stack the boxes one on top of the other, climb on top of them, and get the banana. This implies that they could visualize the result of stacking the boxes even before they had performed the action. This type of learning is much more powerful and versatile than conditioning.

Cognitive learning is not limited to primates, although they are the most efficient in using it. Maze running experiments done with rats by H.C. Blodgett in the 1920s were the first to show cognitive skills in a simple mammal. The motivation for the animals to work their way through the maze was a piece of food at its end. In these studies, the animals in Group I were run in one trial per day and had food available to them each day on completion of the run (Figure **53.6.9**). Group II rats were not fed in the maze for the first six days and then subsequent runs were done with food for several days after. Group III rats had food available on the third day and every day thereafter. The results were that the control rats, Group I, learned quickly, and figured out how to run the maze in seven days. Group III did not learn much during the three days without food, but rapidly caught up to the control group when given the food reward. Group II learned very slowly for the six days with no reward to motivate them, and they did not begin to catch up to the control group until the day food was given, and then it took two days longer to learn the maze.



Redrawn after H. C. Blodgett, The effect of the introduction of reward upon the maze performance of rats. Univ. Calif. Publ. Psychol., 1929, 4, No. 8, pages 117 and 120.

Figure **53.6.9**: Group I (the green solid line) found food at the end of each trial, group II (the blue dashed line) did not find food for the first 6 days, and group III (the red dotted line) did not find food during runs on the first three days. Notice that rats given food earlier learned faster and eventually caught up to the control group. The orange dots on the group II and III lines show the days when food rewards were added to the mazes.

It may not be immediately obvious that this type of learning is different than conditioning. Although one might be tempted to believe that the rats simply learned how to find their way through a conditioned series of right and left turns, E.C. Tolman proved a decade later that the rats were making a representation of the maze in their minds, which he called a “cognitive map.” This was an early demonstration of the power of cognitive learning and how these abilities were not just limited to humans.

Sociobiology

Sociobiology is an interdisciplinary science originally popularized by social insect researcher E.O. Wilson in the 1970s. Wilson defined the science as “the extension of population biology and evolutionary theory to social organization.”[1] The main thrust of sociobiology is that animal and human behavior, including aggressiveness and other social interactions, can be explained almost solely in terms of genetics and natural selection. This science is controversial; noted scientist such as the late Stephen Jay Gould criticized the approach for ignoring the environmental effects on behavior. This is another example of the “nature versus nurture” debate of the role of genetics versus the role of environment in determining an organism’s characteristics.

Sociobiology also links genes with behaviors and has been associated with “biological determinism,” the belief that all behaviors are hardwired into our genes. No one disputes that certain behaviors can be inherited and that natural selection plays a role retaining them. It is the application of such principles to human behavior that sparks this controversy, which remains active today.

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53.7: Orientation and Migratory Behavior

Animal migration

Adapted from Wikipedia, the free encyclopedia. Animal migration - Wikipedia



Mexican free-tailed bats on their long aerial migration

Animal migration is the relatively long-distance movement of individual animals, usually on a seasonal basis. It is the most common form of migration in ecology. It is found in all major animal groups, including birds, mammals, fish, reptiles, amphibians, insects, and crustaceans.[1] The trigger for the migration may be local climate, local availability of food, the season of the year or for mating reasons.[2]

To be counted as a true migration, and not just a local dispersal or irruption, the movement of the animals should be an annual or seasonal occurrence, such as Northern Hemisphere birds migrating south for the winter; wildebeest migrating annually for seasonal grazing; or a major habitat change as part of their life, such as young Atlantic salmon or sea lamprey leaving the river of their birth when they have reached a few inches in size.[3][4]



A Christmas Island red crab on its migration

Migration can take very different forms in different species, and as such there is no simple accepted definition of migration. One of the most commonly used definitions, proposed by Kennedy[5] is

> *Migratory behavior is persistent and straightened out movement effected by the animal's own locomotory exertions or by its active embarkation upon a vehicle. It depends on some temporary inhibition of station keeping responses but promotes their eventual disinhibition and recurrence.*[5]

Migration encompasses four related concepts: persistent straight movement; relocation of an individual on a greater scale (both spatially and temporally) than its normal daily activities; seasonal to-and-fro movement of a population between two areas; and movement leading to the redistribution of individuals within a population.[1] Migration can be either obligate, meaning individuals must migrate, or facultative, meaning individuals can "choose" to migrate or not. Within a migratory species or even within a single population, often not all individuals migrate. *Complete migration* is when all individuals migrate, *partial migration* is when some individuals migrate while others do not, and *differential migration* is when the difference between migratory and non-migratory individuals is based on age or sex (for example).[1]

While most migratory movements occur on an annual cycle, some daily movements are also referred to as migration. Many aquatic animals make a diel vertical migration, travelling a few hundred meters up and down the water column,[6] while some jellyfish make daily horizontal migrations, traveling a few hundred meters across a lake.[7]

Irregular (non-cyclical) migrations such as irruptions can occur under pressure of famine, overpopulation of a locality, or some more obscure influence.[8]

Seasonal migration is the movement of various species from one habitat to another during the year. Resource availability changes depending on seasonal fluctuations, which influence migration patterns. Some species such as Pacific salmon migrate to reproduce; every year they swim upstream to mate and then return to the ocean.[9] Temperature is a driving factor of migration that is dependent on the time of year. Many species, especially birds, migrate to warmer locations during the winter to escape poor environmental conditions.[10]

Circadian migration is where birds utilize circadian rhythm (CR) to regulate migration in both the fall and the spring. In circadian migration clocks of both circadian (daily) and circannual (annual) patterns are utilized to determine the birds' orientation in both time and space as they migrate from one destination to the next. This type of migration is advantageous in birds that during the winter remain close to the equator, and also allows the monitoring of the auditory and spatial memory of the birds' brain to remember an optimal site of migration. These birds also have timing mechanisms that provide avians with the distance required to travel in order to reach their destination.[11] To regulate the migration patterns of these birds, the mammalian circadian clock is utilized. This clock allows birds to determine when the appropriate time is to migrate, which location will best help them regulate their metabolism, and whether land or water travel will be most advantageous.[12]

Tidal migration is the use of tides by organisms to move periodically from one habitat to another. This type of migration is often used in order to find food or mates. Tides can carry organisms horizontally and vertically for as little as a few nanometers to even thousands of kilometers.[13] The most common form of tidal migration is to and from Intertidal zone during daily tidal cycles.[13] These zones are often populated by many different species and are nutrient rich. Organisms like crabs, nematodes, small fish, corals, and other species cycle to these areas as the tides rise and fall typically about every twelve hours. The cycle movements are associated with foraging of marine and bird species. Typically, during low tide smaller or younger species will emerge to forage because they can survive in the shallower water and have less chance of being preyed upon. During high tide, larger species can be found due to the deeper water and nutrient upwelling from the tidal movements. Tidal migration is often facilitated by ocean currents.[14]

In specific groups



Flocks of birds assembling before migration southwards

Different kinds of animal migrate in different ways.

In birds

Main article: Bird migration

Approximately 1,800 of the world's 10,000 bird species migrate long distances each year in response to the seasons.[15] Many of these migrations are north-south, with species feeding and breeding in high northern latitudes in the summer, and moving some hundreds of kilometres south for the winter.[16] Some species extend this strategy to migrate annually between the Northern and Southern Hemispheres. The Arctic tern is famous for its migration; it flies from its Arctic breeding grounds to the Antarctic and back again each year, a distance of at least 19,000 km (12,000 mi), giving it two summers every year.[17]

In fish

Main article: Fish migration



Many species of salmon migrate up rivers to spawn

Most fish species are relatively limited in their movements, remaining in a single geographical area and making short migrations for wintering, to spawn, or to feed. A few hundred species migrate long distances, in some cases of thousands of kilometres. About 120 species of fish, including several species of salmon, migrate between saltwater and freshwater (they are 'diadromous').[18][19]

Forage fish such as herring and capelin migrate around substantial parts of the North Atlantic ocean. The capelin for example spawn around the southern and western coasts of Iceland; their larvae drift clockwise around Iceland, while the fish swim northwards towards Jan Mayen island to feed, and return to Iceland parallel with Greenland's east coast.[20]

In the 'sardine run', billions of Southern African pilchard *Sardinops sagax* spawn in the cool waters of the Agulhas Bank and move northward along the east coast of South Africa between May and July.[21]

In insects

Main articles: Insect migration and Lepidoptera migration



An aggregation of migratory *Pantala flavescens* dragonflies, known as globe skimmers, in Coorg, India

Some winged insects such as locusts and certain butterflies and dragonflies with strong flight migrate long distances. Among the dragonflies, species of *Libellula* and *Sympetrum* are known for mass migration, while *Pantala flavescens*, known as the globe skimmer or wandering glider dragonfly, makes the longest ocean crossing of any insect, between India and Africa.[22] Exceptionally, swarms of the desert locust, *Schistocerca gregaria*, flew westwards across the Atlantic Ocean for 4500 km during October 1988, using air currents in the Inter-Tropical Convergence Zone.[23]

In some migratory butterflies, such as the monarch butterfly and the painted lady, no individual completes the whole migration. Instead the butterflies mate and reproduce on the journey, and successive generations travel the next stage of the migration.[24]

In mammals



Wildebeest on the Serengeti 'great migration'

Further information: List of mammals that perform mass migrations

Some mammals exhibit extraordinary migrations, with caribou having one of the longest known terrestrial migrations on the planet, reaching as much as 4868 km/year in North America. However, over the course of a year, gray wolves move the most. One gray wolf, in particular, covered a total cumulative annual distance (TCAD) of 7247 km.[25]

Mass migration occurs in mammals such as the Serengeti 'great migration', an annual circular pattern of movement with some 1.7 million wildebeest and hundreds of thousands of other large game animals including gazelles and zebra.[26][27] A literature survey in 2009 found more than 20 species which engage, or used to engage, in mass migrations.[28] Of these migrations, those of the springbok, black wildebeest, blesbok, scimitar-horned oryx, and kulan have ceased.[29] Long-distance migrations occur in some bats, notably the mass migration of the Mexican free-tailed bat between Oregon and southern Mexico.[30] Migration is important in cetaceans, including whales, dolphins and porpoises.[31]

In other animals

Some reptiles, especially the sea turtles, and amphibians migrate.[32] Some crustaceans migrate, most spectacularly the Christmas Island red crab which moves en masse each year by the million.[33]

Animal migration tracking

Adapted from Wikipedia, the free encyclopedia. Animal migration tracking - Wikipedia



Radio-collared wolf in Yellowstone National Park



Employee of US Fish and Wildlife Service tracking a mountain lion tagged with a radio collar

Animal migration tracking is used in wildlife biology, conservation biology, ecology, and wildlife management to study animals' behavior in the wild. One of the first techniques was bird banding, placing passive ID tags on birds legs, to identify the bird in a future catch-and-release. Radio tracking involves attaching a small radio transmitter to the animal and following the signal with a RDF receiver. Sophisticated modern techniques use satellites to track tagged animals, and GPS tags which keep a log of the animal's location. One of the many goals of animal migration research has been to determine where the animals are going; however, researchers also want to know why they are going "there". Researchers not only look at the animals' migration but also what is between the migration endpoints to determine if a species is moving to new locations based on food density, a change in water temperature, or other stimulus, and the animal's ability to adapt to these changes. Migration tracking is a vital tool in efforts to control the impact of human civilization on populations of wild animals, and prevent or mitigate the ongoing extinction of endangered species.

Technologies



A monarch butterfly shortly after tagging at the Cape May Bird Observatory Cape May Bird Observatory is one of the organizations that has a monarch identification tagging program. Plastic stickers are placed on the wing of the insect with identification information. Tracking information is used to study the migration patterns of monarchs, including how far and where they fly.

In the fall of 1803, American Naturalist John James Audubon wondered whether migrating birds returned to the same place each year. So he tied a string around the leg of a bird before it flew south. The following spring, Audubon saw the bird had indeed come back.

Scientists today still attach tags, such as metal bands, to track movement of animals. Metal bands require the re-capture of animals for the scientists to gather data; the data is thus limited to the animal's release and destination points.

Recent technologies have helped solve this problem. Some electronic tags give off repeating signals that are picked up by radio devices or satellites while other electronic tags could include archival tags (or data loggers). Scientists can track the locations and movement of the tagged animals without recapturing them using this RFID technology or satellites. These electronic tags can provide a great deal of data. Modern technologies are also smaller, minimizing the negative impact of the tag on the animal.[1]

Radio tracking



The right one of these two brush-tailed rock-wallabies is wearing a radio tracking collar.

Tracking an animal by radio telemetry involves two devices. Telemetry, in general, involves the use of a transmitter that is attached to an animal and sends out a signal in the form of radio waves, just as a radio station does.[2] A scientist might place the transmitter around an animal's ankle, neck, wing, carapace, or dorsal fin. Alternatively, they may surgically implant it as internal radio transmitters have the advantage of remaining intact and functioning longer than traditional attachments, being protected from environmental variables and wear.[3] The transmitter typically uses a frequency in the VHF band as antennas in this band are conveniently small. To conserve battery power the transmitter usually transmits brief pulses, perhaps one per second. A specialized radio receiver called a radio direction finding (RDF) receiver picks up the signal. The receiver is usually in a truck, an ATV, or an airplane.[2] The receiver has a directional antenna (usually a simple Yagi antenna) which receives most strongly from a single direction, and some means of indicating the strength of the received signal, either by a meter or by the loudness of the pulses in earphones. The antenna is rotated until the received radio signal is strongest; then the antenna is pointing toward the animal. To

keep track of the signal, the scientist follows the animal using the receiver. This approach of using radio tracking can be used to track the animal manually but is also used when animals are equipped with other payloads. The receiver is used to home in on the animal to get the payload back.

Another form of radio tracking that can be utilized, especially in the case of small bird migration, is the use of geolocators or "geologgers".[4] This technology utilizes a light sensor that tracks the light-level data during regular intervals in order to determine a location based on the length of the day and the time of solar noon.[4] While there are benefits and challenges with using this method of tracking, it is one of the only practical means of tracking small birds over long distances during migration.[4][5]

Passive integrated transponders (PIT) are another method of telemetry used to track the movements of a species [4] Passive integrated transponders, or "PIT tags", are electronic tags that allow researchers to collect data from a specimen without the need to recapture and handle the animal.[6] Data is captured and monitored via electronic interrogation antennae, which records the time and location of the individual.[6] Pit tags are a humane method of tracking that has little risk of infection or mortality due to the limited contact necessary to monitor the specimens. They are also cost-efficient in that they can be used repeatedly should the need arise to remove the tag from the animal.[7]

Satellite tracking



A saltwater crocodile with GPS-based satellite transmitter for migration tracking

Receivers can be placed in Earth-orbiting satellites such as ARGOS. Networks, or groups, of satellites are used to track animals. Each satellite in a network picks up electronic signals from a transmitter on an animal. Together, the signals from all satellites determine the precise location of the animal. The satellites also track the animal's path as it moves. Satellite-received transmitters fitted to animals can also provide information about the animals' physiological characteristics (e.g. temperature and habitat use.)[8][9] Satellite tracking is especially useful because the scientists do not have to follow after the animal nor do they have to recover the tag to get the data on where the animal is going or has gone. Satellite networks have tracked the migration and territorial movements of caribou, sea turtles,[10] whales, great white sharks, seals, elephants, bald eagles, ospreys and vultures.[8] Additionally Pop-up satellite archival tags are used on marine mammals and various species of fish. There are two main systems, the above-mentioned Argos and the GPS.[11] Thanks to these systems, conservationists can find the key sites for migratory species.[11] Another form of satellite tracking would be the use of acoustic telemetry. This involves the use of electronic tags that emit sound in order for the researchers to track and monitor an animal within three dimensions, which is helpful in instances when large quantities of a species are being tracked at a time.[12]

Stable isotopes



Sea turtle eggs being laid by the mother. Unhatched eggs can be used in stable isotope analysis.

Stable isotopes are one of the intrinsic markers used for studying migration of animals.[13] One of the benefits of intrinsic markers in general, including stable isotope analysis, is that it does not require an organism to be capture and tagged and then recaptured at a later time. Each capture of an organism provides information on where it has been based on diet. The three types of intrinsic markers that can be used as tools for animal migration studies are: (1) contaminants, parasites and pathogens, (2) trace elements, and (3) stable isotopes. Certain geographic regions have specific stable isotope ratios that affect the chemistry of organisms foraging in those locations, this creates "isoscapes" that scientists can use to understand where the organism has been eating. A couple prerequisites must be met in order to use stable isotope analysis successfully: (1) the animal must have at least one light isotope of interest in specific tissues that can be sampled (this condition is almost always met since these light isotopes are building blocks of most animal tissues), and (2) the organism needs to migrate between isotopically different regions and these isotopes must be retained in the tissue in order for the differences to be measured.[13]

Stable isotope analysis has a lot of benefits and has been used in terrestrial and aquatic organisms. For example, stable isotope analysis has been confirmed to work in determining foraging locations of nesting loggerhead sea turtles.[14] Satellite telemetry was used to confirm that the location derived from the analysis were accurate to where these turtles actually traveled. This is important because it allows for greater sample sizes to be used in migration studies, since satellite telemetry is expensive and tissue, blood, and egg samples can be taken from the female turtles laying eggs.[14]

Importance

Electronic tags are giving scientists a complete, accurate picture of migration patterns. For example, when scientists used radio transmitters to track one herd of caribou, they learned two important things. First, they learned that the herd moves much more than previously thought. Second, they learned that each year the herd returns to about the same place to give birth. This information would have been difficult or impossible to obtain with "low tech" tags.

Tracking migrations is an important tool to better understand and protect species. For example, Florida manatees are an endangered species, and therefore they need protection. Radio tracking showed that Florida manatees may travel as far as Rhode Island when they migrate. This information suggests that the manatees may need protection along much of the Atlantic Coast of the United States. Previously, protection efforts focused mainly in the Florida area.

In the wake of the BP oil spill, efforts in tracking animals has increased in the Gulf. Most researchers who use electronic tags have only a few options: pop-up satellite tags, archival tags, or satellite tags. Historically these tags were generally expensive and could cost several thousands of dollars per tag. However, with current advancements in technology prices are now allowing researchers to tag more animals. With this increase in the number of species and individuals that can be tagged it is important to record and acknowledge the potential negative effects these devices might have.[15][16]

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16. ^ *Weiser, E. L.; et al. (2016). "Effects of geolocators on hatching success, return rates, breeding movements, and change in body mass in 16 species of Arctic-breeding shorebirds". Movement Ecology.* ***4*** *(12): 734–743. doi:10.1111/ibi.12493. PMC 4850671. PMID 27134752.*

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53.8: Animal Communication

Communication within a Species

Animals communicate with each other using stimuli known as signals. An example of this is seen in the three-spined stickleback, where the visual signal of a red region in the lower half of a fish signals males to become aggressive and signals females to mate. Other signals are chemical (pheromones), aural (sound), visual (courtship and aggressive displays), or tactile (touch). These types of communication may be instinctual or learned or a combination of both. These are not the same as the communication we associate with language, which has been observed only in humans and perhaps in some species of primates and cetaceans.

A pheromone is a secreted chemical signal used to obtain a response from another individual of the same species. The purpose of pheromones is to elicit a specific behavior from the receiving individual. Pheromones are especially common among social insects, but they are used by many species to attract the opposite sex, to sound alarms, to mark food trails, and to elicit other, more complex behaviors. Even humans are thought to respond to certain pheromones called axillary steroids. These chemicals influence human perception of other people, and in one study were responsible for a group of women synchronizing their menstrual cycles. The role of pheromones in human-to-human communication is still somewhat controversial and continues to be researched.

Songs are an example of an aural signal, one that needs to be heard by the recipient. Perhaps the best known of these are songs of birds, which identify the species and are used to attract mates. Other well-known songs are those of whales, which are of such low frequency that they can travel long distances underwater. Dolphins communicate with each other using a wide variety of vocalizations. Male crickets make chirping sounds using a specialized organ to attract a mate, repel other males, and to announce a successful mating.

Courtship displays are a series of ritualized visual behaviors (signals) designed to attract and convince a member of the opposite sex to mate. These displays are ubiquitous in the animal kingdom. Often these displays involve a series of steps, including an initial display by one member followed by a response from the other. If at any point, the display is performed incorrectly or a proper response is not given, the mating ritual is abandoned and the mating attempt will be unsuccessful. The mating display of the common stork is shown in Figure 53.8.1.

Aggressive displays are also common in the animal kingdom. An example is when a dog bares its teeth when it wants another dog to back down. Presumably, these displays communicate not only the willingness of the animal to fight, but also its fighting ability. Although these displays do signal aggression on the part of the sender, it is thought that these displays are actually a mechanism to reduce the amount of actual fighting that occurs between members of the same species: they allow individuals to assess the fighting ability of their opponent and thus decide whether it is “worth the fight.” The testing of certain hypotheses using game theory has led to the conclusion that some of these displays may overstate an animal’s actual fighting ability and are used to “bluff” the opponent. This type of interaction, even if “dishonest,” would be favored by natural selection if it is successful more times than not.

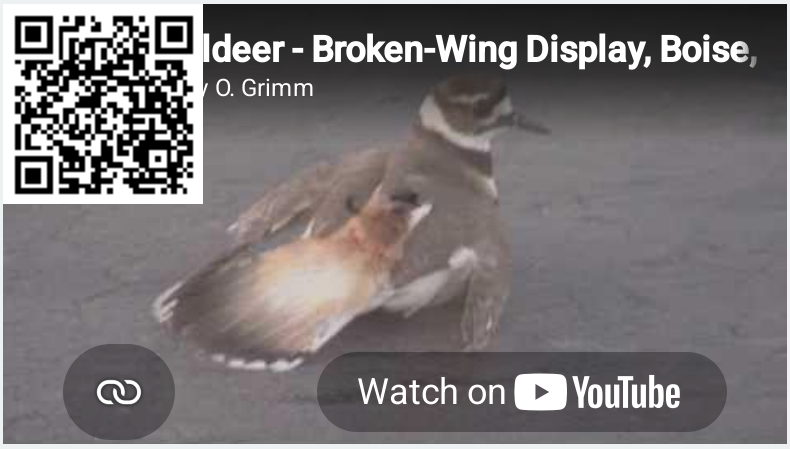


Figure 53.8.1: This stork’s courtship display is designed to attract potential mates. (credit: Linda “jinterwas”/Flickr)

Distraction displays are seen in birds and some fish. They are designed to attract a predator away from the nest that contains their young. This is an example of an altruistic behavior: it benefits the young more than the individual performing the display, which is putting itself at risk by doing so.

Many animals, especially primates, communicate with other members in the group through touch. Activities such as grooming, touching the shoulder or root of the tail, embracing, lip contact, and greeting ceremonies have all been observed in the Indian langur, an Old World monkey. Similar behaviors are found in other primates, especially in the great apes.

Link to Learning



The killdeer bird distracts predators from its eggs by faking a broken wing display in this video taken in Boise, Idaho.

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53.8.1: Honeybee Navigation

The domestic honeybee, ***Apis mellifera***, is a colonial insect living in hives containing one queen — a fertile female, a few drones (males), and thousands of workers (infertile females). The workers are responsible for keeping the hive clean, building the wax combs of the hive, tending the young and, when they get older (and when their *for* gene gets turned on), and **foraging** for food - nectar and pollen.

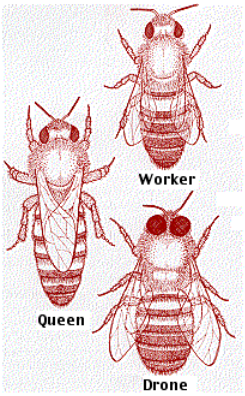


Figure 15.11.5.1 Honeybee castes

ome 5–25% of the workers in the hive are **scouts**. Their job is to search for new sources of food for the other workers, the **foragers**, to harvest. While both scouts and foragers look alike, recent research suggests that they represent stable subpopulations with distinctive patterns of gene expression in their brains. (See Liang, Z. S., *et al.*, in the 9 March 2012 issue of **Science**.)

When food is discovered by scouts, they return to the hive. Shortly after their return, many foragers leave the hive and fly directly to the food. The remarkable thing about this is that the foragers do not follow the scouts back. The scouts may remain in the hive for hours and those that leave continue to hunt for new sources of food even though the foragers are continuing to bring back ample supplies of food from the sites the scouts discovered earlier. So the scout bees have communicated to the foragers the necessary information for them to find the food on their own.

It turns out that the scouts can convey to the foragers information about

- the odor of the food
- its direction from the hive
- its distance from the hive

Distance

When food is within 50–75 meters of the hive, the scouts dance the **"round dance"** on the surface of the comb (left). But when the food is farther than 75 meters from the hive, the scouts dance the **"waggle dance"** (right). The waggle dance has two components: (1) a straight run - the direction of which conveys information about the **direction** of the food and (2) the speed at which the dance is repeated which indicates how far away the food is.

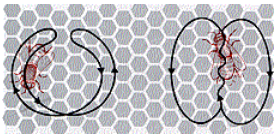


Figure 15.11.5.2 Round Dance

The graph shows the relationship between the speed of the dance and the distance to the food. It is based on data collected by the German ethologist **Karl von Frisch**. It was he who discovered much of what we know today about honeybee communication (and was honored with a Nobel Prize in 1973).

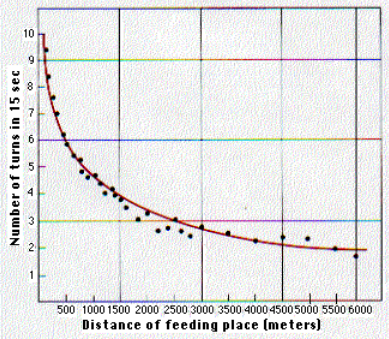


Figure 15.11.5.3 von Frisch graph

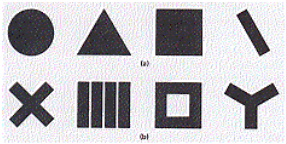
How do the bees calculate distance? von Frisch thought they measured the distance by assessing the amount of energy it took to get there. But the mechanism turns out to be quite different. The bees measure distance by the motion of images received by their eyes as they fly.

Flicker Effect

Honeybees, like all insects, have compound eyes. These give little information about depth but are very sensitive to "flicker effect". It has long been known to bee keepers that honeybees respond better to flowers

- moving in the breeze
- with complex petals

The importance of flicker effect can be demonstrated by training honeybees to visit food placed on cards with patterns. For example, the bees can distinguish any figure in the top row from any figure in the bottom row more easily than they can distinguish between any of the figures in either row.


Figure 15.11.5.4 Flicker patterns

Evidence of distance measuring

Working at the University of Notre Dame (Indiana), Esch and Burns found that when the hive and food were placed on top of tall (50 m) buildings, the speed of the waggle dance indicated a distance only half of the distance indicated by bees travelling the same distance (230 m) at ground level. Features of the scenery pass the retina faster when near than when far (compare the changes in your view from an airliner at cruising altitude and as it approaches the runway).

Tests of Searching Behavior

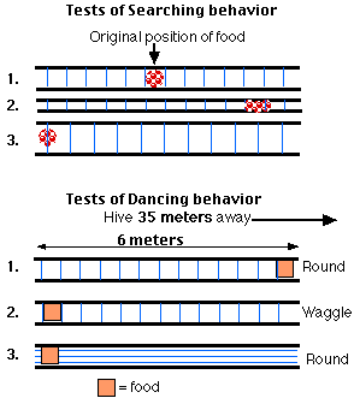


Figure 15.11.5.5 Searching and Dancing behavior in bees

Working at the Australian National University, Srinivasan and his colleagues built tunnels decorating the interior walls with patterns to create flicker. In these three experiments, the bees were first fed in the middle of the tunnel of standard diameter. Then the food was removed.

1. Using the same tunnel, foragers came to same spot in the tunnel.
2. Using a narrower tunnel, foragers began searching for food near its entrance. Forced to fly closer to the vertical stripes, the images moved by faster.
3. Using a tunnel with a larger diameter, foragers searched for food at its far end. Flying farther from the stripes, the images moved by more slowly.

Tests of Dancing Behavior

All tunnels were 6 meters long and located 35 meters from the hive — well within the distance (50–75 m) that normally elicits the **round** dance.

1. Bees were fed at the entrance. Back at the hive, they danced the **round** dance as you would expect.
2. Bees fed at end of tunnel. Back at the hive, they danced the **waggle** dance. Even though the total distance from the hive (41 m) was still well within the "round" range, the complexity of the scenery passed in the last 6 m, elicited the waggle dance.
3. Bees fed at end of tunnel decorated with horizontal stripes. These created no flicker as the bees flew, and on their return to the hive they danced the **round** dance.

You can read about this second set of experiments in Srinivasan, et. al., **Science**, 4 February 2000.

Recruits respond to the misinformation given by returning scouts

More recently, the Esch and Srinivasan groups have teamed up to show that naive foragers are fooled by the misinformation that the returning scouts give them. When scouts were fed only 11 m from the hive but at the far end of a striped tunnel, they danced the waggle dance back at the hive as though the food had been 70 m away. Most of the workers they recruited flew out (bypassing the tunnel) 70 m looking for food. You can read about these experiments in Ungless, et. al., **Nature**, 31 May 2001.

Direction

By itself, the knowledge that food is 6 kilometers (3.7 miles) away is not very useful. But von Frisch also noted that the direction of the straight portion of the waggle dance varied with the direction of the food source from the hive and the time of day.

- At any one time, the direction changes with the location of the food.
- With a fixed source of food, the direction changes by the same angle as the sun during its passage through the sky.

But

- The sun is not visible within the hive.
- The scouts dance on the **vertical** surface of the combs.

How, then, do they translate flight angles in the darkened hive?

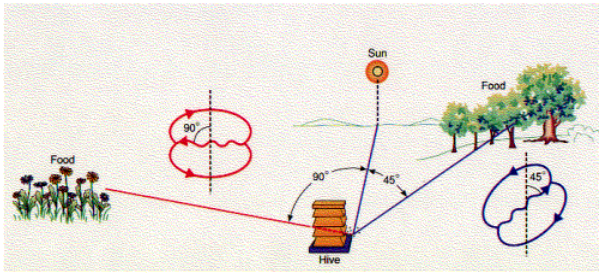


Figure 15.11.5.6 Bee dance

The picture shows the relationship between the angle of the dance on the vertical comb and the bearing of the sun with respect to the location of food. When the food and sun are in the same direction, the straight portion of the waggle dance is directed upward. When the food is at some angle to the right (blue) or left (red) of the sun, the bee orients the straight portion of her dance at the same angle to the right or left of the vertical.

Using radar to track individual bees recruited by the waggle dance, Riley, J. R., *et al*., (**Nature**, 12 May 2005) have shown that the recruits do fly in the indicated direction. They even adjust their flight path to compensate for being blown off course by the wind. However, their course is seldom so precise that they can find the food without the aid of vision and/or smell as they neared it.

Other features

Time Sense

When scouts remain in the hive for a long period, they shift the direction of the straight portion of the waggle dance as the day wears on (and the direction of the sun shifts). But they cannot see the sun in the darkened hive. Evidently, they are "aware" of the passing time and make the necessary corrections.

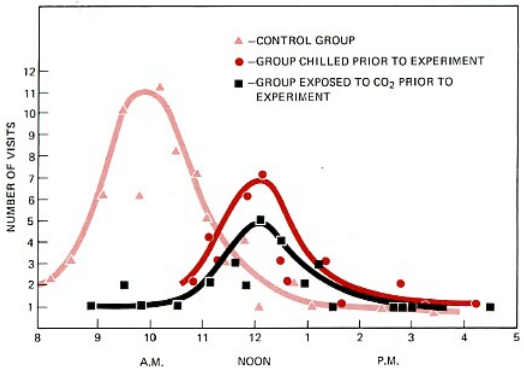


Figure 15.11.5.7 Time Sense

The time sense of honeybees has long been known to people who have sweet snacks in their garden at a set time every day. Within minutes of the regular time, foraging bees arrive for their share of the jam. The speed of the bee's clock seems to be related to its metabolic rate. If normally punctual bees are chilled (to lower their metabolic rate) or exposed to an anesthetizing concentration of carbon dioxide they arrive late to the picnic table (graph above).

Polarized light

von Frisch also discovered that scouts (and foragers) don't actually have to see the sun to navigate. As long as they can see a small patch of clear blue sky, they get along fine. This is because sky light is partially polarized, and the plane of polarization in any part of the sky is determined by the location of the sun. Try it by rotating a pair of polaroid® sun glasses!

Swarming

Before a new queen emerges, the old queen leaves the hive, taking many of the workers with her. The swarm usually settles somewhere, e.g., on a tree branch, while scouts go searching for a new home. Each scout that finds a promising site, returns to the swarm and dances on it just as though she had found food. Eventually, the swarm departs for the location promoted most vigorously. Once the new hive is established, many of the scouts that found the site will become food scouts.

Grooming

Workers have another type of dance — rapidly vibrating from side to side — that tells other workers that she needs help removing dust, pollen, etc. from hard-to-reach places on her body.

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53.8.2: Pheromones

Pheromones are chemicals released by an organism into its environment enabling it to communicate with other members of its own species.

Pheromones in Insects

Alarm Pheromone: When an ant is disturbed, it releases a pheromone that can be detected by other ants several centimeters away. They are attracted by low concentrations of the pheromone and begin to move toward the region of increasing concentration. As they get nearer to their disturbed nestmate, their response changes to one of alarm. The higher concentration causes them to run about as they work to remedy the disturbance. Unless additional amounts of the alarm pheromone are released, it soon dissipates. This ensures that once the emergency is over, the ants return quietly to their former occupations. Honeybees also have an alarm pheromone (which is a good thing not to elicit around a colony of "Africanized" bees).

Trail Pheromone: Certain ants, as they return to the nest with food, lay down a trail pheromone. This trail attracts and guides other ants to the food. It is continually renewed as long as the food holds out. When the supply begins to dwindle, trailmaking ceases. The trail pheromone evaporates quickly so other ants stop coming to the site and are not confused by old trails when food is found elsewhere. And at least in one species of ant, trails that no longer lead to food are also marked with a repellant pheromone.



Figure 15.11.7.1: Trail pheromone

A stick treated with the trail pheromone of an ant (left) can be used to make an artificial trail which is followed closely by other ants emerging from their nest (right). The trail will not be maintained by other ants unless food is placed at its end. (Photos courtesy of Sol Mednick and Scientific American).

Queen Pheromone: Honeybee queens spend their lives literally surrounded by a retinue of worker bees. The queen emits a pheromone that is a complex mixture of unsaturated hydrocarbons, fatty acids, and other organic molecules. Among its effects:

- inducing the workers to feed and groom her
- inhibiting the workers from building queen cells and rearing new queens
- inhibiting ovary development in the workers

Sex Attractants

Hundreds of pheromones are known with which one sex (usually the female) of an insect species attracts its mates. Many of these sex attractants or their close chemical relatives are available commercially. They have proved useful weapons against insect pests in two ways:

- **Male Confusion**: Distributing a sex attractant throughout an area masks the insect's own attractant and thus may prevent the sexes getting together. This "communication disruption" has been used successfully against a wide variety of important pests. For example, the sex attractant of the cotton boll weevil has reduced the need for conventional chemical insecticides by more than half in some cotton-growing areas.
- **Insect Monitoring**: Insect sex attractants are also valuable in monitoring pest populations. By baiting traps with the appropriate pheromone, a build-up of the pest population can be spotted early. Even if a conventional insecticide is the weapon chosen, its early use reduces
  - the amount needed
  - damage to the crop
  - cost to the grower

- possible damage to the environment.

Early detection of pest build-up is a key ingredient in the system known as integrated pest management (IPM).



Figure 15.11.7.2 Gypsy moth

The photo (courtesy of USDA) shows the feathery antennae of a male gypsy moth. These detect the pheromone released by the females (who do not fly). In some insects, a single molecule of sex attractant is enough to elicit a response.

Sexual Deception

- By an animal: Many species of spiders prey exclusively on moths of certain species and only on the males. Studies of one species of spider, *Mastophora cornigera*, show that it releases a mixture of volatile compounds that mimic the sex pheromone of the moth species it preys upon. Male moths flying upwind in search of a female end up eaten instead!
- By a plant: A number of species of orchids - each pollinated by the males of a single species of insect (wasps or bees) — emit the same pheromone that is the sex attractant by which females of the insect species attract the males for mating.

Pheromones in Mammals

Releaser Pheromones: Many mammals (e.g., dogs and cats) deposit chemicals in and/or around their "territory". As these vaporize, they signal to other members of the species of the presence of the occupant of the territory. Domestic rabbit mothers release a mammary pheromone that triggers immediate nursing behavior by their babies (pups). A good thing, too, as mothers devote only 5–7 minutes a day to feeding their pups so they had better be quick about it.

Many animals, including mammals, signal with alarm pheromones. Although neither the source nor the chemical nature of alarm pheromones are known in any mammal, stressed animals release something that triggers quick behavior (e.g., flight or fight) in other members of their species. The pheromone is detected in a special cluster of cells located at the very tip of the nose and thus in a position to detected airborne molecules even before the vomeronasal organ (see below) or nasal epithelium can. The detectors on these cells are primary cilia.

Primer Pheromones: Rats and mice give off pheromones that elicit mating behavior. However, the response is not immediate as it is in the releaser pheromones of mother rabbits and insects. Instead, detection of the pheromone primes the endocrine system of the recipient to make the changes, e.g., ovulation, needed for successful mating. Primer pheromones are detected by the olfactory epithelium with which normal odors are detected and also in most mammals (but not humans) by the *vomeronasal organ (VNO)*. The VNO is a patch of receptor tissue in the nasal cavity distinct from the olfactory epithelium. The receptors are G-protein-coupled transmembrane proteins similar to those that mediate olfaction, but encoded by entirely different genes. The neurons leading from the VNO take a separate path into and through the brain.

Human pheromones: It has long been noticed that women living close together (e.g., college roommates) develop synchronous menstrual cycles. This is thought to be because they release two (as yet uncharacterized) primer pheromones: (1) one prior to ovulation that tends to speed up the onset of ovulation in others and (2) one after ovulation that tends to delay the onset of ovulation in other women. Both pheromones are released from the armpits. The pheromones are not detected consciously as odors, but presumably trigger the hormonal changes that mediate the menstrual cycle.

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53.9: Behavioral Ecology

Behavioral ecology is the study of the evolutionary basis for animal behavior due to ecological pressures (**Figure 53.9.1**). Behavioral ecology emerged after Nikolaas Tinbergen outlined four questions to address when studying animal behaviors (**Figure 53.9.2**) that focused on two levels of answers: What are the ultimate (evolutionary) explanations of behavior, and what are the proximate (physiological or developmental) explanations of behavior?

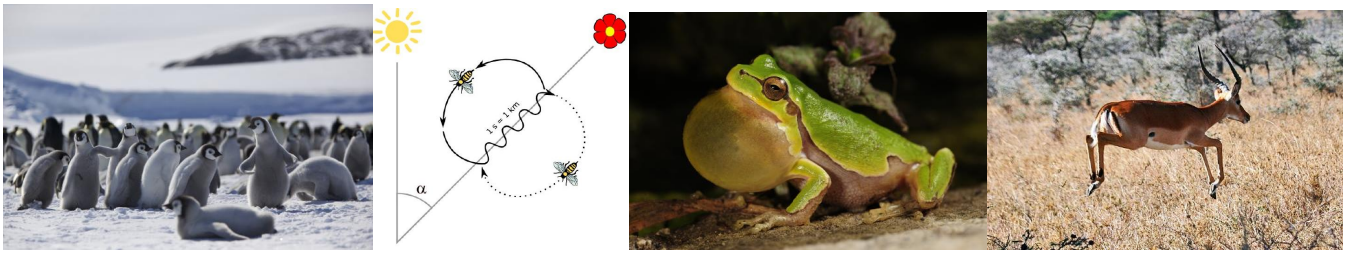


Figure 53.9.1: The study of behavioral ecology focuses on the ways organisms behaviorally interact with their physical and social environment. Here we see penguins huddling in the Antarctic (Ian Duffy), the bee waggle dance communicating information (Emmanuel Boutet), a frog with inflated vocal sac (Benny Trapp), and a stotting gazelle (Rick Wilhelmsen).

Tinbergen's four questions are complementary categories of explanations for animal behaviour. These are also commonly referred to as levels of analysis.[1] It suggests that an integrative understanding of behaviour must include: **ultimate (evolutionary) explanations**, in particular the behaviour (1) **adaptive function** and (2) **phylogenetic** history; and the **proximate explanations**, in particular the (3) underlying **physiological mechanisms** and (4) **ontogenetic/developmental history**.[2]

When asked about the purpose of sight in humans and animals, even elementary-school children can answer that animals have vision to help them find food and avoid danger (function/adaptation). Biologists have three additional explanations: sight is caused by a particular series of evolutionary steps (phylogeny), the mechanics of the eye (mechanism/causation), and even the process of an individual's development (ontogeny).

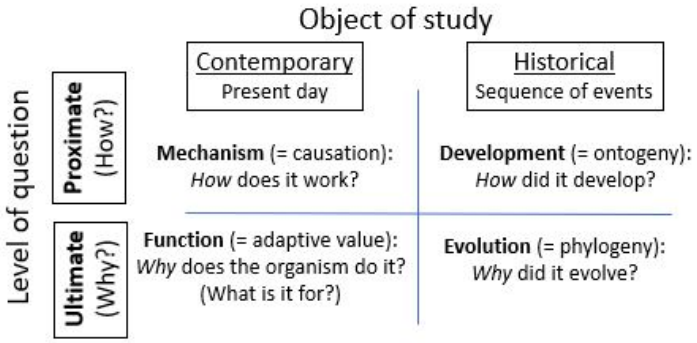


Figure 53.9.3: Summary of Tinbergen's four questions (Dan Wetzel).

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53.10: Behavior and Evolution

Evolutionary (ultimate) explanations

1. Function (adaptation)

Darwin's theory of evolution by natural selection is the only scientific explanation for why an animal's behavior is usually well adapted for survival and reproduction in its environment. However, claiming that a particular mechanism is well suited to the present environment is different from claiming that this mechanism was selected for in the past due to its history of being adaptive.[4] The literature conceptualizes the relationship between function and evolution in two ways. On the one hand, function and evolution are often presented as separate and distinct explanations of behaviour.[4]

On the other hand, the common definition of adaptation, a central concept in evolution, is a trait that was functional to the reproductive success of the organism and that is thus now present due to being selected for; that is, function and evolution are inseparable. However a trait can have a current function that is adaptive without being an adaptation in this sense, if for instance the environment has changed. Imagine an environment in which having a small body suddenly conferred benefit on an organism when previously body size had had no effect on survival.[4]

A small body's function in the environment would then be adaptive, but it wouldn't become an adaptation until enough generations had passed in which small bodies were advantageous to reproduction for small bodies to be selected for. Given this, it is best to understand that presently functional traits might not all have been produced by natural selection.[4] The term "function" is preferable to "adaptation", because adaptation is often construed as implying that it was selected for due to past function.

2. Phylogeny (evolution)

Evolution captures both the history of an organism via its phylogeny, and the history of natural selection working on function to produce adaptations.[5] There are several reasons why natural selection may fail to achieve optimal design. One entails random processes such as mutation and environmental events acting on small populations. Another entails the constraints resulting from early evolutionary development. Each organism harbors traits, both anatomical and behavioral, of previous phylogenetic stages, since many traits are retained as populations evolve.

Reconstructing the phylogeny of a species often makes it possible to understand the "uniqueness" of recent characteristics: Earlier phylogenetic stages and (pre-) conditions which persist often also determine the form of more modern characteristics. For instance, the vertebrate eye (including the human eye) has a blind spot, whereas octopus eyes do not. In those two lineages, the eye was originally constructed one way or the other. Once the vertebrate eye was constructed, there were no intermediate forms that were both adaptive and would have enabled it to evolve without a blind spot.

Proximate explanations

3. Mechanism (causation)

In examining living organisms, biologists are confronted with diverse levels of complexity (e.g. chemical, physiological, psychological, social). They therefore investigate causal and functional relations within and between these levels. A biochemist might examine, for instance, the influence of social and ecological conditions on the release of certain neurotransmitters and hormones, and the effects of such releases on behaviour, e.g. stress during birth has a tocolytic (contraction-suppressing) effect.

Some prominent classes of causal mechanisms include:

- The brain: Broca's area, a small section of the human brain, has a critical role in linguistic capability.
- Hormones: chemicals used to communicate among cells of an individual organism. Testosterone, for instance, stimulates aggressive behaviour in a number of species.
- Pheromones: chemicals used to communicate among members of the same species. Some species (e.g., dogs and some moths) use pheromones to attract mates.

4. Ontogeny

Ontogeny is the process of development of an individual organism from the zygote through the embryo to the adult form.

In the latter half of the twentieth century, social scientists debated whether human behaviour was the product of nature (genes) or nurture (environment in the developmental period, including culture). Many forms of developmental learning have a critical period, for instance, for imprinting among geese and language acquisition among humans. In such cases, genes determine the timing of the environmental impact.

Causal relationships

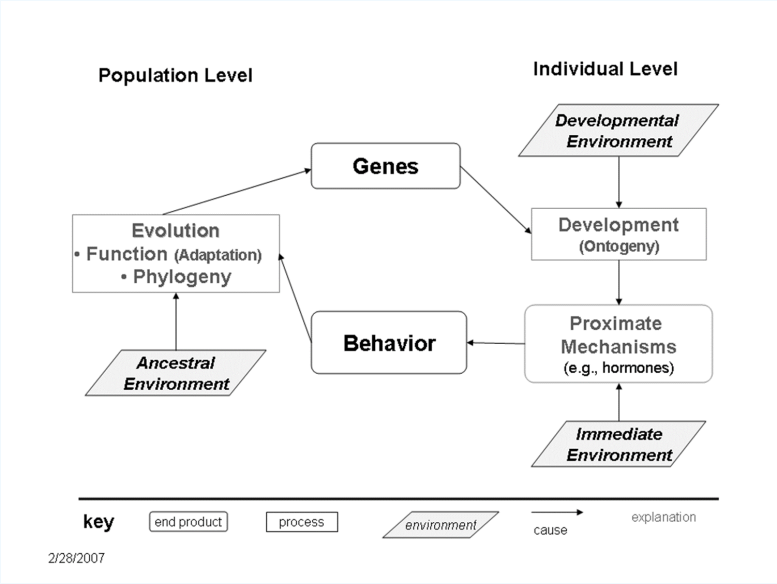


Figure 53.10.3: Diagrammatic explanation of behavioral ecology: the interaction between an organisms behavior, its genes, the environment, and evolutionary forces (W. Pete Welch; public domain); Adopted from Tinbergen (1963).

The figure shows the causal relationships among the categories of explanations. The left-hand side represents the evolutionary explanations at the species level; the right-hand side represents the proximate explanations at the individual level. In the middle are those processes' end products—genes (i.e., genome) and behaviour, both of which can be analyzed at both levels.

Evolution, which is determined by both function and phylogeny, results in the genes of a population. The genes of an individual interact with its developmental environment, resulting in mechanisms, such as a nervous system. A mechanism (which is also an end-product in its own right) interacts with the individual's immediate environment, resulting in its behaviour.

Here we return to the population level. Over many generations, the success of the species' behaviour in its ancestral environment—or more technically, the environment of evolutionary adaptedness may result in evolution as measured by a change in its genes.

In sum, there are two processes—one at the population level and one at the individual level—which are influenced by environments in three time periods.

Examples

Let's look at a couple of examples of explaining a trait or behavior using Tinbergen's four questions:

Visual perception

- Function: to find food and avoid danger.
- Phylogeny: the vertebrate eye initially developed with a blind spot, but the lack of adaptive intermediate forms prevented the loss of the blind spot.
- Causation: the lens of the eye focuses light on the retina.
- Development: neurons need the stimulation of light to wire the eye to the brain (Moore, 2001:98–99).

Sleep (Bode & Kuula, 2021):[7]

- Function: energy restoration, metabolic regulation, thermoregulation, boosting immune system, detoxification, brain maturation, circuit reorganization, synaptic optimization, avoiding danger.
- Phylogeny: sleep exists in invertebrates, lower vertebrates, and higher vertebrates. NREM and REM sleep exist in eutheria, marsupialiformes, and also evolved in birds.
- Mechanisms: mechanisms regulate wakefulness, sleep onset, and sleep. Specific mechanisms involve neurotransmitters, genes, neural structures, and the circadian rhythm.
- Ontogeny: sleep manifests differently in babies, infants, children, adolescents, adults, and older adults. Differences include the stages of sleep, sleep duration, and sex differences.

Contributors and Attributions

Modified by Dan Wetzel (University of Pittsburgh) from the following sources:

- Wikipedia, Behavioral ecology
- Wikipedia, Tinbergen's four questions.

Sources

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2. Daly, M. & Wilson, M. (1983). *Sex, evolution, and behaviour*. Brooks-Cole.
3. p411 in Tinbergen, Niko (1963) "On Aims and Methods in Ethology," Zeitschrift für Tierpsychologie, 20: 410–433.
4. Nikolaas Tinbergen, ethology, Cartwright 2000:10; Buss 2004:12)
5. "Phylogeny" often emphasizes the evolutionary genealogical relationships among species (Alcock 2001:492; Mayr, 2001:289) as distinct from the categories of explanations. Although the categories are more relevant in a conceptual discussion, the traditional term is retained here.
6. Bode, Adam; Kuula, Liisa (September 2021). "Romantic Love and Sleep Variations: Potential Proximate Mechanisms and Evolutionary Functions". *Biology*. **10** (9): 923. doi:10.3390/biology10090923.

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53.11: Reproductive Strategies

Population ecologists have hypothesized that suites of characteristics may evolve in species that lead to particular adaptations to their environments. These adaptations impact the kind of population growth their species experience. Population ecologists have described a continuum of life-history “strategies” with *K*-selected species on one end and *r*-selected species on the other (table **53.11.*a***). ***K*-selected species** are adapted to stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity (which is represented by the letter "K" in the equation for logistic population growth). These species tend to have larger, but fewer, offspring, contribute large amounts of resources to each offspring, and have long generation times. Elephants would be an example of a *K*-selected species (figure **53.11.*a***). When a habitat becomes filled with a diverse collection of creatures competing with one another for the necessities of life, the advantage shifts to *K*-strategists. *K*-strategists have stable populations that are close to *K*. There is nothing to be gained from a high growth rate (*r*). The species will benefit most by a close adaptation to the conditions of its environment.

Table 53.11.*a*: Comparison of *K*- and *r*-selected species

Characteristics of *K*-selected species	Characteristics of *r*-selected species
Mature late	Mature early
Greater longevity	Lower longevity
Increased parental care	Decreased parental care
Strong competitors	Weak competitors (strong colonizers)
Fewer offspring	More offspring
Larger offspring	Smaller offspring



(a) K-selected species



(b) r-selected species

Figure **53.11.*a***: (a) Elephants are considered K-selected species as they live long, mature late, and provide long-term parental care to few offspring. Oak trees produce many offspring that do not receive parental care, but are considered K-selected species based on longevity and late maturation. (b) Dandelions and jellyfish are both considered r-selected species as they mature early, have short lifespans, and produce many offspring that receive no parental care.

r*-selected species** are adapted to unstable and unpredictable environments. They have large numbers of small offspring. Animals that are *r*-selected do not provide a lot of resources or parental care to offspring, and the offspring are relatively self-sufficient at birth. Examples of *r*-selected species are marine invertebrates such as jellyfish and plants such as the dandelion (figure **53.11.*a). *r*-strategists have short life spans and reproduce quickly, resulting in short generation times. For example, the housefly can produce 7 generations each year (each of about 120 young). Ragweed is well-adapted to exploiting its environment in a hurry - before competitors can become established. It grows rapidly and produces a huge number of seeds (after releasing its pollen, the bane of many hay fever sufferers). Because ragweed's approach to continued survival is through rapid reproduction (a high value of *r)* it is called an *r*-strategist. Other weeds, many insects, and many rodents are also *r*-strategists. If fact, if we consider an organism a pest, it is probably an *r*-strategist.

The two extreme strategies are at two ends of a continuum on which real species life histories will exist. In addition, life history strategies do not need to evolve as suites but can evolve independently of each other; therefore, each species may have some characteristics that trend toward one extreme or the other. Nevertheless, the *r*- and *K*-selection theory provides a foundation for a more accurate life history framework. New demographic-based models of life history evolution have been developed, which incorporate many ecological concepts included in *r*- and *K*-selection theory as well as population age structure and mortality factors.

Another tool used by population ecologists is a **survivorship curve**, which is a graph of the number of individuals surviving at each age interval versus time. These curves allow us to compare the life histories of different populations (figure **53.11.*c***). There are

three types of survivorship curves. In a **type I survivorship curve**, mortality is low in the early and middle years and occurs mostly in older individuals. Organisms exhibiting a type I survivorship typically produce few offspring and provide good care to the offspring increasing the likelihood of their survival. Humans and most mammals exhibit a type I survivorship curve. In **type II survivorship curves**, mortality is relatively constant throughout the entire life span, and mortality is equally likely to occur at any point in the life span. Many bird populations provide examples of an intermediate or type II survivorship curve. In **type III survivorship curves**, early ages experience the highest mortality with much lower mortality rates for organisms that make it to advanced years. Type III organisms typically produce large numbers of offspring, but provide very little or no care for them. Trees and marine invertebrates exhibit a type III survivorship curve because very few of these organisms survive their younger years, but those that do make it to an old age are more likely to survive for a relatively long period of time.

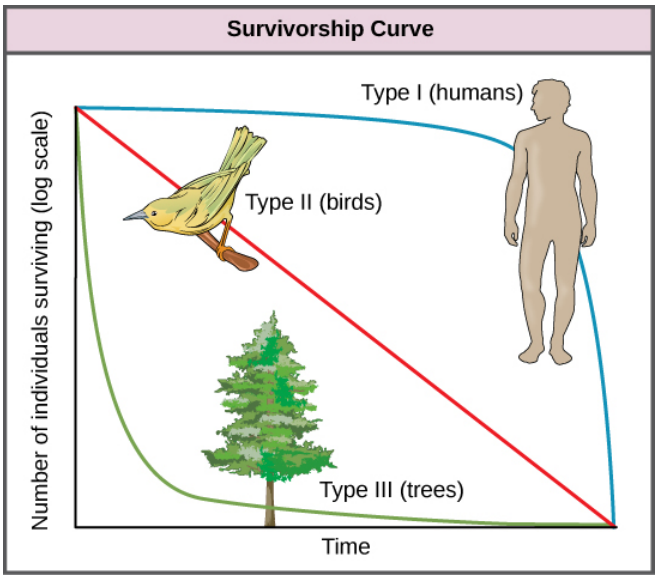


Figure **53.11.*c***: Survivorship curves show the chance of survival in a population according to age. The number of individuals surviving (on a log scale) is on the y-axis, and time (representing relative age) is on the x-axis. Humans and most mammals have a Type I survivorship curve, because death primarily occurs in the older years. The Type I survivorship curve is represented by a convex curve, which rapidly declines at the end. Birds have a Type II survivorship curve, as death at any age is equally probable. The Type II survivorship curve is represented by a straight line, going from the upper left to lower right of the graph. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive. The Type III survivorship curve is represented by a concave curve, which initially declines rapidly and then flattens.

While is no exact association between reproductive strategies (*K*- or *r*-selected) and survivorship curves (Type I, II, or III), *K*-selected species are more likely to have a Type III survivorship curve. *r*-selected species tend to have a Type I survivorship curve.

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53.12: Altruism

Learning Objectives

- Explain how altruistic behaviors can benefit populations

Altruistic Behaviors

Behaviors that lower the fitness of the individual engaging in the behavior, but increase the fitness of another individual, are termed altruistic. Examples of such behaviors are seen widely across the animal kingdom. Social insects, such as worker bees, have no ability to reproduce, yet they maintain the queen so she can populate the hive with her offspring. Meerkats keep a sentry standing guard to warn the rest of the colony about intruders, even though the sentry is putting itself at risk. Wolves and wild dogs bring meat to pack members not present during a hunt. Lemurs take care of infants unrelated to them. Although on the surface these behaviors appear to be altruistic, it may not be so simple.

Why Does Altruism Exist?

There has been much discussion over why altruistic behaviors exist. Do these behaviors lead to overall evolutionary advantages for their species ? Do they help the altruistic individual pass on its own genes? And what about such activities between unrelated individuals? One explanation for altruistic-type behaviors is found in the genetics of natural selection. In the 1976 book, *The Selfish Gene*, scientist Richard Dawkins attempted to explain many seemingly-altruistic behaviors from the viewpoint of the gene itself. Although a gene obviously cannot be selfish in the human sense, it may appear that way if the sacrifice of an individual benefits related individuals that share genes that are identical by descent (present in relatives because of common lineage). Mammal parents make this sacrifice to take care of their offspring. Emperor penguins migrate miles in harsh conditions to bring food back for their young. Selfish gene theory has been controversial over the years and is still discussed among scientists in related fields.



Figure **53.12.1**: Altruistic actions: Emperor penguins migrate miles in harsh conditions to bring back food for their young. Are extreme, altruistic actions such as these motivated by the selfish need to pass on genes?

Even less-related individuals (those with less genetic identity than that shared by parent and offspring) benefit from seemingly altruistic behavior. The activities of social insects such as bees, wasps, ants, and termites are good examples. Sterile workers in these societies take care of the queen because they are closely related to it; as the queen has offspring, she is passing on genes from the workers indirectly. Thus, it is of fitness benefit for the worker to maintain the queen without having any direct chance of passing on its genes due to its sterility. The lowering of individual fitness to enhance the reproductive fitness of a relative and, thus, one's inclusive fitness evolves through kin selection. This phenomenon can explain many superficially-altruistic behaviors seen in animals. However, these behaviors may not be truly defined as altruism in these cases because the actor is actually increasing its own fitness either directly (through its own offspring) or indirectly (through the inclusive fitness it gains through relatives that share genes with it).

Unrelated individuals may also act altruistically to each other; this seems to defy the "selfish gene" explanation. An example of this is observed in many monkey species where a monkey will present its back to an unrelated monkey to have that individual pick the parasites from its fur. After a certain amount of time, the roles are reversed and the first monkey now grooms the second monkey. Thus, there is reciprocity in the behavior. Both benefit from the interaction and their fitness is raised more than if neither cooperated or if one cooperated and the other did not. This behavior is still not necessarily altruism, as the "giving" behavior of the

actor is based on the expectation that it will be the "receiver" of the behavior in the future; a concept termed reciprocal altruism. Reciprocal altruism requires that individuals repeatedly encounter each other, often the result of living in the same social group, and that cheaters (those that never "give back") are punished.

Evolutionary Game Theory and Altruism

According to evolutionary game theory, a modification of classical game theory in mathematics, many of these so-called "altruistic behaviors" are not altruistic at all. The definition of "pure" altruism, based on human behavior, is an action that benefits another without any direct benefit to oneself. Most of the behaviors previously described do not seem to satisfy this definition; game theorists are good at finding "selfish" components in them. Others have argued that the terms "selfish" and "altruistic" should be dropped completely when discussing animal behavior, as they describe human behavior and may not be directly applicable to instinctual animal activity. What is clear, though, is that heritable behaviors that improve the chances of passing on one's genes or a portion of one's genes are favored by natural selection and will be retained in future generations as long as those behaviors convey a fitness advantage.

Key Points

- Behaviors that lower the fitness of the individual, but increase the fitness of another individual are termed altruistic; why altruistic behaviors exist has been the topic of some debate.
- One explanation for altruistic-type behaviors is found in the genetics of natural selection and the "selfish gene " theory: although a gene cannot be selfish in the human sense, it may appear that way if the sacrifice of an individual benefits related individuals that share genes that are identical.
- Even less-related individuals, those with less genetic identity than that shared by parent and offspring, benefit from seemingly-altruistic behavior, such as sterile worker bees protecting the queen.
- Unrelated individuals may also act altruistically to each other, which seems to defy the "selfish gene" explanation; however, this altruism is typically reciprocal, in that both benefit from the interaction.
- Most of the behaviors described when speaking of altruism do not seem to satisfy the definition of "pure" altruism; some evolutionary game theorists suggest that we get rid of the terms "altruistic" and "selfish" altogether since they describe human behavior.

Key Terms

- **kin selection**: an evolutionary mechanism by which an organism's behavior benefits the reproductive success of its relatives, including at the expense of its own survival or reproduction
- **altruism**: devotion to the interests of others; brotherly kindness; opposed to egoism or selfishness
- **game theory**: a branch of applied mathematics that studies strategic situations in which individuals or organizations choose various actions in an attempt to maximize their returns

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CHAPTER OVERVIEW

54: Ecology of Individuals and Populations

54.1: The Environmental Challenges

54.2: Populations, Groups of Single Species in One Place

54.3: Population Demography and Dynamics

54.4: Life History and the Cost of Reproduction

54.5: Environmental Limits to Population Growth

54.6: Factors that Regulate Populations

54.7: Human Population Growth

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54.1: The Environmental Challenges

Imagine sailing down a river in a small motorboat on a weekend afternoon; the water is smooth and you are enjoying the warm sunshine and cool breeze when suddenly you are hit in the head by a 20-pound silver carp. This is a risk now on many rivers and canal systems in Illinois and Missouri because of the presence of Asian carp.



Figure **54.1.1**: Asian carp jump out of the water in response to electrofishing. The Asian carp in the inset photograph were harvested from the Little Calumet River in Illinois in May, 2010, using rotenone, a toxin often used as an insecticide, in an effort to learn more about the population of the species. (credit main image: modification of work by USGS; credit inset: modification of work by Lt. David French, USCG)

This fish—actually a group of species including the silver, black, grass, and big head carp—has been farmed and eaten in China for over 1000 years. It is one of the most important aquaculture food resources worldwide. In the United States, however, Asian carp is considered a dangerous invasive species that disrupts community structure and composition to the point of threatening native species.

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54.2: Populations, Groups of Single Species in One Place

Imagine sailing down a river in a small motorboat on a weekend afternoon; the water is smooth and you are enjoying the warm sunshine and cool breeze when suddenly you are hit in the head by a 20-pound silver carp. This is a risk now on many rivers and canal systems in Illinois and Missouri because of the presence of Asian carp.



Figure **54.2.1**: Asian carp jump out of the water in response to electrofishing. The Asian carp in the inset photograph were harvested from the Little Calumet River in Illinois in May, 2010, using rotenone, a toxin often used as an insecticide, in an effort to learn more about the population of the species. (credit main image: modification of work by USGS; credit inset: modification of work by Lt. David French, USCG)

This fish—actually a group of species including the silver, black, grass, and big head carp—has been farmed and eaten in China for over 1000 years. It is one of the most important aquaculture food resources worldwide. In the United States, however, Asian carp is considered a dangerous invasive species that disrupts community structure and composition to the point of threatening native species.

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54.3: Population Demography and Dynamics

Skills to Develop

- Describe how ecologists measure population size and density
- Describe three different patterns of population distribution
- Use life tables to calculate mortality rates
- Describe the three types of survivorship curves and relate them to specific populations

Populations are dynamic entities. Populations consist all of the species living within a specific area, and populations fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. The statistical study of population dynamics, demography, uses a series of mathematical tools to investigate how populations respond to changes in their biotic and abiotic environments. Many of these tools were originally designed to study human populations. For example, life tables, which detail the life expectancy of individuals within a population, were initially developed by life insurance companies to set insurance rates. In fact, while the term “demographics” is commonly used when discussing humans, all living populations can be studied using this approach.

Population Size and Density

The study of any population usually begins by determining how many individuals of a particular species exist, and how closely associated they are with each other. Within a particular habitat, a population can be characterized by its population size (*N*), the total number of individuals, and its population density, the number of individuals within a specific area or volume. Population size and density are the two main characteristics used to describe and understand populations. For example, populations with more individuals may be more stable than smaller populations based on their genetic variability, and thus their potential to adapt to the environment. Alternatively, a member of a population with low population density (more spread out in the habitat), might have more difficulty finding a mate to reproduce compared to a population of higher density. As is shown in Figure **54.3.1**, smaller organisms tend to be more densely distributed than larger organisms.

Art Connection

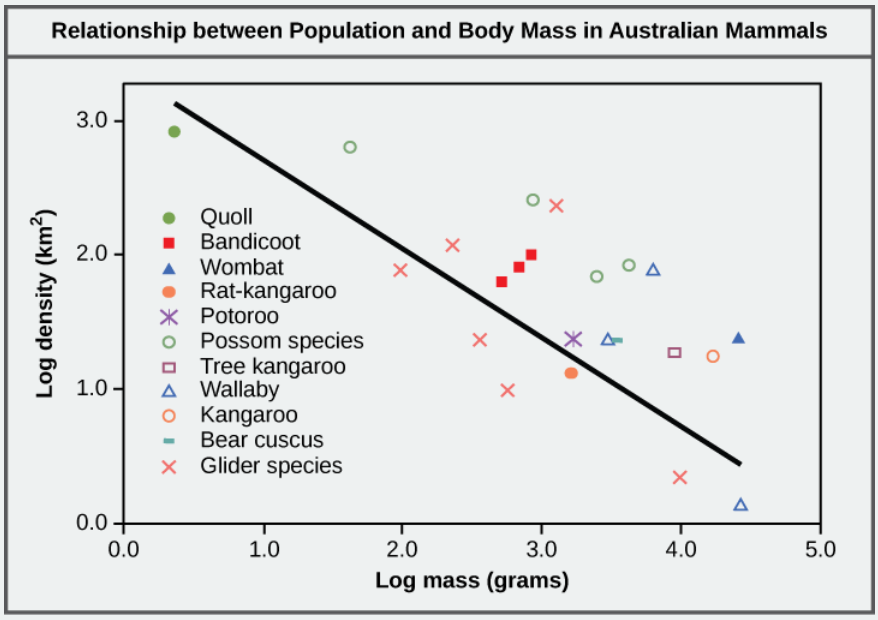


Figure **54.3.1**: Australian mammals show a typical inverse relationship between population density and body size.

As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

Population Research Methods

The most accurate way to determine population size is to simply count all of the individuals within the habitat. However, this method is often not logistically or economically feasible, especially when studying large habitats. Thus, scientists usually study populations by sampling a representative portion of each habitat and using this data to make inferences about the habitat as a whole. A variety of methods can be used to sample populations to determine their size and density. For immobile organisms such as plants, or for very small and slow-moving organisms, a quadrat may be used (Figure **54.3.2**). A quadrat is a way of marking off square areas within a habitat, either by staking out an area with sticks and string, or by the use of a wood, plastic, or metal square placed on the ground. After setting the quadrats, researchers then count the number of individuals that lie within their boundaries. Multiple quadrat samples are performed throughout the habitat at several random locations. All of this data can then be used to estimate the population size and population density within the entire habitat. The number and size of quadrat samples depends on the type of organisms under study and other factors, including the density of the organism. For example, if sampling daffodils, a 1 m^2 quadrat might be used whereas with giant redwoods, which are larger and live much further apart from each other, a larger quadrat of 100 m^2 might be employed. This ensures that enough individuals of the species are counted to get an accurate sample that correlates with the habitat, including areas not sampled.

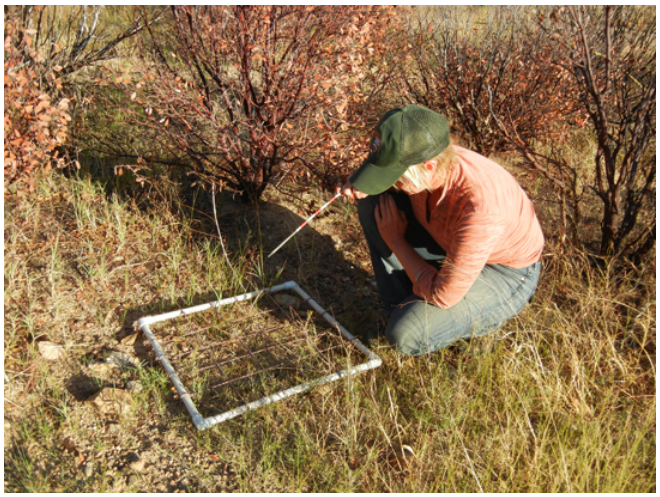
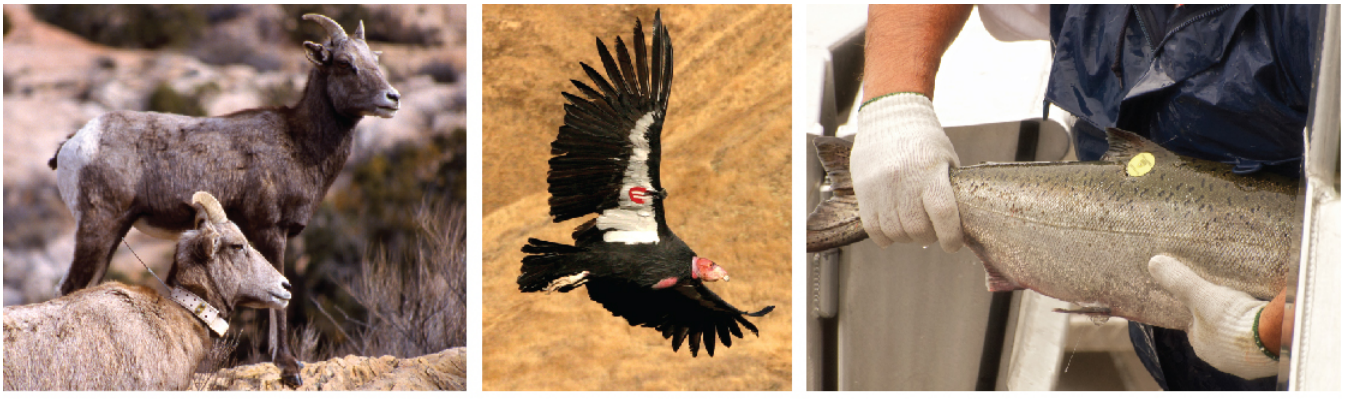


Figure **54.3.2**: A scientist uses a quadrat to measure population size and density. (credit: NPS Sonoran Desert Network)

For mobile organisms, such as mammals, birds, or fish, a technique called mark and recapture is often used. This method involves marking a sample of captured animals in some way (such as tags, bands, paint, or other body markings), and then releasing them back into the environment to allow them to mix with the rest of the population; later, a new sample is collected, including some individuals that are marked (recaptures) and some individuals that are unmarked (Figure **54.3.3**).



(a) (b) (c)

Figure **54.3.3**: Mark and recapture is used to measure the population size of mobile animals such as (a) bighorn sheep, (b) the California condor, and (c) salmon. (credit a: modification of work by Neal Herbert, NPS; credit b: modification of work by Pacific Southwest Region USFWS; credit c: modification of work by Ingrid Taylar)

Using the ratio of marked and unmarked individuals, scientists determine how many individuals are in the sample. From this, calculations are used to estimate the total population size. This method assumes that the larger the population, the lower the percentage of tagged organisms that will be recaptured since they will have mixed with more untagged individuals. For example, if 80 deer are captured, tagged, and released into the forest, and later 100 deer are captured and 20 of them are already marked, we can determine the population size (N) using the following equation:

$$\frac{\text{number marked first catch} * \text{total number of second catch}}{\text{number marked second catch}} = N$$

Using our example, the population size would be estimated at 400.

$$\frac{(80 * 100)}{20} = 400$$

Therefore, there are an estimated 400 total individuals in the original population.

There are some limitations to the mark and recapture method. Some animals from the first catch may learn to avoid capture in the second round, thus inflating population estimates. Alternatively, animals may preferentially be retrapped (especially if a food reward is offered), resulting in an underestimate of population size. Also, some species may be harmed by the marking technique, reducing their survival. A variety of other techniques have been developed, including the electronic tracking of animals tagged with radio transmitters and the use of data from commercial fishing and trapping operations to estimate the size and health of populations and communities.

Species Distribution

In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals. Species dispersion patterns (or distribution patterns) show the spatial relationship between members of a population within a habitat at a particular point in time. In other words, they show whether members of the species live close together or far apart, and what patterns are evident when they are spaced apart.

Individuals in a population can be more or less equally spaced apart, dispersed randomly with no predictable pattern, or clustered in groups. These are known as uniform, random, and clumped dispersion patterns, respectively (Figure **54.3.4**). Uniform dispersion is observed in plants that secrete substances inhibiting the growth of nearby individuals (such as the release of toxic chemicals by the sage plant *Salvia leucophylla*, a phenomenon called allelopathy) and in animals like the penguin that maintain a defined territory. An example of random dispersion occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in a favorable environment. A clumped dispersion may be seen in plants that drop their seeds straight to the ground, such as oak trees, or animals that live in groups (schools of fish or herds of elephants). Clumped dispersions may also be a function of habitat heterogeneity. Thus, the dispersion of the individuals within a population provides more information about how they interact with each other than does a simple density measurement. Just as lower density species might have more difficulty finding a mate, solitary species with a random distribution might have a similar difficulty when compared to social species clumped together in groups.

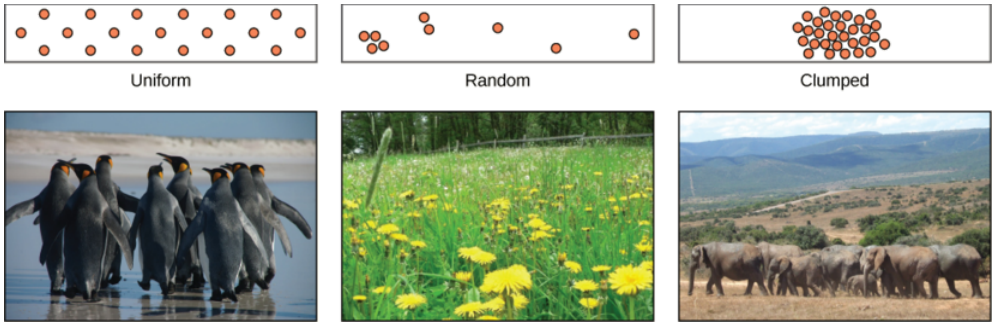


Figure **54.3.4**: Species may have uniform, random, or clumped distribution. Territorial birds such as penguins tend to have uniform distribution. Plants such as dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as elephants that travel in groups exhibit clumped distribution. (credit a: modification of work by Ben Tubby; credit b: modification of work by Rosendahl; credit c: modification of work by Rebecca Wood)

Demography

While population size and density describe a population at one particular point in time, scientists must use demography to study the dynamics of a population. Demography is the statistical study of population changes over time: birth rates, death rates, and life expectancies. Each of these measures, especially birth rates, may be affected by the population characteristics described above. For example, a large population size results in a higher birth rate because more potentially reproductive individuals are present. In contrast, a large population size can also result in a higher death rate because of competition, disease, and the accumulation of waste. Similarly, a higher population density or a clumped dispersion pattern results in more potential reproductive encounters between individuals, which can increase birth rate. Lastly, a female-biased sex ratio (the ratio of males to females) or age structure (the proportion of population members at specific age ranges) composed of many individuals of reproductive age can increase birth rates.

In addition, the demographic characteristics of a population can influence how the population grows or declines over time. If birth and death rates are equal, the population remains stable. However, the population size will increase if birth rates exceed death rates; the population will decrease if birth rates are less than death rates. Life expectancy is another important factor; the length of time individuals remain in the population impacts local resources, reproduction, and the overall health of the population. These demographic characteristics are often displayed in the form of a life table.

Life Tables

Life tables provide important information about the life history of an organism. Life tables divide the population into age groups and often sexes, and show how long a member of that group is likely to live. They are modeled after actuarial tables used by the insurance industry for estimating human life expectancy. Life tables may include the probability of individuals dying before their next birthday (i.e., their mortality rate), the percentage of surviving individuals dying at a particular age interval, and their life expectancy at each interval. An example of a life table is shown in Table **54.3.1** from a study of Dall mountain sheep, a species native to northwestern North America. Notice that the population is divided into age intervals (column A). The mortality rate (per 1000), shown in column D, is based on the number of individuals dying during the age interval (column B) divided by the number of individuals surviving at the beginning of the interval (Column C), multiplied by 1000.

$$\text{mortality rate} = \frac{\text{number of individuals dying}}{\text{number of individuals surviving}} * 1000$$

For example, between ages three and four, 12 individuals die out of the 776 that were remaining from the original 1000 sheep. This number is then multiplied by 1000 to get the mortality rate per thousand.

$$\text{mortality rate} = \frac{12}{776} * 1000 \approx 15.5$$

As can be seen from the mortality rate data (column D), a high death rate occurred when the sheep were between 6 and 12 months old, and then increased even more from 8 to 12 years old, after which there were few survivors. The data indicate that if a sheep in this population were to survive to age one, it could be expected to live another 7.7 years on average, as shown by the life expectancy numbers in column E.

Table 54.3.1: Life Table of Dall Mountain Sheep[1]

Age interval (years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 alive at beginning of age interval	Life expectancy or mean lifetime remaining to those attaining age interval
0-0.5	54	1000	54.0	7.06
0.5-1	145	946	153.3	--
1-2	12	801	15.0	7.7
2-3	13	789	16.5	6.8
3-4	12	776	15.5	5.9
4-5	30	764	39.3	5.0
5-6	46	734	62.7	4.2
6-7	48	688	69.8	3.4
7-8	69	640	107.8	2.6
8-9	132	571	231.2	1.9
9-10	187	439	426.0	1.3
10-11	156	252	619.0	0.9
11-12	90	96	937.5	0.6
12-13	3	6	500.0	1.2
13-14	3	3	1000	0.7

Survivorship Curves

Another tool used by population ecologists is a survivorship curve, which is a graph of the number of individuals surviving at each age interval plotted versus time (usually with data compiled from a life table). These curves allow us to compare the life histories of different populations (Figure **54.3.5**). Humans and most primates exhibit a Type I survivorship curve because a high percentage of offspring survive their early and middle years—death occurs predominantly in older individuals. These types of species usually have small numbers of offspring at one time, and they give a high amount of parental care to them to ensure their survival. Birds are an example of an intermediate or Type II survivorship curve because birds die more or less equally at each age interval. These organisms also may have relatively few offspring and provide significant parental care. Trees, marine invertebrates, and most fishes exhibit a Type III survivorship curve because very few of these organisms survive their younger years; however, those that make it to an old age are more likely to survive for a relatively long period of time. Organisms in this category usually have a very large number of offspring, but once they are born, little parental care is provided. Thus these offspring are “on their own” and vulnerable to predation, but their sheer numbers assure the survival of enough individuals to perpetuate the species.

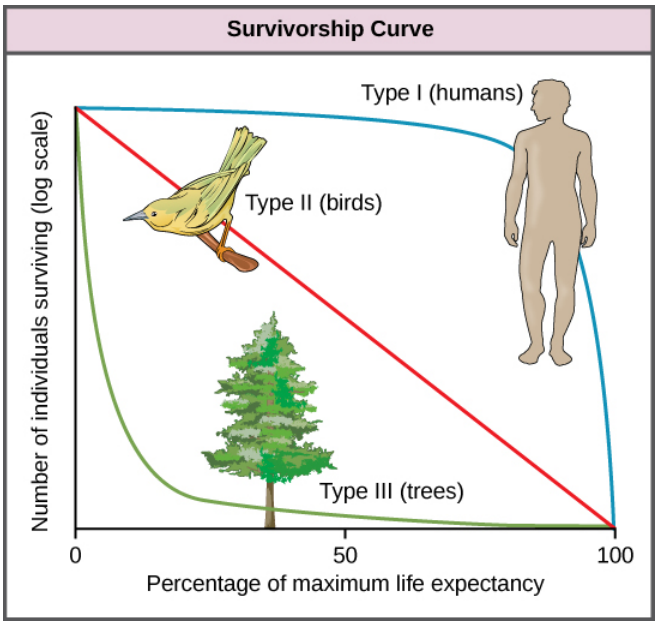


Figure **54.3.5**: Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

Summary

Populations are individuals of a species that live in a particular habitat. Ecologists measure characteristics of populations: size, density, dispersion pattern, age structure, and sex ratio. Life tables are useful to calculate life expectancies of individual population members. Survivorship curves show the number of individuals surviving at each age interval plotted versus time.

Art Connections

Figure **54.3.1**: As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

Answer

Smaller animals require less food and other resources, so the environment can support more of them.

Footnotes

1. 1 Data Adapted from Edward S. Deevey, Jr., "Life Tables for Natural Populations of Animals," *The Quarterly Review of Biology* 22, no. 4 (December 1947): 283-314.

Glossary

demography

statistical study of changes in populations over time

life table

table showing the life expectancy of a population member based on its age

mark and recapture

technique used to determine population size in mobile organisms

mortality rate

proportion of population surviving to the beginning of an age interval that die during the age interval

population density

number of population members divided by the area or volume being measured

population size (*N*)

number of population members in a habitat at the same time

quadrat

square made of various materials used to determine population size and density in slow moving or stationary organisms

species dispersion pattern

(also, species distribution pattern) spatial location of individuals of a given species within a habitat at a particular point in time

survivorship curve

graph of the number of surviving population members versus the relative age of the member

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54.4: Life History and the Cost of Reproduction

Skills to Develop

- Describe how life history patterns are influenced by natural selection
- Explain different life history patterns and how different reproductive strategies affect species' survival

A species' life history describes the series of events over its lifetime, such as how resources are allocated for growth, maintenance, and reproduction. Life history traits affect the life table of an organism. A species' life history is genetically determined and shaped by the environment and natural selection.

Life History Patterns and Energy Budgets

Energy is required by all living organisms for their growth, maintenance, and reproduction; at the same time, energy is often a major limiting factor in determining an organism's survival. Plants, for example, acquire energy from the sun via photosynthesis, but must expend this energy to grow, maintain health, and produce energy-rich seeds to produce the next generation. Animals have the additional burden of using some of their energy reserves to acquire food. Furthermore, some animals must expend energy caring for their offspring. Thus, all species have an energy budget: they must balance energy intake with their use of energy for metabolism, reproduction, parental care, and energy storage (such as bears building up body fat for winter hibernation).

Parental Care and Fecundity

Fecundity is the potential reproductive capacity of an individual within a population. In other words, fecundity describes how many offspring could ideally be produced if an individual has as many offspring as possible, repeating the reproductive cycle as soon as possible after the birth of the offspring. In animals, fecundity is inversely related to the amount of parental care given to an individual offspring. Species, such as many marine invertebrates, that produce many offspring usually provide little if any care for the offspring (they would not have the energy or the ability to do so anyway). Most of their energy budget is used to produce many tiny offspring. Animals with this strategy are often self-sufficient at a very early age. This is because of the energy tradeoff these organisms have made to maximize their evolutionary fitness. Because their energy is used for producing offspring instead of parental care, it makes sense that these offspring have some ability to be able to move within their environment and find food and perhaps shelter. Even with these abilities, their small size makes them extremely vulnerable to predation, so the production of many offspring allows enough of them to survive to maintain the species.

Animal species that have few offspring during a reproductive event usually give extensive parental care, devoting much of their energy budget to these activities, sometimes at the expense of their own health. This is the case with many mammals, such as humans, kangaroos, and pandas. The offspring of these species are relatively helpless at birth and need to develop before they achieve self-sufficiency.

Plants with low fecundity produce few energy-rich seeds (such as coconuts and chestnuts) with each having a good chance to germinate into a new organism; plants with high fecundity usually have many small, energy-poor seeds (like orchids) that have a relatively poor chance of surviving. Although it may seem that coconuts and chestnuts have a better chance of surviving, the energy tradeoff of the orchid is also very effective. It is a matter of where the energy is used, for large numbers of seeds or for fewer seeds with more energy.

Early versus Late Reproduction

The timing of reproduction in a life history also affects species survival. Organisms that reproduce at an early age have a greater chance of producing offspring, but this is usually at the expense of their growth and the maintenance of their health. Conversely, organisms that start reproducing later in life often have greater fecundity or are better able to provide parental care, but they risk that they will not survive to reproductive age. Examples of this can be seen in fishes. Small fish like guppies use their energy to reproduce rapidly, but never attain the size that would give them defense against some predators. Larger fish, like the bluegill or shark, use their energy to attain a large size, but do so with the risk that they will die before they can reproduce or at least reproduce to their maximum. These different energy strategies and tradeoffs are key to understanding the evolution of each species as it maximizes its fitness and fills its niche. In terms of energy budgeting, some species "blow it all" and use up most of their energy

reserves to reproduce early before they die. Other species delay having reproduction to become stronger, more experienced individuals and to make sure that they are strong enough to provide parental care if necessary.

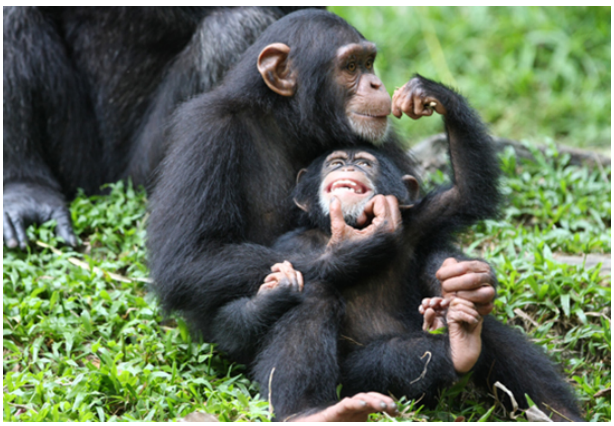
Single versus Multiple Reproductive Events

Some life history traits, such as fecundity, timing of reproduction, and parental care, can be grouped together into general strategies that are used by multiple species. Semelparity occurs when a species reproduces only once during its lifetime and then dies. Such species use most of their resource budget during a single reproductive event, sacrificing their health to the point that they do not survive. Examples of semelparity are bamboo, which flowers once and then dies, and the Chinook salmon (Figure 54.4.1a), which uses most of its energy reserves to migrate from the ocean to its freshwater nesting area, where it reproduces and then dies. Scientists have posited alternate explanations for the evolutionary advantage of the Chinook's post-reproduction death: a programmed suicide caused by a massive release of corticosteroid hormones, presumably so the parents can become food for the offspring, or simple exhaustion caused by the energy demands of reproduction; these are still being debated.

Iteroparity describes species that reproduce repeatedly during their lives. Some animals are able to mate only once per year, but survive multiple mating seasons. The pronghorn antelope is an example of an animal that goes into a seasonal estrus cycle ("heat"): a hormonally induced physiological condition preparing the body for successful mating (Figure 54.4.1b). Females of these species mate only during the estrus phase of the cycle. A different pattern is observed in primates, including humans and chimpanzees, which may attempt reproduction at any time during their reproductive years, even though their menstrual cycles make pregnancy likely only a few days per month during ovulation (Figure 54.4.1c).



a b



c

Figure 54.4.1: The (a) Chinook salmon mates once and dies. The (b) pronghorn antelope mates during specific times of the year during its reproductive life. Primates, such as humans and (c) chimpanzees, may mate on any day, independent of ovulation. (credit a: modification of work by Roger Tabor, USFWS; credit b: modification of work by Mark Gocke, USDA; credit c: modification of work by "Shiny Things"/Flickr)

Evolution Connection: Energy Budgets, Reproductive Costs, and Sexual Selection in *Drosophila*

Research into how animals allocate their energy resources for growth, maintenance, and reproduction has used a variety of experimental animal models. Some of this work has been done using the common fruit fly, *Drosophila melanogaster*. Studies have shown that not only does reproduction have a cost as far as how long male fruit flies live, but also fruit flies that have already mated several times have limited sperm remaining for reproduction. Fruit flies maximize their last chances at reproduction by selecting optimal mates.

In a 1981 study, male fruit flies were placed in enclosures with either virgin or inseminated females. The males that mated with virgin females had shorter life spans than those in contact with the same number of inseminated females with which they were unable to mate. This effect occurred regardless of how large (indicative of their age) the males were. Thus, males that did not mate lived longer, allowing them more opportunities to find mates in the future.

More recent studies, performed in 2006, show how males select the female with which they will mate and how this is affected by previous matings (Figure **54.4.2**).[1] Males were allowed to select between smaller and larger females. Findings showed that larger females had greater fecundity, producing twice as many offspring per mating as the smaller females did. Males that had previously mated, and thus had lower supplies of sperm, were termed "resource-depleted," while males that had not mated were termed "non-resource-depleted." The study showed that although non-resource-depleted males preferentially mated with larger females, this selection of partners was more pronounced in the resource-depleted males. Thus, males with depleted sperm supplies, which were limited in the number of times that they could mate before they replenished their sperm supply, selected larger, more fecund females, thus maximizing their chances for offspring. This study was one of the first to show that the physiological state of the male affected its mating behavior in a way that clearly maximizes its use of limited reproductive resources.

	Ratio large/small females mated
Non sperm-depleted	8 ± 5
Sperm-depleted	15 ± 5

Figure **54.4.2**: Male fruit flies that had previously mated (sperm-depleted) picked larger, more fecund females more often than those that had not mated (non-sperm-depleted). This change in behavior causes an increase in the efficiency of a limited reproductive resource: sperm.

These studies demonstrate two ways in which the energy budget is a factor in reproduction. First, energy expended on mating may reduce an animal's lifespan, but by this time they have already reproduced, so in the context of natural selection this early death is not of much evolutionary importance. Second, when resources such as sperm (and the energy needed to replenish it) are low, an organism's behavior can change to give them the best chance of passing their genes on to the next generation. These changes in behavior, so important to evolution, are studied in a discipline known as behavioral biology, or ethology, at the interface between population biology and psychology.

Summary

All species have evolved a pattern of living, called a life history strategy, in which they partition energy for growth, maintenance, and reproduction. These patterns evolve through natural selection; they allow species to adapt to their environment to obtain the resources they need to successfully reproduce. There is an inverse relationship between fecundity and parental care. A species may reproduce early in life to ensure surviving to a reproductive age or reproduce later in life to become larger and healthier and better able to give parental care. A species may reproduce once (semelparity) or many times (iteroparity) in its life.

Footnotes

1. 1 Adapted from Phillip G. Byrne and William R. Rice, "Evidence for adaptive male mate choice in the fruit fly *Drosophila melanogaster,*" Proc Biol Sci. 273, no. 1589 (2006): 917-922, doi: 10.1098/rspb.2005.3372.

Glossary

energy budget

allocation of energy resources for body maintenance, reproduction, and parental care

fecundity

potential reproductive capacity of an individual

iteroparity

life history strategy characterized by multiple reproductive events during the lifetime of a species

life history

inherited pattern of resource allocation under the influence of natural selection and other evolutionary forces

semelparity

life history strategy characterized by a single reproductive event followed by death

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54.5: Environmental Limits to Population Growth

Skills to Develop

- Explain the characteristics of and differences between exponential and logistic growth patterns
- Give examples of exponential and logistic growth in natural populations
- Describe how natural selection and environmental adaptation led to the evolution of particular life history patterns

Although life histories describe the way many characteristics of a population (such as their age structure) change over time in a general way, population ecologists make use of a variety of methods to model population dynamics mathematically. These more precise models can then be used to accurately describe changes occurring in a population and better predict future changes. Certain models that have been accepted for decades are now being modified or even abandoned due to their lack of predictive ability, and scholars strive to create effective new models.

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, and then population growth decreases as resources become depleted. This accelerating pattern of increasing population size is called exponential growth.

The best example of exponential growth is seen in bacteria. Bacteria are prokaryotes that reproduce by prokaryotic fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour, there is one round of division and each organism divides, resulting in 2000 organisms—an increase of 1000. In another hour, each of the 2000 organisms will double, producing 4000, an increase of 2000 organisms. After the third hour, there should be 8000 bacteria in the flask, an increase of 4000 organisms. The important concept of exponential growth is that the population growth rate—the number of organisms added in each reproductive generation—is accelerating; that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the population would have increased from 1000 to more than 16 billion. When the population size, *N*, is plotted over time, a J-shaped growth curve is produced (Figure **54.5.1**).

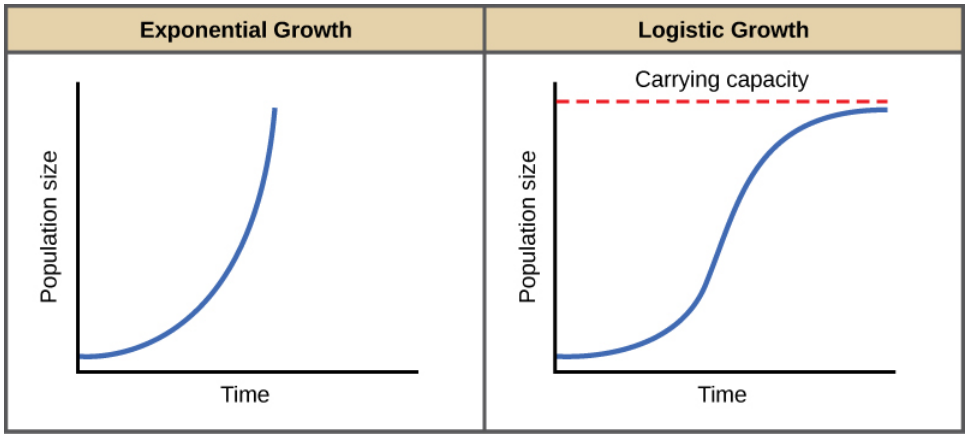


Figure **54.5.1**: When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

The bacteria example is not representative of the real world where resources are limited. Furthermore, some bacteria will die during the experiment and thus not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the death rate (*D*) (number organisms that die during a particular time interval) is subtracted from the birth rate (*B*) (number organisms that are born during that interval). This is shown in the following formula:

$$\frac{\Delta N \text{ (change in number)}}{\Delta T \text{ (change in time)}} = B \text{ (birth rate)} - D \text{ (death rate)}$$

The birth rate is usually expressed on a per capita (for each individual) basis. Thus, *B* (birth rate) = *bN* (the per capita birth rate "*b*" multiplied by the number of individuals "*N*") and *D* (death rate) =*dN* (the per capita death rate "d" multiplied by the number of individuals "*N*"). Additionally, ecologists are interested in the population at a particular point in time, an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the "instantaneous" growth rate, replacing the *change* in number and time with an instant-specific measurement of number and time.

$$\frac{dN}{dT} = bN - dN = (b - d)N$$

Notice that the "*d*" associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called "*d*." The difference between birth and death rates is further simplified by substituting the term "*r*" (intrinsic rate of increase) for the relationship between birth and death rates:

$$\frac{dN}{dT} = rN$$

The value "r" can be positive, meaning the population is increasing in size; or negative, meaning the population is decreasing in size; or zero, where the population's size is unchanging, a condition known as zero population growth. A further refinement of the formula recognizes that different species have inherent differences in their intrinsic rate of increase (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its biotic potential, or r_{max}, thus changing the equation to:

$$\frac{dN}{dT} = r_{\max}N$$

Logistic Growth

Exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the "struggle for existence," which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the logistic growth model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off (Figure 54.5.1). This population size, which represents the maximum population size that a particular environment can support, is called the carrying capacity, or K.

The formula we use to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression "K–N" is indicative of how many individuals may be added to a population at a given stage, and "K–N" divided by "K" is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:

$$\begin{aligned}\frac{dN}{dT} &= r_{\max}\frac{dN}{dT} \\ &= r_{\max}N\frac{(K-N)}{K}\end{aligned}$$

Notice that when N is very small, $(K - N)/K$ becomes close to K/K or 1, and the right side of the equation reduces to $r_{max}N$, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when N is large, $(K - N)/K$ come close to zero, which means that population growth will be slowed greatly or even stopped. Thus, population growth is greatly slowed in large populations by the carrying capacity K. This model also allows for the population of a negative population growth, or a population decline. This occurs when the number of individuals in the population exceeds the carrying capacity (because the value of $(K - N)/K$ is negative).

A graph of this equation yields an S-shaped curve (Figure **54.5.1**), and it is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition** (intra- = "within"; -specific = "species"). Intraspecific competition for resources may not affect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment's carrying capacity.

Examples of Logistic Growth

Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube (Figure **54.5.2**a). Its growth levels off as the population depletes the nutrients that are necessary for its growth. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals (Figure **54.5.2**b). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

Art Connection

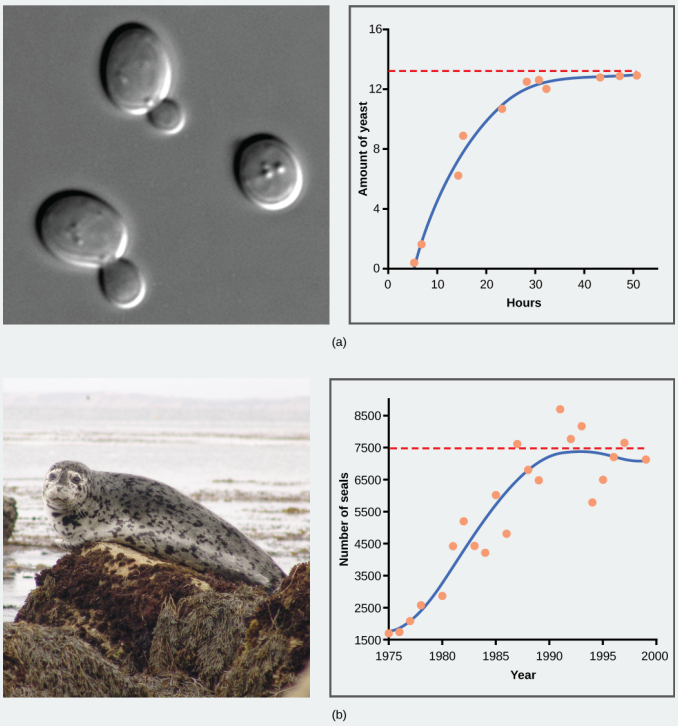


Figure **54.5.2**: (a) Yeast grown in ideal conditions in a test tube show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.

If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

A. The carrying capacity of seals would decrease, as would the seal population.

B. The carrying capacity of seals would decrease, but the seal population would remain the same.
C. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
D. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Summary

Populations with unlimited resources grow exponentially, with an accelerating growth rate. When resources become limiting, populations follow a logistic growth curve. The population of a species will level off at the carrying capacity of its environment.

Art Connections

Figure 54.5.2b If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

A. The carrying capacity of seals would decrease, as would the seal population.
B. The carrying capacity of seals would decrease, but the seal population would remain the same.
C. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
D. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Answer

A

Glossary

biotic potential (r_{max})
maximal potential growth rate of a species

birth rate (*B*)
number of births within a population at a specific point in time

carrying capacity (*K*)
number of individuals of a species that can be supported by the limited resources of a habitat

death rate (*D*)
number of deaths within a population at a specific point in time

exponential growth
accelerating growth pattern seen in species under conditions where resources are not limiting

intraspecific competition
competition between members of the same species

J-shaped growth curve
shape of an exponential growth curve

logistic growth
leveling off of exponential growth due to limiting resources

population growth rate
number of organisms added in each reproductive generation

S-shaped growth curve

shape of a logistic growth curve

zero population growth

steady population size where birth rates and death rates are equal

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54.6: Factors that Regulate Populations

Skills to Develop

- Give examples of how the carrying capacity of a habitat may change
- Compare and contrast density-dependent growth regulation and density-independent growth regulation, giving examples
- Give examples of exponential and logistic growth in wild animal populations
- Describe how natural selection and environmental adaptation leads to the evolution of particular life-history patterns

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. The carrying capacity varies annually: for example, some summers are hot and dry whereas others are cold and wet. In many areas, the carrying capacity during the winter is much lower than it is during the summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They engage in interspecific competition: that is, they share the environment with other species, competing with them for the same resources. These factors are also important to understanding how a specific population will grow.

Nature regulates population growth in a variety of ways. These are grouped into density-dependent factors, in which the density of the population at a given time affects growth rate and mortality, and density-independent factors, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Density-dependent Regulation

Most density-dependent factors are biological in nature (biotic), and include predation, inter- and intraspecific competition, accumulation of waste, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown in Figure **54.6.1** with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals.[1] Denser populations of the parasite exhibited lower fecundity: they contained fewer eggs. One possible explanation for this is that females would be smaller in more dense populations (due to limited resources) and that smaller females would have fewer eggs. This hypothesis was tested and disproved in a 2009 study which showed that female weight had no influence.[2] The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

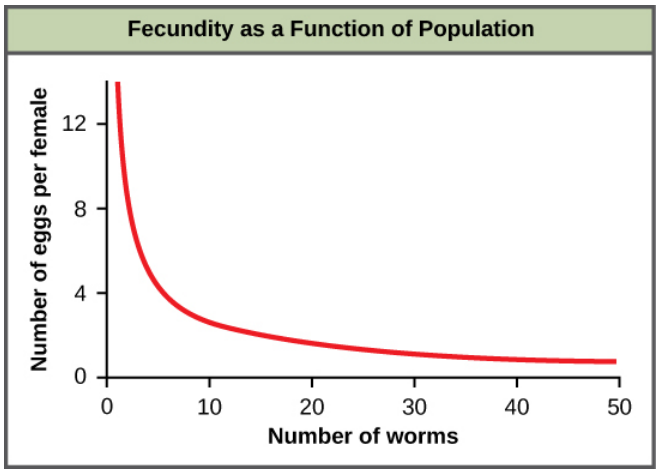


Figure **54.6.1**: In this population of roundworms, fecundity (number of eggs) decreases with population density.[3]

Density-independent Regulation and Interaction with Density-dependent Factors

Many factors, typically physical or chemical in nature (abiotic), influence the mortality of a population regardless of its density, including weather, natural disasters, and pollution. An individual deer may be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

Evolution Connection: Why Did the Woolly Mammoth Go Extinct?

It's easy to get lost in the discussion of dinosaurs and theories about why they went extinct 65 million years ago. Was it due to a meteor slamming into Earth near the coast of modern-day Mexico, or was it from some long-term weather cycle that is not yet understood? One hypothesis that will never be proposed is that humans had something to do with it. Mammals were small, insignificant creatures of the forest 65 million years ago, and no humans existed.



a b c

Figure 54.6.2: The three photos include: (a) 1916 mural of a mammoth herd from the American Museum of Natural History, (b) the only stuffed mammoth in the world, from the Museum of Zoology located in St. Petersburg, Russia, and (c) a one-month-old baby mammoth, named Lyuba, discovered in Siberia in 2007. (credit a: modification of work by Charles R. Knight; credit b: modification of work by “Tanapon”/Flickr; credit c: modification of work by Matt Howry)

Woolly mammoths, however, began to go extinct about 10,000 years ago, when they shared the Earth with humans who were no different anatomically than humans today (Figure **54.6.2**). Mammoths survived in isolated island populations as recently as 1700 BC. We know a lot about these animals from carcasses found frozen in the ice of Siberia and other regions of the north. Scientists have sequenced at least 50 percent of its genome and believe mammoths are between 98 and 99 percent identical to modern elephants.

It is commonly thought that climate change and human hunting led to their extinction. A 2008 study estimated that climate change reduced the mammoth’s range from 3,000,000 square miles 42,000 years ago to 310,000 square miles 6,000 years ago.[4] It is also well documented that humans hunted these animals. A 2012 study showed that no single factor was exclusively responsible for the extinction of these magnificent creatures.[5] In addition to human hunting, climate change, and reduction of habitat, these scientists demonstrated another important factor in the mammoth’s extinction was the migration of humans across the Bering Strait to North America during the last ice age 20,000 years ago.

The maintenance of stable populations was and is very complex, with many interacting factors determining the outcome. It is important to remember that humans are also part of nature. Once we contributed to a species’ decline using primitive hunting technology only.

Life Histories of *K*-selected and *r*-selected Species

While reproductive strategies play a key role in life histories, they do not account for important factors like limited resources and competition. The regulation of population growth by these factors can be used to introduce a classical concept in population biology, that of *K*-selected versus *r*-selected species.

Early Theories about Life History: *K*-selected and *r*-selected Species

By the second half of the twentieth century, the concept of K- and r-selected species was used extensively and successfully to study populations. The concept relates not only reproductive strategies, but also to a species' habitat and behavior, especially in the way that they obtain resources and care for their young. It includes length of life and survivorship factors as well. For this analysis, population biologists have grouped species into the two large categories—*K*-selected and *r*-selected—although they are really two ends of a continuum.

K-selected species are species selected by stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity (hence the term *K*-selected) where intraspecific competition is high. These species have few, large offspring, a long gestation period, and often give long-term care to their offspring (Table **54.6.1**). While larger in size when born, the offspring are relatively helpless and immature at birth. By the time they reach adulthood, they must develop skills to compete for natural resources. In plants, scientists think of parental care more broadly: how long fruit takes to develop or how long it remains on the plant are determining factors in the time to the next reproductive event. Examples of *K*-selected species are primates including humans), elephants, and plants such as oak trees (Figure **54.6.3**a).

Oak trees grow very slowly and take, on average, 20 years to produce their first seeds, known as acorns. As many as 50,000 acorns can be produced by an individual tree, but the germination rate is low as many of these rot or are eaten by animals such as squirrels. In some years, oaks may produce an exceptionally large number of acorns, and these years may be on a two- or three-year cycle depending on the species of oak (*r*-selection).

As oak trees grow to a large size and for many years before they begin to produce acorns, they devote a large percentage of their energy budget to growth and maintenance. The tree's height and size allow it to dominate other plants in the competition for sunlight, the oak's primary energy resource. Furthermore, when it does reproduce, the oak produces large, energy-rich seeds that use their energy reserve to become quickly established (*K*-selection).



(a) K-selected species



(b) r-selected species

Figure 54.6.3: (a) Elephants are considered K-selected species as they live long, mature late, and provide long-term parental care to few offspring. Oak trees produce many offspring that do not receive parental care, but are considered K-selected species based on longevity and late maturation. (b) Dandelions and jellyfish are both considered r-selected species as they mature early, have short lifespans, and produce many offspring that receive no parental care.

In contrast, *r*-selected species have a large number of small offspring (hence their *r* designation (Table 54.6.1). This strategy is often employed in unpredictable or changing environments. Animals that are *r*-selected do not give long-term parental care and the offspring are relatively mature and self-sufficient at birth. Examples of *r*-selected species are marine invertebrates, such as jellyfish, and plants, such as the dandelion (Figure 54.6.3b). Dandelions have small seeds that are wind dispersed long distances. Many seeds are produced simultaneously to ensure that at least some of them reach a hospitable environment. Seeds that land in inhospitable environments have little chance for survival since their seeds are low in energy content. Note that survival is not necessarily a function of energy stored in the seed itself.

Table 54.6.1: Characteristics of *K*-selected and *r*-selected species

Characteristics of *K*-selected species	Characteristics of *r*-selected species
Mature late	Mature early
Greater longevity	Lower longevity
Increased parental care	Decreased parental care
Increased competition	Decreased competition
Fewer offspring	More offspring
Larger offspring	Smaller offspring

Modern Theories of Life History

The *r*- and *K*-selection theory, although accepted for decades and used for much groundbreaking research, has now been reconsidered, and many population biologists have abandoned or modified it. Over the years, several studies attempted to confirm the theory, but these attempts have largely failed. Many species were identified that did not follow the theory's predictions. Furthermore, the theory ignored the age-specific mortality of the populations which scientists now know is very important. New demographic-based models of life history evolution have been developed which incorporate many ecological concepts included in *r*- and *K*-selection theory as well as population age structure and mortality factors.

Summary

Populations are regulated by a variety of density-dependent and density-independent factors. Species are divided into two categories based on a variety of features of their life history patterns: *r*-selected species, which have large numbers of offspring, and *K*-selected species, which have few offspring. The *r*- and *K*-selection theory has fallen out of use; however, many of its key features are still used in newer, demographically-based models of population dynamics.

Footnotes

1. 1 N.A. Croll et al., "The Population Biology and Control of *Ascaris lumbricoides* in a Rural Community in Iran." *Transactions of the Royal Society of Tropical Medicine and Hygiene* 76, no. 2 (1982): 187-197, doi:10.1016/0035-9203(82)90272-3.
2. 2 Martin Walker et al., "Density-Dependent Effects on the Weight of Female *Ascaris lumbricoides* Infections of Humans and its Impact on Patterns of Egg Production." *Parasites & Vectors* 2, no. 11 (February 2009), doi:10.1186/1756-3305-2-11.
3. 3 N.A. Croll et al., "The Population Biology and Control of *Ascaris lumbricoides* in a Rural Community in Iran." *Transactions of the Royal Society of Tropical Medicine and Hygiene* 76, no. 2 (1982): 187-197, doi:10.1016/0035-9203(82)90272-3.
4. 4 David Nogués-Bravo et al., "Climate Change, Humans, and the Extinction of the Woolly Mammoth." *PLoS Biol* 6 (April 2008): e79, doi:10.1371/journal.pbio.0060079.
5. 5 G.M. MacDonald et al., "Pattern of Extinction of the Woolly Mammoth in Beringia." *Nature Communications* 3, no. 893 (June 2012), doi:10.1038/ncomms1881.

Glossary

demographic-based population model
: modern model of population dynamics incorporating many features of the *r*- and *K*-selection theory

density-dependent regulation
: regulation of population that is influenced by population density, such as crowding effects; usually involves biotic factors

density-independent regulation
: regulation of populations by factors that operate independent of population density, such as forest fires and volcanic eruptions; usually involves abiotic factors

interspecific competition
: competition between species for resources in a shared habitat or environment

***K*-selected species**

species suited to stable environments that produce a few, relatively large offspring and provide parental care

***r*-selected species**

species suited to changing environments that produce many offspring and provide little or no parental care

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54.7: Human Population Growth

Skills to Develop

- Discuss how human population growth can be exponential
- Explain how humans have expanded the carrying capacity of their habitat
- Relate population growth and age structure to the level of economic development in different countries
- Discuss the long-term implications of unchecked human population growth

Concepts of animal population dynamics can be applied to human population growth. Humans are not unique in their ability to alter their environment. For example, beaver dams alter the stream environment where they are built. Humans, however, have the ability to alter their environment to increase its carrying capacity sometimes to the detriment of other species (e.g., via artificial selection for crops that have a higher yield). Earth's human population is growing rapidly, to the extent that some worry about the ability of the earth's environment to sustain this population, as long-term exponential growth carries the potential risks of famine, disease, and large-scale death.

Although humans have increased the carrying capacity of their environment, the technologies used to achieve this transformation have caused unprecedented changes to Earth's environment, altering ecosystems to the point where some may be in danger of collapse. The depletion of the ozone layer, erosion due to acid rain, and damage from global climate change are caused by human activities. The ultimate effect of these changes on our carrying capacity is unknown. As some point out, it is likely that the negative effects of increasing carrying capacity will outweigh the positive ones—the carrying capacity of the world for human beings might actually decrease.

The world's human population is currently experiencing exponential growth even though human reproduction is far below its biotic potential (Figure **54.7.1**). To reach its biotic potential, all females would have to become pregnant every nine months or so during their reproductive years. Also, resources would have to be such that the environment would support such growth. Neither of these two conditions exists. In spite of this fact, human population is still growing exponentially.

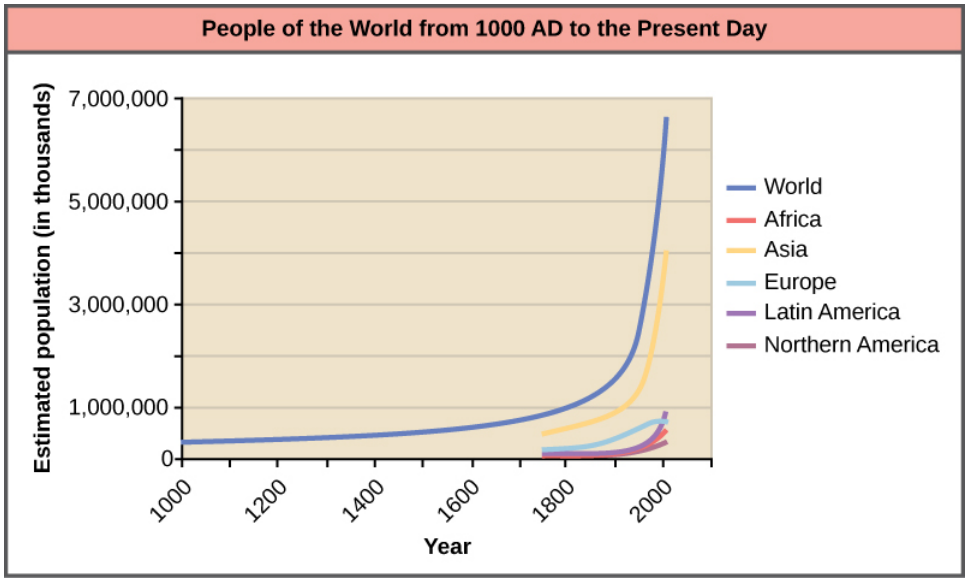


Figure **54.7.1**: Human population growth since 1000 AD is exponential (dark blue line). Notice that while the population in Asia (yellow line), which has many economically underdeveloped countries, is increasing exponentially, the population in Europe (light blue line), where most of the countries are economically developed, is growing much more slowly.

A consequence of exponential human population growth is the time that it takes to add a particular number of humans to the Earth is becoming shorter. Figure **54.7.2** shows that 123 years were necessary to add 1 billion humans in 1930, but it only took 24 years to add two billion people between 1975 and 1999. As already discussed, at some point it would appear that our ability to increase our carrying capacity indefinitely on a finite world is uncertain. Without new technological advances, the human growth rate has been predicted to slow in the coming decades. However, the population will still be increasing and the threat of overpopulation remains.

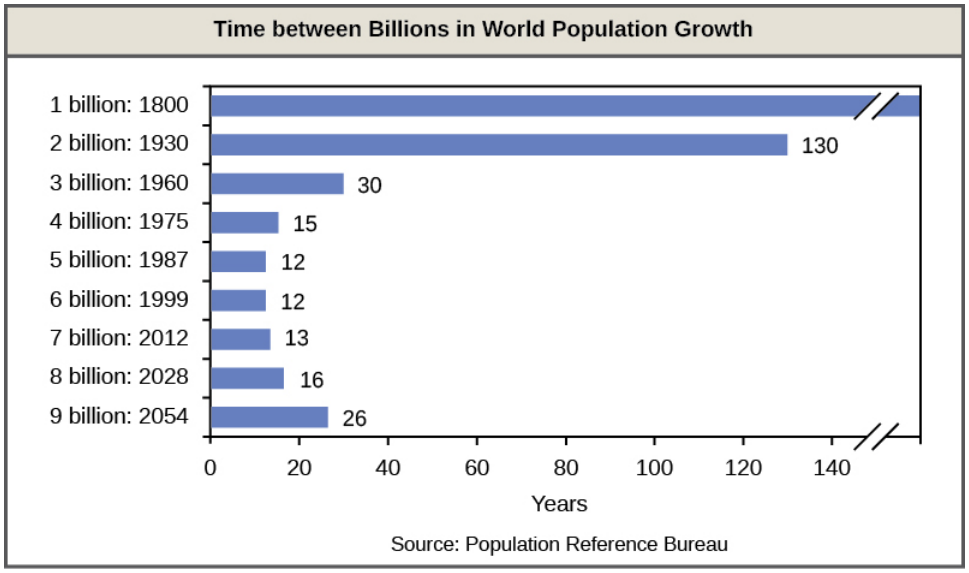


Figure 54.7.2: The time between the addition of each billion human beings to Earth decreases over time. (credit: modification of work by Ryan T. Cragun)

Link to Learning



Click through this interactive view of how human populations have changed over time.

Overcoming Density-Dependent Regulation

Humans are unique in their ability to alter their environment with the conscious purpose of increasing its carrying capacity. This ability is a major factor responsible for human population growth and a way of overcoming density-dependent growth regulation. Much of this ability is related to human intelligence, society, and communication. Humans can construct shelter to protect them from the elements and have developed agriculture and domesticated animals to increase their food supplies. In addition, humans use language to communicate this technology to new generations, allowing them to improve upon previous accomplishments.

Other factors in human population growth are migration and public health. Humans originated in Africa, but have since migrated to nearly all inhabitable land on the Earth. Public health, sanitation, and the use of antibiotics and vaccines have decreased the ability of infectious disease to limit human population growth. In the past, diseases such as the bubonic plaque of the fourteenth century killed between 30 and 60 percent of Europe's population and reduced the overall world population by as many as 100 million people. Today, the threat of infectious disease, while not gone, is certainly less severe. According to the World Health Organization, global death from infectious disease declined from 16.4 million in 1993 to 14.7 million in 1992. To compare to some of the epidemics of the past, the percentage of the world's population killed between 1993 and 2002 decreased from 0.30 percent of the world's population to 0.24 percent. Thus, it appears that the influence of infectious disease on human population growth is becoming less significant.

Age Structure, Population Growth, and Economic Development

The age structure of a population is an important factor in population dynamics. Age structure is the proportion of a population at different age ranges. Age structure allows better prediction of population growth, plus the ability to associate this growth with the level of economic development in the region. Countries with rapid growth have a pyramidal shape in their age structure diagrams, showing a preponderance of younger individuals, many of whom are of reproductive age or will be soon (Figure **54.7.3**). This pattern is most often observed in underdeveloped countries where individuals do not live to old age because of less-than-optimal living conditions. Age structures of areas with slow growth, including developed countries such as the United States, still have a pyramidal structure, but with many fewer young and reproductive-aged individuals and a greater proportion of older individuals. Other developed countries, such as Italy, have zero population growth. The age structure of these populations is more conical, with an even greater percentage of middle-aged and older individuals. The actual growth rates in different countries are shown in Figure **54.7.4**, with the highest rates tending to be in the less economically developed countries of Africa and Asia.

Art Connection

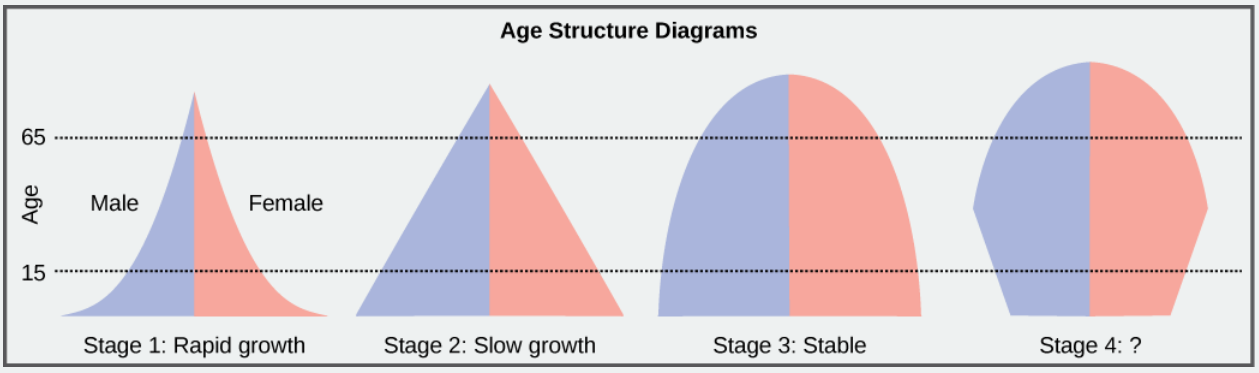


Figure **54.7.3**: Typical age structure diagrams are shown. The rapid growth diagram narrows to a point, indicating that the number of individuals decreases rapidly with age. In the slow growth model, the number of individuals decreases steadily with age. Stable population diagrams are rounded on the top, showing that the number of individuals per age group decreases gradually, and then increases for the older part of the population.

Age structure diagrams for rapidly growing, slow growing and stable populations are shown in stages 1 through 3. What type of population change do you think stage 4 represents?

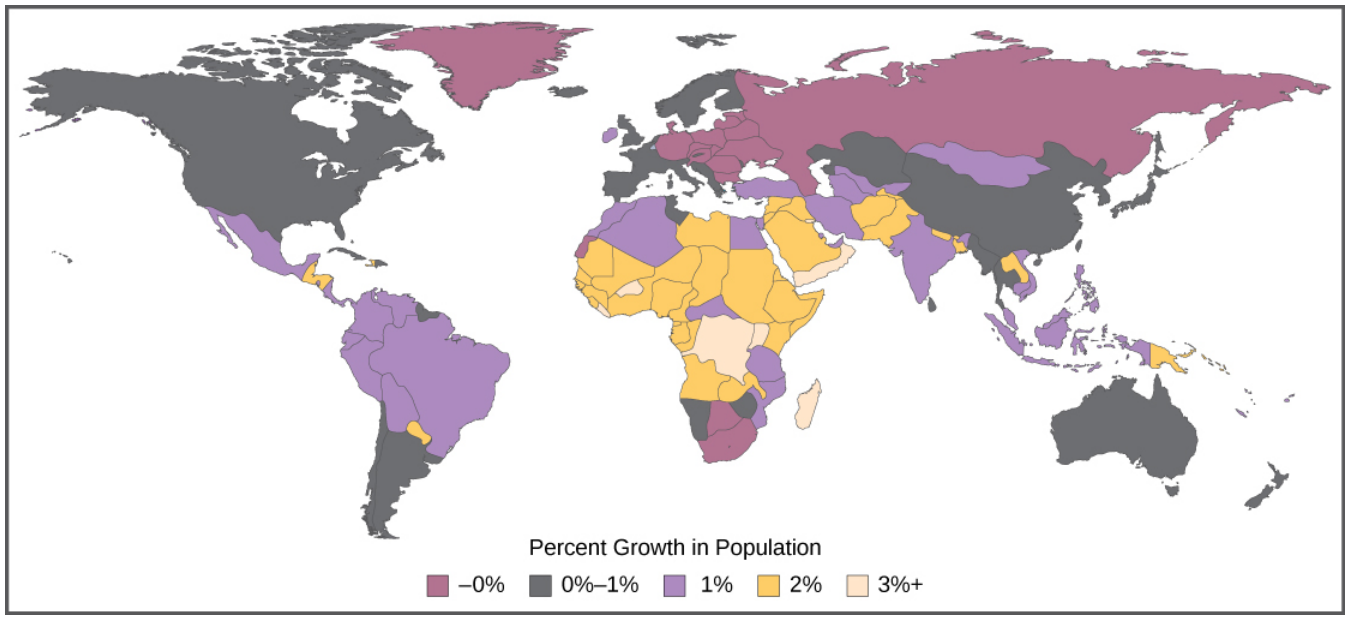


Figure **54.7.4**: The percent growth rate of population in different countries is shown. Notice that the highest growth is occurring in less economically developed countries in Africa and Asia.

Long-Term Consequences of Exponential Human Population Growth

Many dire predictions have been made about the world's population leading to a major crisis called the "population explosion." In the 1968 book *The Population Bomb*, biologist Dr. Paul R. Ehrlich wrote, "The battle to feed all of humanity is over. In the 1970s hundreds of millions of people will starve to death in spite of any crash programs embarked upon now. At this late date nothing can prevent a substantial increase in the world death rate."[1] While many critics view this statement as an exaggeration, the laws of exponential population growth are still in effect, and unchecked human population growth cannot continue indefinitely.

Efforts to control population growth led to the one-child policy in China, which used to include more severe consequences, but now imposes fines on urban couples who have more than one child. Due to the fact that some couples wish to have a male heir, many Chinese couples continue to have more than one child. The policy itself, its social impacts, and the effectiveness of limiting overall population growth are controversial. In spite of population control policies, the human population continues to grow. At some point the food supply may run out because of the subsequent need to produce more and more food to feed our population. The United Nations estimates that future world population growth may vary from 6 billion (a decrease) to 16 billion people by the year 2100. There is no way to know whether human population growth will moderate to the point where the crisis described by Dr. Ehrlich will be averted.

Another result of population growth is the endangerment of the natural environment. Many countries have attempted to reduce the human impact on climate change by reducing their emission of the greenhouse gas carbon dioxide. However, these treaties have not been ratified by every country, and many underdeveloped countries trying to improve their economic condition may be less likely to agree with such provisions if it means slower economic development. Furthermore, the role of human activity in causing climate change has become a hotly debated socio-political issue in some developed countries, including the United States. Thus, we enter the future with considerable uncertainty about our ability to curb human population growth and protect our environment.

Link to Learning

Visit this website and select "Launch movie" for an animation discussing the global impacts of human population growth.

Summary

The world's human population is growing at an exponential rate. Humans have increased the world's carrying capacity through migration, agriculture, medical advances, and communication. The age structure of a population allows us to predict population growth. Unchecked human population growth could have dire long-term effects on our environment.

Art Connections

Figure **54.7.3**: Age structure diagrams for rapidly growing, slow growing and stable populations are shown in stages 1 through 3. What type of population change do you think stage 4 represents?

Answer

Stage 4 represents a population that is decreasing.

Footnotes

1. 1 Paul R. Erlich, prologue to *The Population Bomb*, (1968; repr., New York: Ballantine, 1970).

Glossary

age structure

proportion of population members at specific age ranges

one-child policy

China’s policy to limit population growth by limiting urban couples to have only one child or face the penalty of a fine

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CHAPTER OVERVIEW

55: Community Ecology

55.1: Biological Communities- Species Living Together

55.1.1: Biogeography

55.1.2: Community Ecology

55.2: The Ecological Niche Concept

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55.3: Predator-Prey Relationships

55.3.1: Community Ecology

55.4: The Many Types of Species Interactions

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55.5: Ecological Successions, Disturbance, and Species Richness

55.5.1: Community Ecology

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55.1: Biological Communities- Species Living Together

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55.1.1: Biogeography

Skills to Develop

- Define biogeography
- List and describe abiotic factors that affect the global distribution of plant and animal species
- Compare the impact of abiotic forces on aquatic and terrestrial environments
- Summarize the affect of abiotic factors on net primary productivity

Many forces influence the communities of living organisms present in different parts of the biosphere (all of the parts of Earth inhabited by life). The biosphere extends into the atmosphere (several kilometers above Earth) and into the depths of the oceans. Despite its apparent vastness to an individual human, the biosphere occupies only a minute space when compared to the known universe. Many abiotic forces influence where life can exist and the types of organisms found in different parts of the biosphere. The abiotic factors influence the distribution of biomes: large areas of land with similar climate, flora, and fauna.

Biogeography

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors such as temperature and rainfall vary based mainly on latitude and elevation. As these abiotic factors change, the composition of plant and animal communities also changes. For example, if you were to begin a journey at the equator and walk north, you would notice gradual changes in plant communities. At the beginning of your journey, you would see tropical wet forests with broad-leaved evergreen trees, which are characteristic of plant communities found near the equator. As you continued to travel north, you would see these broad-leaved evergreen plants eventually give rise to seasonally dry forests with scattered trees. You would also begin to notice changes in temperature and moisture. At about 30 degrees north, these forests would give way to deserts, which are characterized by low precipitation.

Moving farther north, you would see that deserts are replaced by grasslands or prairies. Eventually, grasslands are replaced by deciduous temperate forests. These deciduous forests give way to the boreal forests found in the subarctic, the area south of the Arctic Circle. Finally, you would reach the Arctic tundra, which is found at the most northern latitudes. This trek north reveals gradual changes in both climate and the types of organisms that have adapted to environmental factors associated with ecosystems found at different latitudes. However, different ecosystems exist at the same latitude due in part to abiotic factors such as jet streams, the Gulf Stream, and ocean currents. If you were to hike up a mountain, the changes you would see in the vegetation would parallel those as you move to higher latitudes.

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An endemic species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution; therefore, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia (Figure **55.1.1.1**).



(a) (b)

Figure **55.1.1.1**: Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal. (credit a: modification of work by Derrick Coetzee; credit b: modification of work by Allan Whittome)

Sometimes ecologists discover unique patterns of species distribution by determining where species are *not* found. Hawaii, for example, has no native land species of reptiles or amphibians, and has only one native terrestrial mammal, the hoary bat. Most of New Guinea, as another example, lacks placental mammals.

Link to Learning

Check out this video to observe a platypus swimming in its natural habitat in New South Wales, Australia.

Plants can be endemic or generalists: endemic plants are found only on specific regions of the Earth, while generalists are found on many regions. Isolated land masses—such as Australia, Hawaii, and Madagascar—often have large numbers of endemic plant species. Some of these plants are endangered due to human activity. The forest gardenia (*Gardenia brighamii*), for instance, is endemic to Hawaii; only an estimated 15–20 trees are thought to exist (Figure **55.1.1.2**).



Figure 55.1.1.2: Listed as federally endangered, the forest gardenia is a small tree with distinctive flowers. It is found only in five of the Hawaiian Islands in small populations consisting of a few individual specimens. (credit: Forest & Kim Starr)

Energy Sources

Energy from the sun is captured by green plants, algae, cyanobacteria, and photosynthetic protists. These organisms convert solar energy into the chemical energy needed by all living things. Light availability can be an important force directly affecting the evolution of adaptations in photosynthesizers. For instance, plants in the understory of a temperate forest are shaded when the trees above them in the canopy completely leaf out in the late spring. Not surprisingly, understory plants have adaptations to successfully capture available light. One such adaptation is the rapid growth of spring ephemeral plants such as the spring beauty (Figure 55.1.1.3). These spring flowers achieve much of their growth and finish their life cycle (reproduce) early in the season before the trees in the canopy develop leaves.



Figure 55.1.1.3: The spring beauty is an ephemeral spring plant that flowers early in the spring to avoid competing with larger forest trees for sunlight. (credit: John Beetham)

In aquatic ecosystems, the availability of light may be limited because sunlight is absorbed by water, plants, suspended particles, and resident microorganisms. Toward the bottom of a lake, pond, or ocean, there is a zone that light cannot reach. Photosynthesis

cannot take place there and, as a result, a number of adaptations have evolved that enable living things to survive without light. For instance, aquatic plants have photosynthetic tissue near the surface of the water; for example, think of the broad, floating leaves of a water lily—water lilies cannot survive without light. In environments such as hydrothermal vents, some bacteria extract energy from inorganic chemicals because there is no light for photosynthesis.

The availability of nutrients in aquatic systems is also an important aspect of energy or photosynthesis. Many organisms sink to the bottom of the ocean when they die in the open water; when this occurs, the energy found in that living organism is sequestered for some time unless ocean upwelling occurs. Ocean upwelling is the rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline (Figure **55.1.1.4**). As the wind pushes ocean waters offshore, water from the bottom of the ocean moves up to replace this water. As a result, the nutrients once contained in dead organisms become available for reuse by other living organisms.

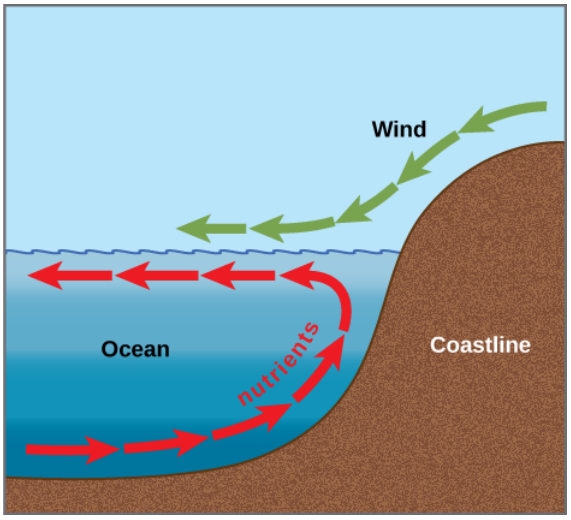


Figure **55.1.1.4**: Ocean upwelling is an important process that recycles nutrients and energy in the ocean. As wind (green arrows) pushes offshore, it causes water from the ocean bottom (red arrows) to move to the surface, bringing up nutrients from the ocean depths.

In freshwater systems, the recycling of nutrients occurs in response to air temperature changes. The nutrients at the bottom of lakes are recycled twice each year: in the spring and fall turnover. The spring and fall turnover is a seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top of a body of water (Figure **55.1.1.5**). These turnovers are caused by the formation of a thermocline: a layer of water with a temperature that is significantly different from that of the surrounding layers. In wintertime, the surface of lakes found in many northern regions is frozen. However, the water under the ice is slightly warmer, and the water at the bottom of the lake is warmer yet at 4 °C to 5 °C (39.2 °F to 41 °F). Water is densest at 4 °C; therefore, the deepest water is also the densest. The deepest water is oxygen poor because the decomposition of organic material at the bottom of the lake uses up available oxygen that cannot be replaced by means of oxygen diffusion into the water due to the surface ice layer.

Art Connection

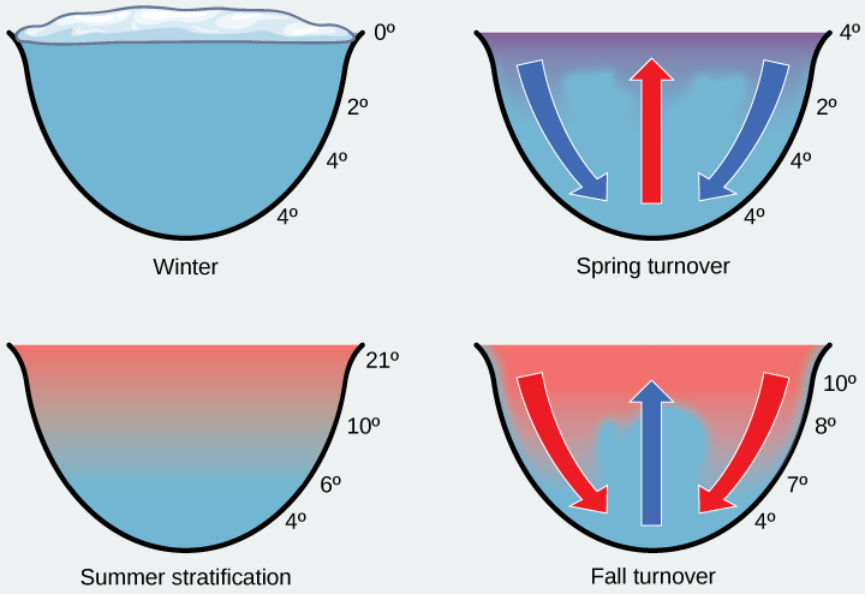


Figure **55.1.1.5**: The spring and fall turnovers are important processes in freshwater lakes that act to move the nutrients and oxygen at the bottom of deep lakes to the top. Turnover occurs because water has a maximum density at 4 °C. Surface water temperature changes as the seasons progress, and denser water sinks.

How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

In springtime, air temperatures increase and surface ice melts. When the temperature of the surface water begins to reach 4 °C, the water becomes heavier and sinks to the bottom. The water at the bottom of the lake is then displaced by the heavier surface water and, thus, rises to the top. As that water rises to the top, the sediments and nutrients from the lake bottom are brought along with it. During the summer months, the lake water stratifies, or forms layers, with the warmest water at the lake surface.

As air temperatures drop in the fall, the temperature of the lake water cools to 4 °C; therefore, this causes fall turnover as the heavy cold water sinks and displaces the water at the bottom. The oxygen-rich water at the surface of the lake then moves to the bottom of the lake, while the nutrients at the bottom of the lake rise to the surface (Figure **55.1.1.5**). During the winter, the oxygen at the bottom of the lake is used by decomposers and other organisms requiring oxygen, such as fish.

Temperature

Temperature affects the physiology of living things as well as the density and state of water. Temperature exerts an important influence on living things because few living things can survive at temperatures below 0 °C (32 °F) due to metabolic constraints. It is also rare for living things to survive at temperatures exceeding 45 °C (113 °F); this is a reflection of evolutionary response to typical temperatures. Enzymes are most efficient within a narrow and specific range of temperatures; enzyme degradation can occur at higher temperatures. Therefore, organisms either must maintain an internal temperature or they must inhabit an environment that will keep the body within a temperature range that supports metabolism. Some animals have adapted to enable their bodies to survive significant temperature fluctuations, such as seen in hibernation or reptilian torpor. Similarly, some bacteria are adapted to surviving in extremely hot temperatures such as geysers. Such bacteria are examples of extremophiles: organisms that thrive in extreme environments.

Temperature can limit the distribution of living things. Animals faced with temperature fluctuations may respond with adaptations, such as migration, in order to survive. Migration, the movement from one place to another, is an adaptation found in many animals, including many that inhabit seasonally cold climates. Migration solves problems related to temperature, locating food, and finding a mate. In migration, for instance, the Arctic Tern (*Sterna paradisaea*) makes a 40,000 km (24,000 mi) round trip flight each year between its feeding grounds in the southern hemisphere and its breeding grounds in the Arctic Ocean. Monarch butterflies (*Danaus plexippus*) live in the eastern United States in the warmer months and migrate to Mexico and the southern United States in the wintertime. Some species of mammals also make migratory forays. Reindeer (*Rangifer tarandus*) travel about 5,000 km (3,100 mi)

each year to find food. Amphibians and reptiles are more limited in their distribution because they lack migratory ability. Not all animals that can migrate do so: migration carries risk and comes at a high energy cost.

Some animals hibernate or estivate to survive hostile temperatures. Hibernation enables animals to survive cold conditions, and estivation allows animals to survive the hostile conditions of a hot, dry climate. Animals that hibernate or estivate enter a state known as torpor: a condition in which their metabolic rate is significantly lowered. This enables the animal to wait until its environment better supports its survival. Some amphibians, such as the wood frog (*Rana sylvatica*), have an antifreeze-like chemical in their cells, which retains the cells' integrity and prevents them from bursting.

Water

Water is required by all living things because it is critical for cellular processes. Since terrestrial organisms lose water to the environment by simple diffusion, they have evolved many adaptations to retain water.

- Plants have a number of interesting features on their leaves, such as leaf hairs and a waxy cuticle, that serve to decrease the rate of water loss via transpiration.
- Freshwater organisms are surrounded by water and are constantly in danger of having water rush into their cells because of osmosis. Many adaptations of organisms living in freshwater environments have evolved to ensure that solute concentrations in their bodies remain within appropriate levels. One such adaptation is the excretion of dilute urine.
- Marine organisms are surrounded by water with a higher solute concentration than the organism and, thus, are in danger of losing water to the environment because of osmosis. These organisms have morphological and physiological adaptations to retain water and release solutes into the environment. For example, Marine iguanas (*Amblyrhynchus cristatus*), sneeze out water vapor that is high in salt in order to maintain solute concentrations within an acceptable range while swimming in the ocean and eating marine plants.

Inorganic Nutrients and Soil

Inorganic nutrients, such as nitrogen and phosphorus, are important in the distribution and the abundance of living things. Plants obtain these inorganic nutrients from the soil when water moves into the plant through the roots. Therefore, soil structure (particle size of soil components), soil pH, and soil nutrient content play an important role in the distribution of plants. Animals obtain inorganic nutrients from the food they consume. Therefore, animal distributions are related to the distribution of what they eat. In some cases, animals will follow their food resource as it moves through the environment.

Other Aquatic Factors

Some abiotic factors, such as oxygen, are important in aquatic ecosystems as well as terrestrial environments. Terrestrial animals obtain oxygen from the air they breathe. Oxygen availability can be an issue for organisms living at very high elevations, however, where there are fewer molecules of oxygen in the air. In aquatic systems, the concentration of dissolved oxygen is related to water temperature and the speed at which the water moves. Cold water has more dissolved oxygen than warmer water. In addition, salinity, current, and tide can be important abiotic factors in aquatic ecosystems.

Other Terrestrial Factors

Wind can be an important abiotic factor because it influences the rate of evaporation and transpiration. The physical force of wind is also important because it can move soil, water, or other abiotic factors, as well as an ecosystem's organisms.

Fire is another terrestrial factor that can be an important agent of disturbance in terrestrial ecosystems. Some organisms are adapted to fire and, thus, require the high heat associated with fire to complete a part of their life cycle. For example, the jack pine—a coniferous tree—requires heat from fire for its seed cones to open (Figure **55.1.1.6**). Through the burning of pine needles, fire adds nitrogen to the soil and limits competition by destroying undergrowth.



Figure **55.1.1.6**: The mature cones of the jack pine (*Pinus banksiana*) open only when exposed to high temperatures, such as during a forest fire. A fire is likely to kill most vegetation, so a seedling that germinates after a fire is more likely to receive ample sunlight than one that germinates under normal conditions. (credit: USDA)

Abiotic Factors Influencing Plant Growth

Temperature and moisture are important influences on plant production (primary productivity) and the amount of organic matter available as food (net primary productivity). Net primary productivity is an estimation of all of the organic matter available as food; it is calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration. In terrestrial environments, net primary productivity is estimated by measuring the aboveground biomass per unit area, which is the total mass of living plants, excluding roots. This means that a large percentage of plant biomass which exists underground is not included in this measurement. Net primary productivity is an important variable when considering differences in biomes. Very productive biomes have a high level of aboveground biomass.

Annual biomass production is directly related to the abiotic components of the environment. Environments with the greatest amount of biomass have conditions in which photosynthesis, plant growth, and the resulting net primary productivity are optimized. The climate of these areas is warm and wet. Photosynthesis can proceed at a high rate, enzymes can work most efficiently, and stomata can remain open without the risk of excessive transpiration; together, these factors lead to the maximal amount of carbon dioxide (CO_2) moving into the plant, resulting in high biomass production. The aboveground biomass produces several important resources for other living things, including habitat and food. Conversely, dry and cold environments have lower photosynthetic rates and therefore less biomass. The animal communities living there will also be affected by the decrease in available food.

Summary

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Endemic species are species that are naturally found only in a specific geographic area. The distribution of living things is influenced by several environmental factors that are, in part, controlled by the latitude or elevation at which an organism is found. Ocean upwelling and spring and fall turnovers are important processes regulating the distribution of nutrients and other abiotic factors important in aquatic ecosystems. Energy sources, temperature, water, inorganic nutrients, and soil are factors limiting the distribution of living things in terrestrial systems. Net primary productivity is a measure of the amount of biomass produced by a biome.

Art Connections

Figure **55.1.1.5**: How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

Answer

Tropical lakes don’t freeze, so they don’t undergo spring turnover in the same way temperate lakes do. However, stratification does occur, as well as seasonal turnover.

aboveground biomass
total mass of aboveground living plants per area

biogeography
study of the geographic distribution of living things and the abiotic factors that affect their distribution

biome
ecological community of plants, animals, and other organisms that is adapted to a characteristic set of environmental conditions

endemic
species found only in a specific geographic area that is usually restricted in size

fall and spring turnover
seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top

net primary productivity
measurement of the energy accumulation within an ecosystem, calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration

ocean upwelling
rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline

thermocline
layer of water with a temperature that is significantly different from that of the surrounding layers

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55.1.2: Community Ecology

Skills to Develop

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Describe community structure and succession

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations inhabiting a specific area at the same time. The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

Predation and Herbivory

Perhaps the classical example of species interaction is predation: the hunting of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests (Figure **55.1.2.1**). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.

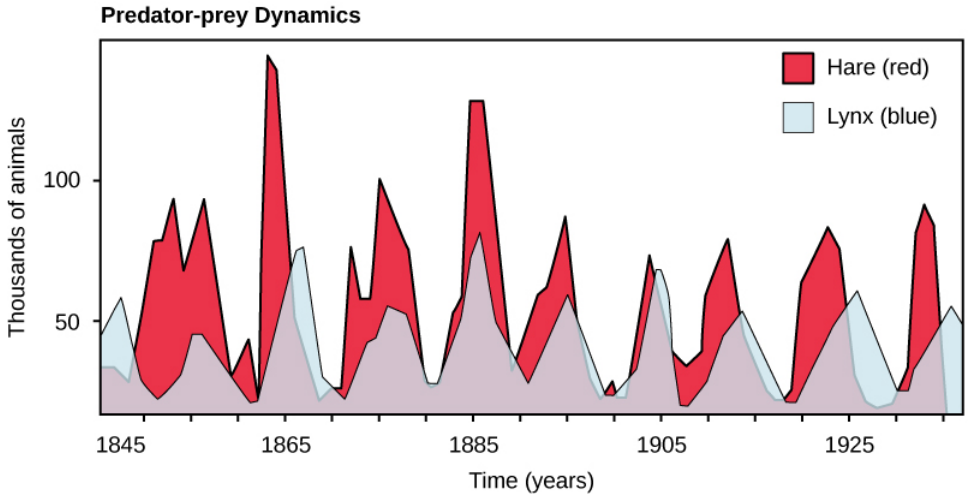


Figure **55.1.2.1**: The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

The idea that the population cycling of the two species is entirely controlled by predation models has come under question. More recent studies have pointed to undefined density-dependent factors as being important in the cycling, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. Figure **55.1.2.2** shows some organisms' defenses against predation and herbivory.



(a)



(b)



(c)



(d)

Figure **55.1.2.2**: The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni*) uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs (Figure **55.1.2.3**a). In another example, the chameleon can change its color to match its surroundings (Figure **55.1.2.3**b). Both of these are examples of camouflage, or avoiding detection by blending in with the background.



a b

Figure 55.1.2.3: (a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemical, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called aposematic coloration, or warning coloration (Figure 55.1.2.4).



(a) (b)

Figure 55.1.2.4: (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In Batesian mimicry, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation (Figure 55.1.2.5).



a b

Figure 55.1.2.5: Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)

In Müllerian mimicry, multiple species share the same warning coloration, but all of them actually have defenses. Figure 55.1.2.6 shows a variety of foul-tasting butterflies with similar coloration. In Emsleyan/Mertensian mimicry, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the non-venomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.



Figure 55.1.2.6: Several unpleasant-tasting *Heliconius* butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Link to Learning

Go to this website to view stunning examples of mimicry.

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The competitive exclusion principle states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in Figure **55.1.2.7**, with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

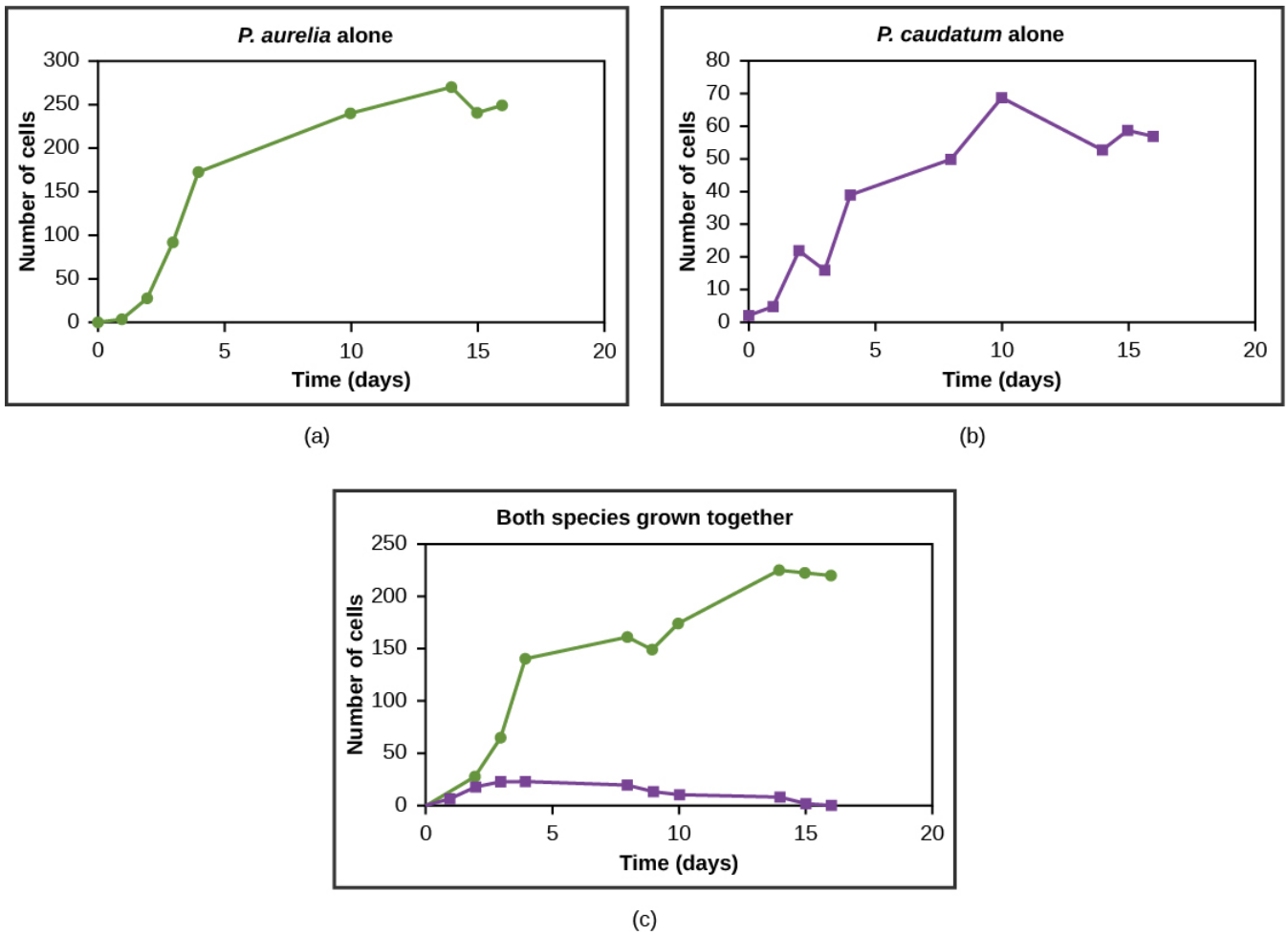


Figure **55.1.2.7**: *Paramecium aurelia* and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These

organisms coexist by minimizing direct competition.

Symbiosis

Symbiotic relationships, or symbioses (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

Commensalism

A commensal relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure **55.1.2.8**). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.



Figure **55.1.2.8**: The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: “Hanay”/Wikimedia Commons)

Mutualism

A second type of symbiotic relationship is called mutualism, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect’s gut (Figure **55.1.2.9**a). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria (Figure **55.1.2.9**b). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.



a b

Figure 55.1.2.9: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Parasitism

A parasite is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the organism being fed upon, the host, is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed (Figure 55.1.2.10). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle. Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.

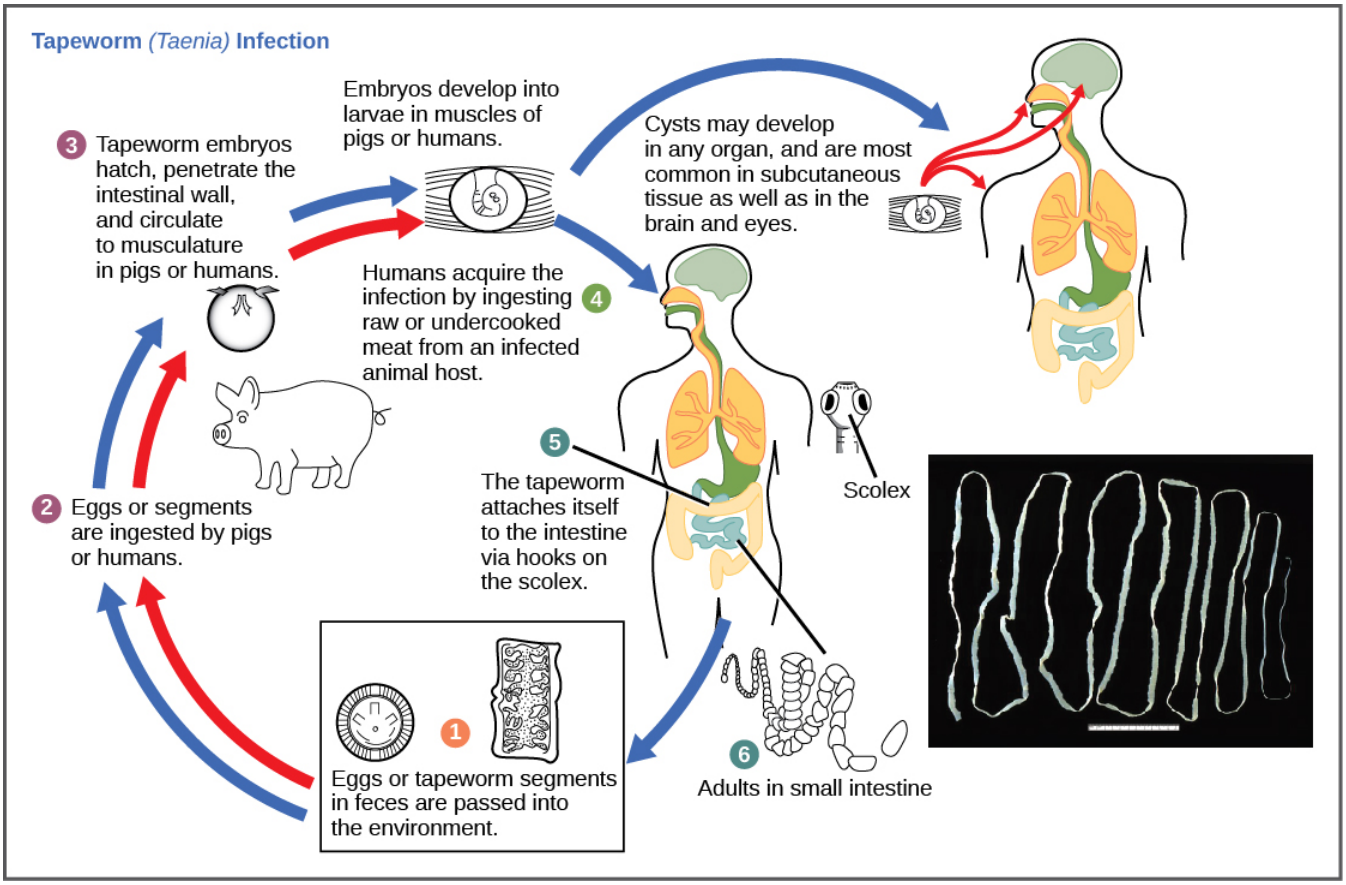


Figure 55.1.2.10: This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef (Figure 55.1.2.11). Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.

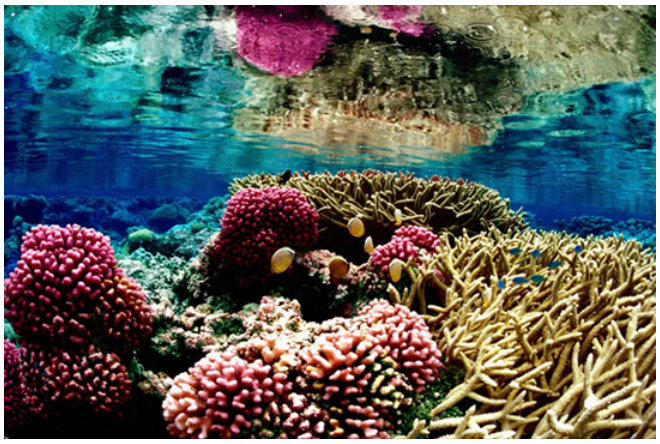


Figure 55.1.2.11: Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS)

Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. Species richness is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe (Figure 55.1.2.12). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of island biogeography attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. Relative species abundance is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.

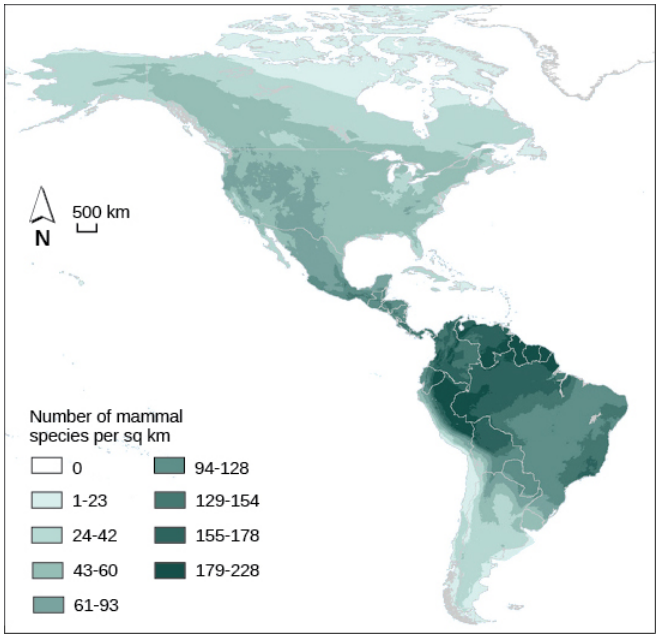


Figure 55.1.2.12: The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

Keystone Species

A keystone species is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species (Figure

55.1.2.13). Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.



Figure 55.1.2.13: The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

Everyday Connection: Invasive Species

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in Figure 55.1.2.14. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

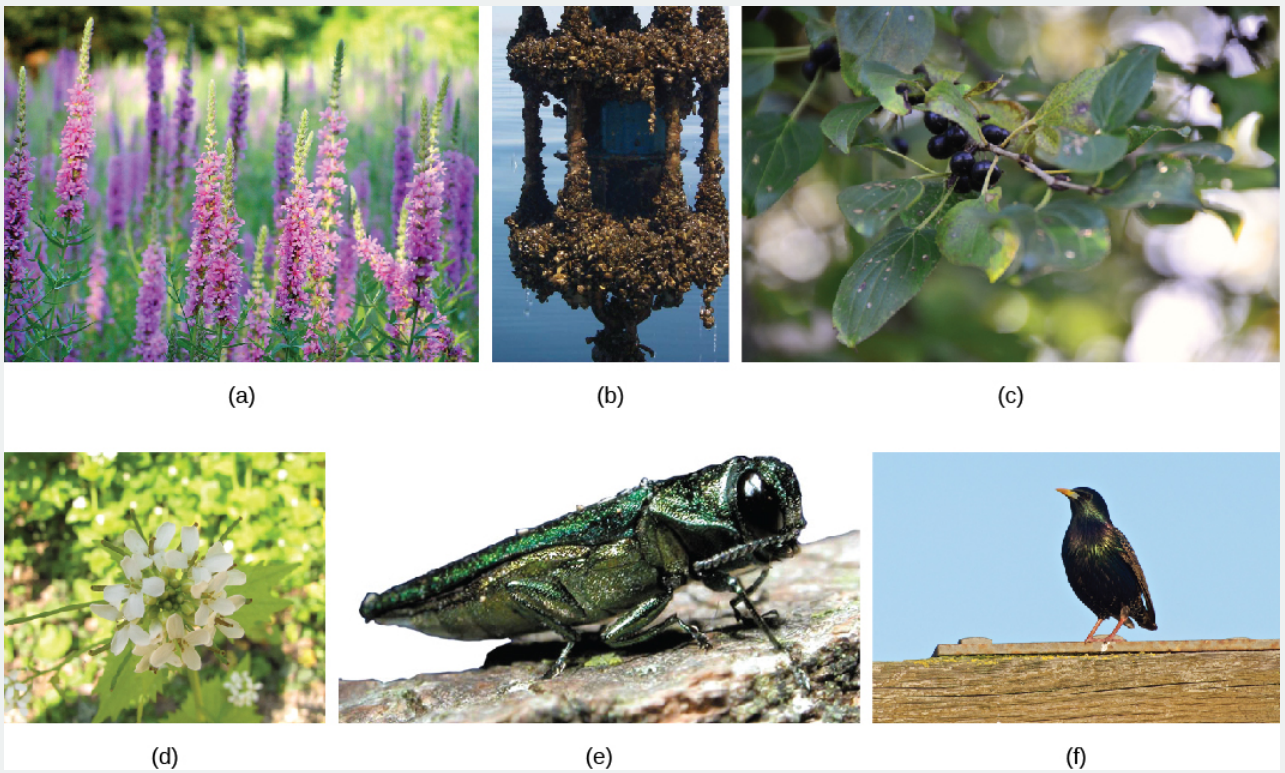


Figure 55.1.2.14: In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as pioneer species (Figure **55.1.2.15**). These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.



Figure 55.1.2.15: During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire (Figure 55.1.2.16). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the climax community, which will remain stable until the next disturbance.

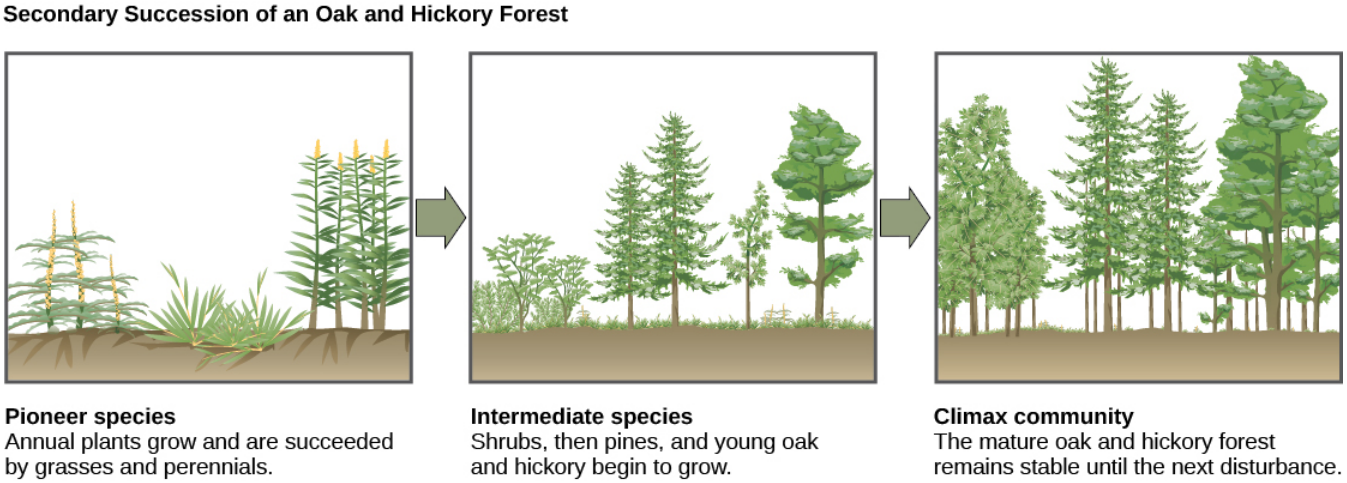


Figure 55.1.2.16: Secondary succession is shown in an oak and hickory forest after a forest fire.

Summary

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism.

Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established.

Glossary

aposematic coloration
warning coloration used as a defensive mechanism against predation

Batesian mimicry
type of mimicry where a non-harmful species takes on the warning colorations of a harmful one

camouflage
avoid detection by blending in with the background.

climax community
final stage of succession, where a stable community is formed by a characteristic assortment of plant and animal species

commensalism
relationship between species wherein one species benefits from the close, prolonged interaction, while the other species neither benefits nor is harmed

competitive exclusion principle
no two species within a habitat can coexist when they compete for the same resources at the same place and time

Emsleyan/Mertensian mimicry
type of mimicry where a harmful species resembles a less harmful one

environmental disturbance
change in the environment caused by natural disasters or human activities

foundation species
species which often forms the major structural portion of the habitat

host
organism a parasite lives on

island biogeography
study of life on island chains and how their geography interacts with the diversity of species found there

keystone species
species whose presence is key to maintaining biodiversity in an ecosystem and to upholding an ecological community's structure

Müllerian mimicry
type of mimicry where species share warning coloration and all are harmful to predators

mutualism
symbiotic relationship between two species where both species benefit

parasite
organism that uses resources from another species, the host

pioneer species
first species to appear in primary and secondary succession

primary succession

succession on land that previously has had no life

relative species abundance

absolute population size of a particular species relative to the population sizes of other species within the community

secondary succession

succession in response to environmental disturbances that move a community away from its equilibrium

species richness

number of different species in a community

symbiosis

close interaction between individuals of different species over an extended period of time that impacts the abundance and distribution of the associating populations

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55.2: The Ecological Niche Concept

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55.2.1: Community Ecology

Skills to Develop

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Describe community structure and succession

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations inhabiting a specific area at the same time. The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

Predation and Herbivory

Perhaps the classical example of species interaction is predation: the hunting of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests (Figure **55.2.1.1**). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.

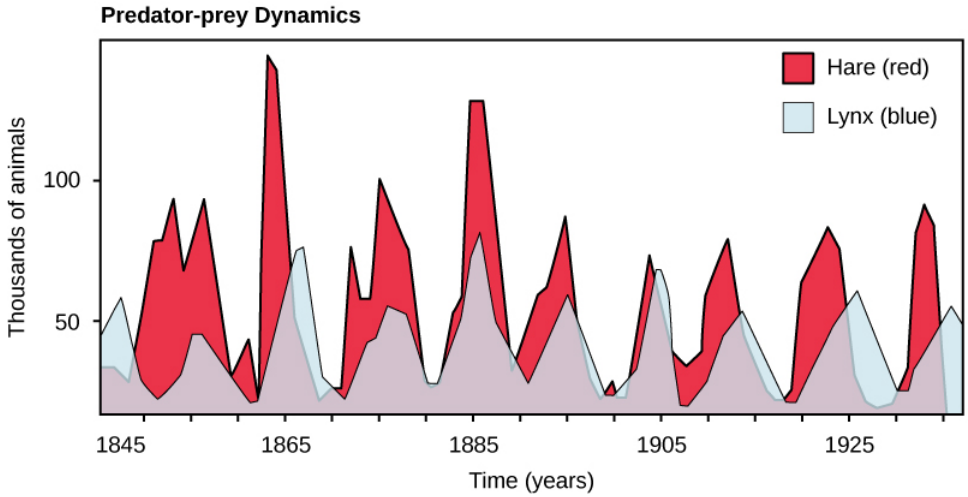


Figure **55.2.1.1**: The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

The idea that the population cycling of the two species is entirely controlled by predation models has come under question. More recent studies have pointed to undefined density-dependent factors as being important in the cycling, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. Figure **55.2.1.2** shows some organisms' defenses against predation and herbivory.



(a)



(b)



(c)



(d)

Figure **55.2.1.2**: The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni*) uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs (Figure **55.2.1.3**a). In another example, the chameleon can change its color to match its surroundings (Figure **55.2.1.3**b). Both of these are examples of camouflage, or avoiding detection by blending in with the background.



a b

Figure 55.2.1.3: (a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemical, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called aposematic coloration, or warning coloration (Figure 55.2.1.4).



(a) (b)

Figure 55.2.1.4: (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In Batesian mimicry, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation (Figure 55.2.1.5).



a b

Figure 55.2.1.5: Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)

In Müllerian mimicry, multiple species share the same warning coloration, but all of them actually have defenses. Figure 55.2.1.6 shows a variety of foul-tasting butterflies with similar coloration. In Emsleyan/Mertensian mimicry, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the non-venomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.



Figure 55.2.1.6: Several unpleasant-tasting *Heliconius* butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Link to Learning

Go to this website to view stunning examples of mimicry.

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The competitive exclusion principle states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in Figure **55.2.1.7**, with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

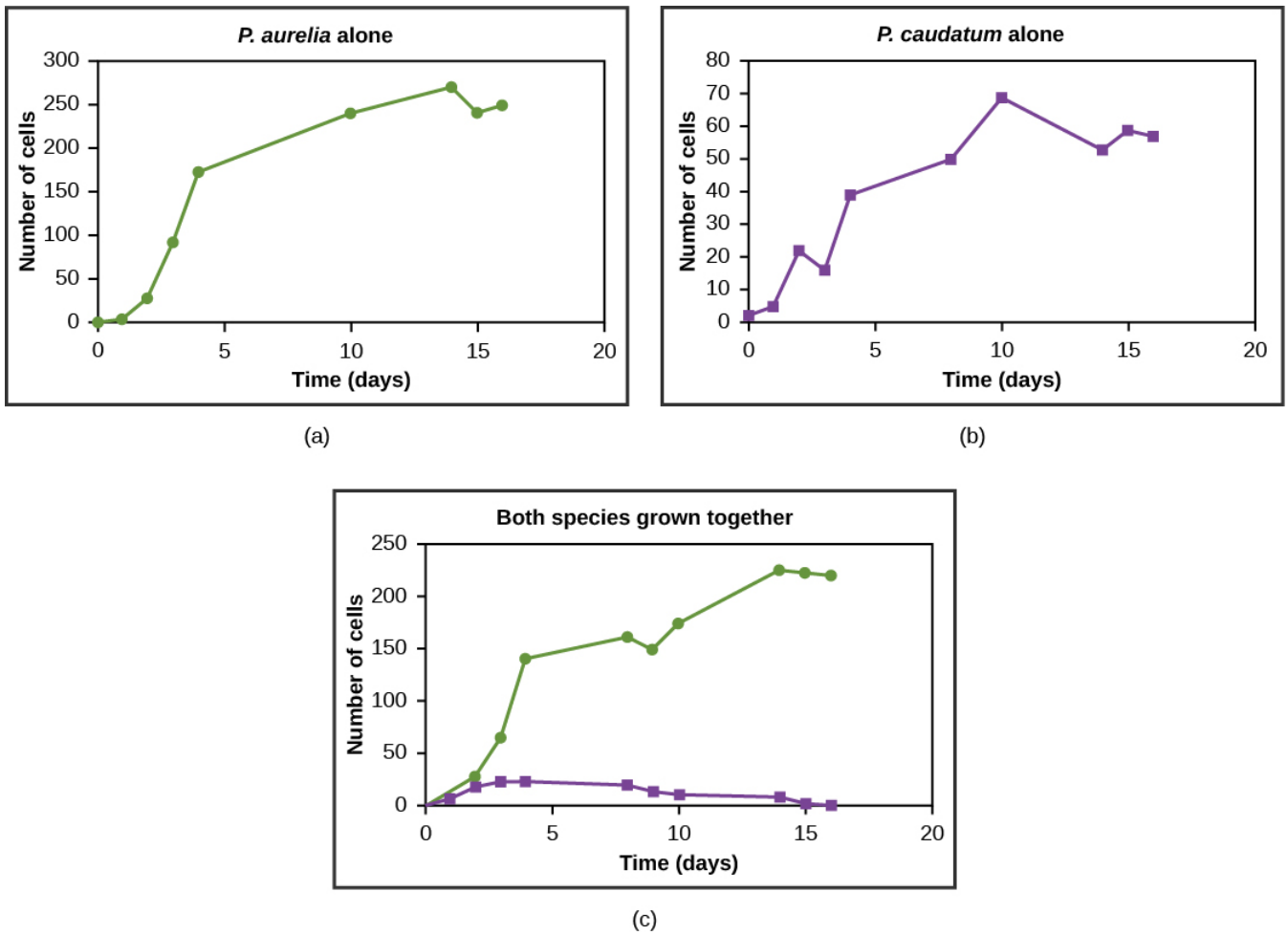


Figure **55.2.1.7**: *Paramecium aurelia* and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These

organisms coexist by minimizing direct competition.

Symbiosis

Symbiotic relationships, or symbioses (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

Commensalism

A commensal relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure **55.2.1.8**). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.



Figure **55.2.1.8**: The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: “Hanay”/Wikimedia Commons)

Mutualism

A second type of symbiotic relationship is called mutualism, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect’s gut (Figure **55.2.1.9**a). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria (Figure **55.2.1.9**b). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.



a b

Figure 55.2.1.9: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Parasitism

A parasite is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the organism being fed upon, the host, is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed (Figure 55.2.1.10). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle. Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.

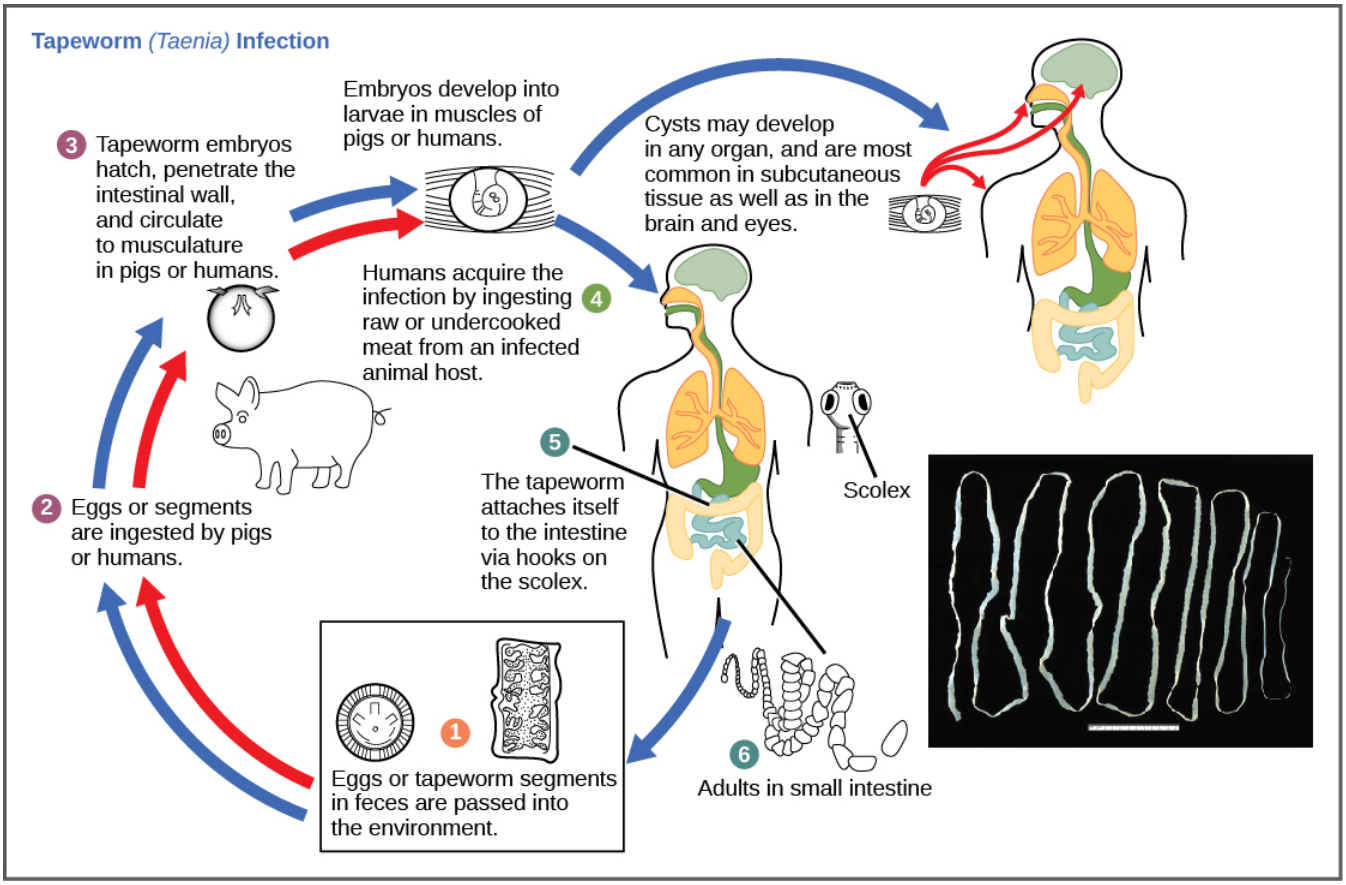


Figure 55.2.1.10: This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef (Figure 55.2.1.11). Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.

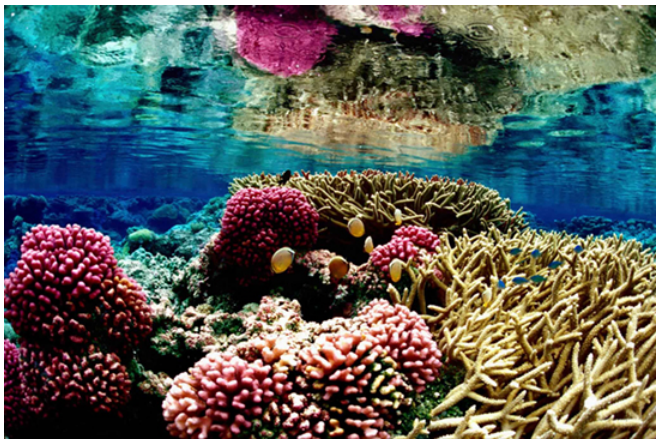


Figure 55.2.1.11: Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS)

Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. Species richness is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe (Figure 55.2.1.12). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of island biogeography attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. Relative species abundance is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.

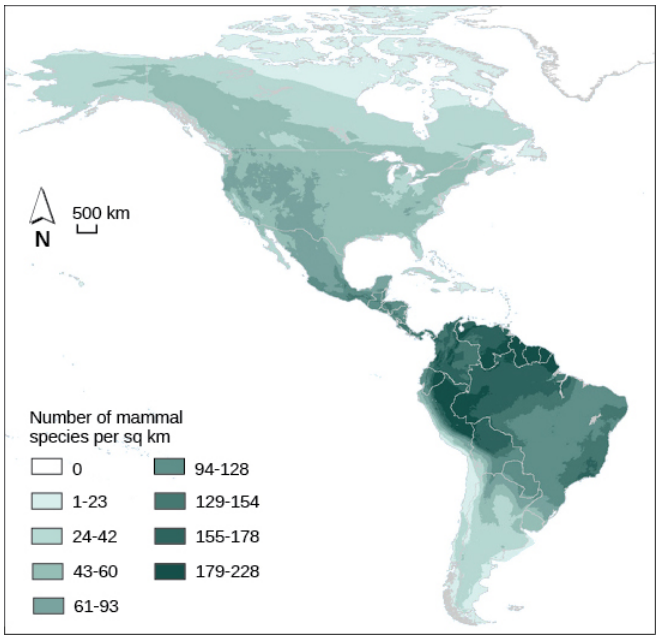


Figure 55.2.1.12: The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

Keystone Species

A keystone species is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species (Figure

55.2.1.13). Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.



Figure 55.2.1.13: The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

Everyday Connection: Invasive Species

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in Figure 55.2.1.14. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

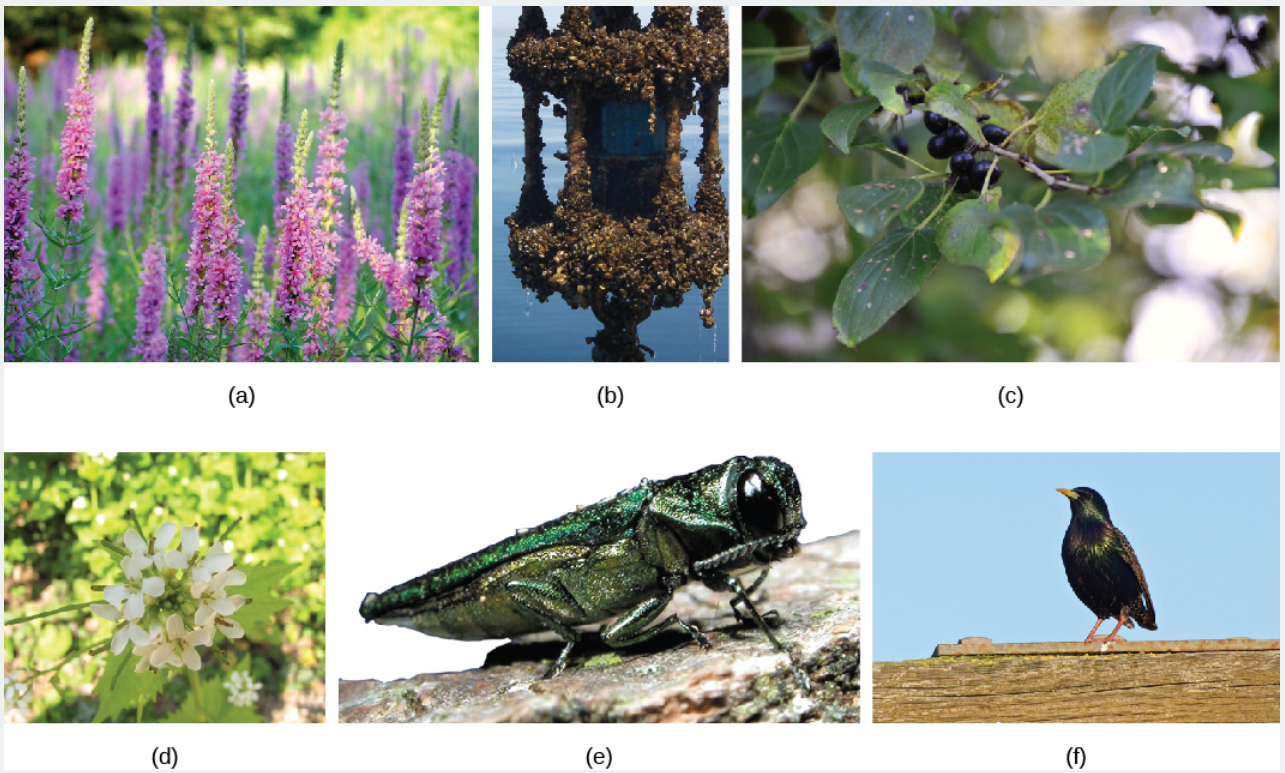


Figure 55.2.1.14: In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as pioneer species (Figure **55.2.1.15**). These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.



Figure **55.2.1.15**: During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire (Figure **55.2.1.16**). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the climax community, which will remain stable until the next disturbance.

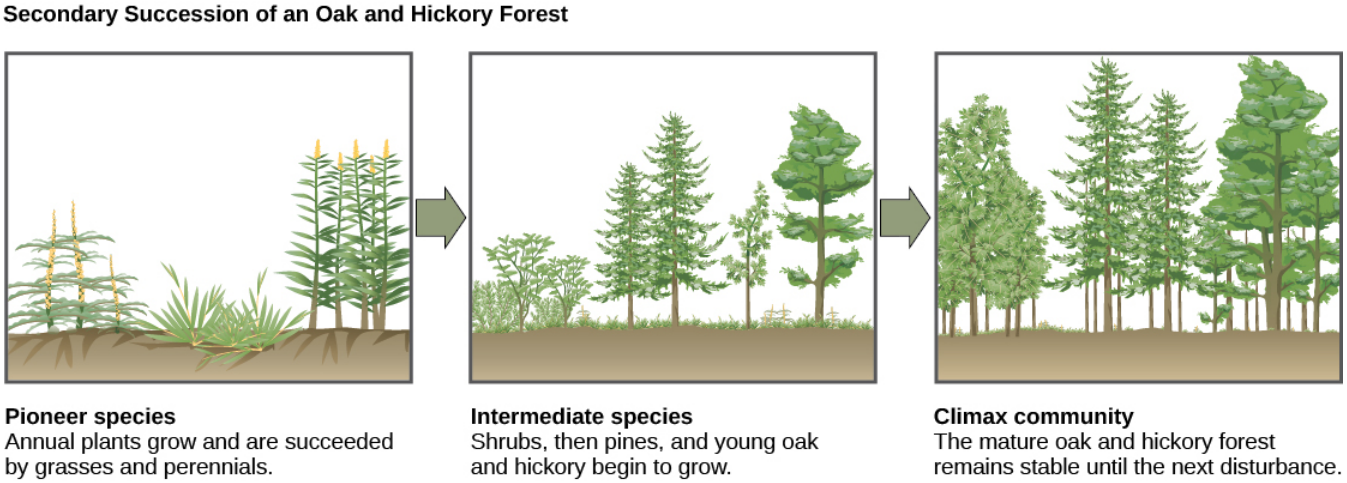


Figure **55.2.1.16**: Secondary succession is shown in an oak and hickory forest after a forest fire.

Summary

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism.

Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established.

Glossary

aposematic coloration
warning coloration used as a defensive mechanism against predation

Batesian mimicry
type of mimicry where a non-harmful species takes on the warning colorations of a harmful one

camouflage
avoid detection by blending in with the background.

climax community
final stage of succession, where a stable community is formed by a characteristic assortment of plant and animal species

commensalism
relationship between species wherein one species benefits from the close, prolonged interaction, while the other species neither benefits nor is harmed

competitive exclusion principle
no two species within a habitat can coexist when they compete for the same resources at the same place and time

Emsleyan/Mertensian mimicry
type of mimicry where a harmful species resembles a less harmful one

environmental disturbance
change in the environment caused by natural disasters or human activities

foundation species
species which often forms the major structural portion of the habitat

host
organism a parasite lives on

island biogeography
study of life on island chains and how their geography interacts with the diversity of species found there

keystone species
species whose presence is key to maintaining biodiversity in an ecosystem and to upholding an ecological community's structure

Müllerian mimicry
type of mimicry where species share warning coloration and all are harmful to predators

mutualism
symbiotic relationship between two species where both species benefit

parasite
organism that uses resources from another species, the host

pioneer species
first species to appear in primary and secondary succession

primary succession

succession on land that previously has had no life

relative species abundance

absolute population size of a particular species relative to the population sizes of other species within the community

secondary succession

succession in response to environmental disturbances that move a community away from its equilibrium

species richness

number of different species in a community

symbiosis

close interaction between individuals of different species over an extended period of time that impacts the abundance and distribution of the associating populations

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55.3: Predator-Prey Relationships

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55.3.1: Community Ecology

Skills to Develop

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Describe community structure and succession

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations inhabiting a specific area at the same time. The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

Predation and Herbivory

Perhaps the classical example of species interaction is predation: the hunting of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests (Figure **55.3.1.1**). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.

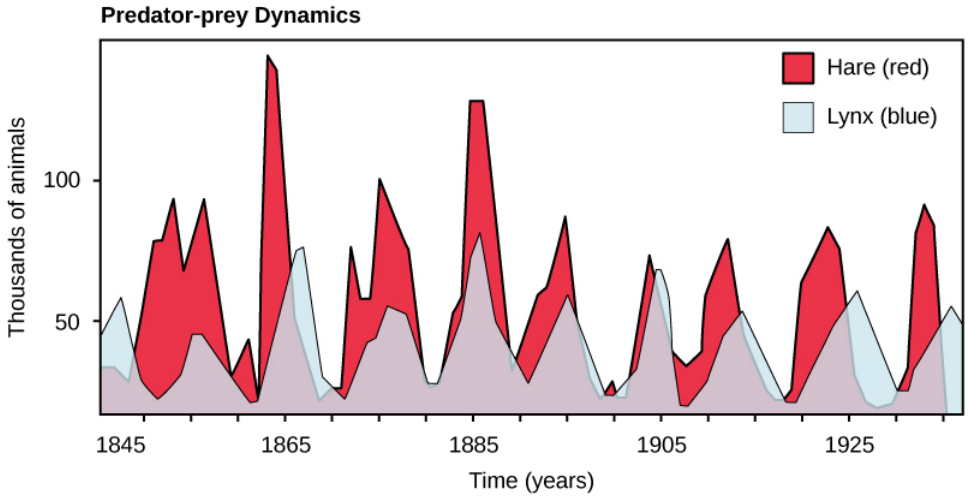


Figure **55.3.1.1**: The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

The idea that the population cycling of the two species is entirely controlled by predation models has come under question. More recent studies have pointed to undefined density-dependent factors as being important in the cycling, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. Figure **55.3.1.2** shows some organisms' defenses against predation and herbivory.



(a)



(b)



(c)



(d)

Figure **55.3.1.2**: The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni*) uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs (Figure **55.3.1.3**a). In another example, the chameleon can change its color to match its surroundings (Figure **55.3.1.3**b). Both of these are examples of camouflage, or avoiding detection by blending in with the background.



a b

Figure 55.3.1.3: (a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemical, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called aposematic coloration, or warning coloration (Figure 55.3.1.4).



(a) (b)

Figure 55.3.1.4: (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In Batesian mimicry, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation (Figure 55.3.1.5).



a b

Figure 55.3.1.5: Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)

In Müllerian mimicry, multiple species share the same warning coloration, but all of them actually have defenses. Figure 55.3.1.6 shows a variety of foul-tasting butterflies with similar coloration. In Emsleyan/Mertensian mimicry, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the non-venomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.



Figure 55.3.1.6: Several unpleasant-tasting *Heliconius* butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Link to Learning

Go to this website to view stunning examples of mimicry.

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The competitive exclusion principle states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in Figure **55.3.1.7**, with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

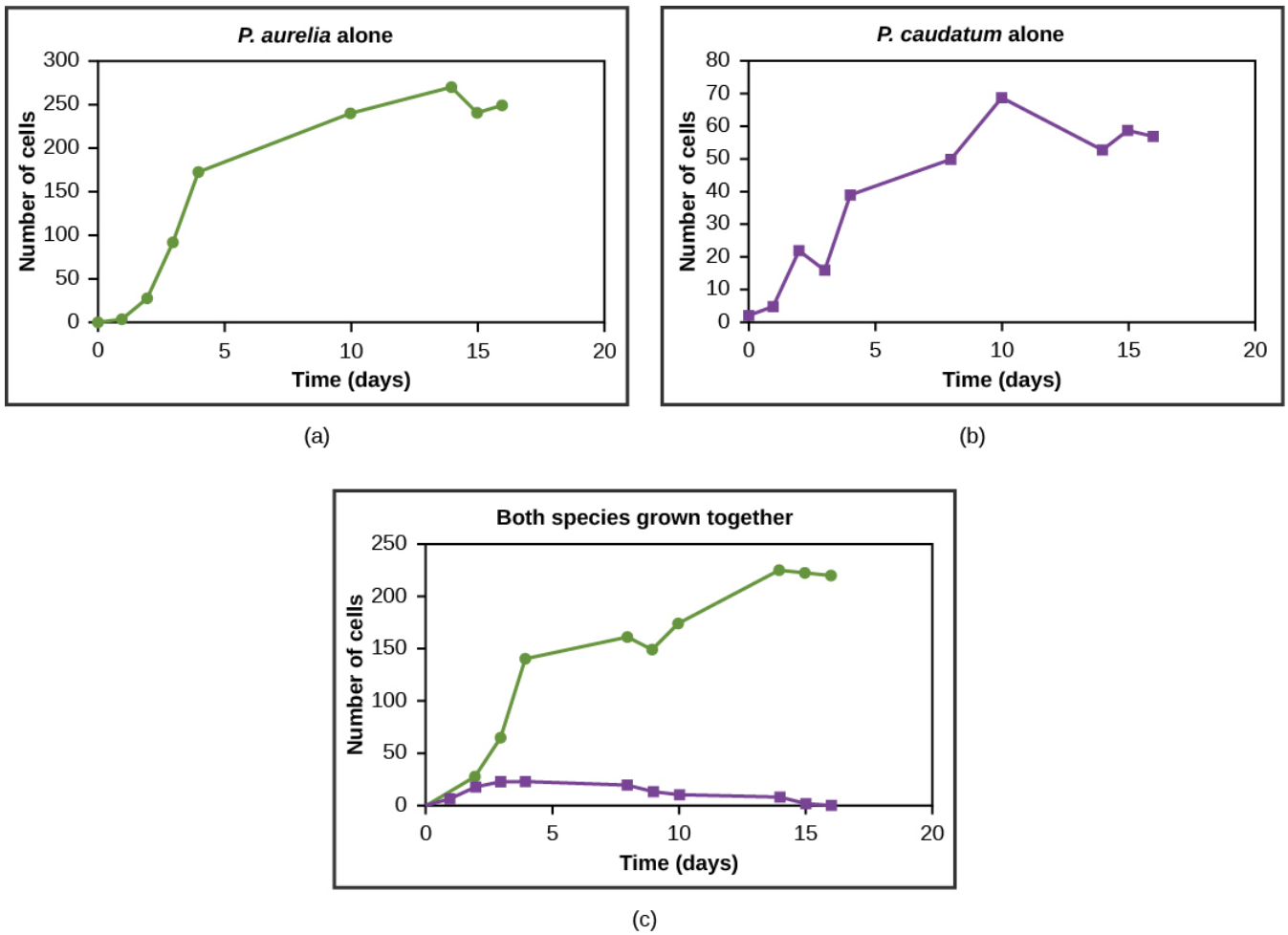


Figure **55.3.1.7**: *Paramecium aurelia* and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These

organisms coexist by minimizing direct competition.

Symbiosis

Symbiotic relationships, or symbioses (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

Commensalism

A commensal relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure **55.3.1.8**). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.



Figure **55.3.1.8**: The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: “Hanay”/Wikimedia Commons)

Mutualism

A second type of symbiotic relationship is called mutualism, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect’s gut (Figure **55.3.1.9**a). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria (Figure **55.3.1.9**b). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.



a b

Figure 55.3.1.9: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Parasitism

A parasite is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the organism being fed upon, the host, is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed (Figure 55.3.1.10). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle. Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.

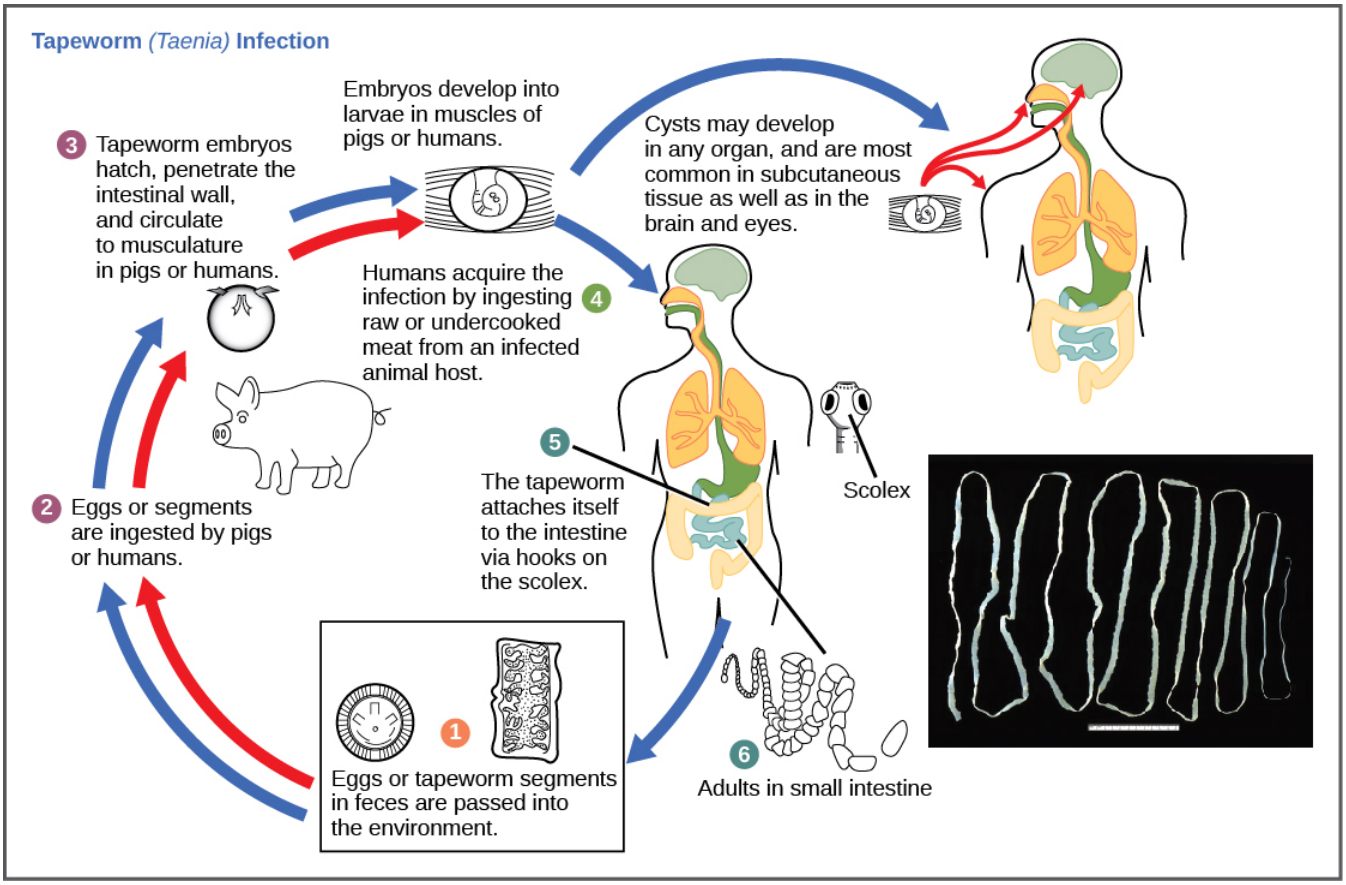


Figure 55.3.1.10: This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef (Figure 55.3.1.11). Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.

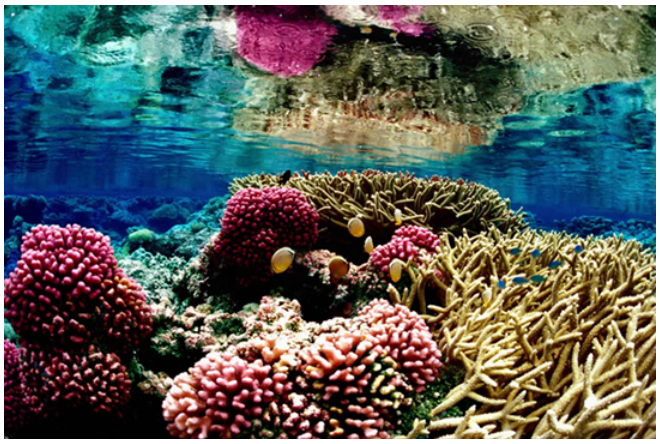


Figure 55.3.1.11: Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS)

Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. Species richness is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe (Figure 55.3.1.12). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of island biogeography attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. Relative species abundance is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.

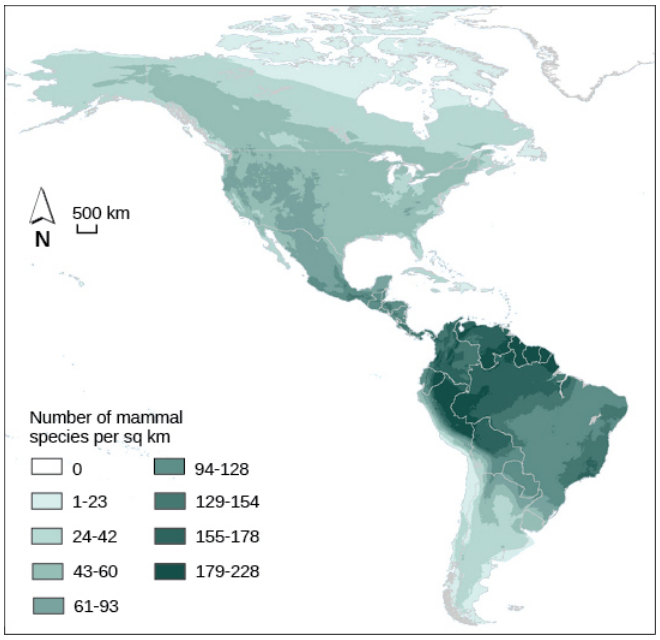


Figure 55.3.1.12: The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

Keystone Species

A keystone species is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species (Figure

55.3.1.13). Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.



Figure 55.3.1.13: The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

Everyday Connection: Invasive Species

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in Figure 55.3.1.14. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

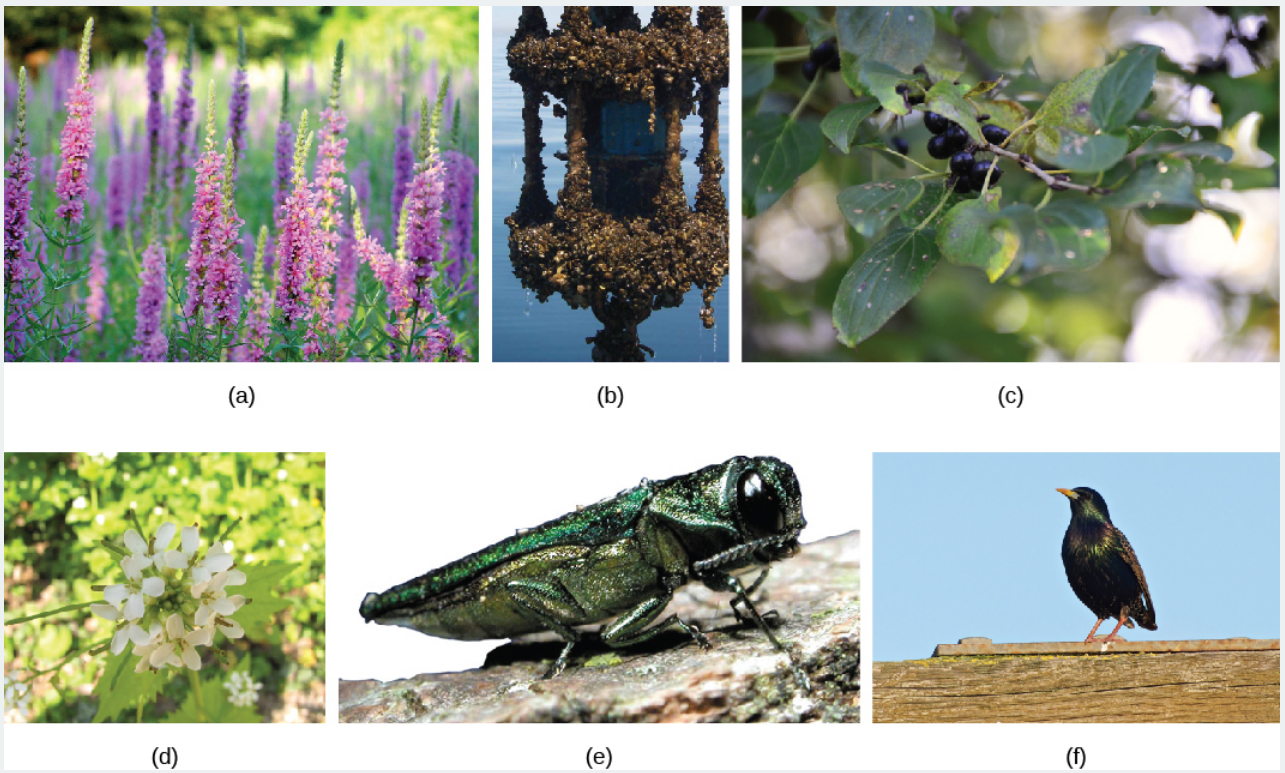


Figure 55.3.1.14: In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as pioneer species (Figure **55.3.1.15**). These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.



Figure **55.3.1.15**: During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire (Figure **55.3.1.16**). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the climax community, which will remain stable until the next disturbance.

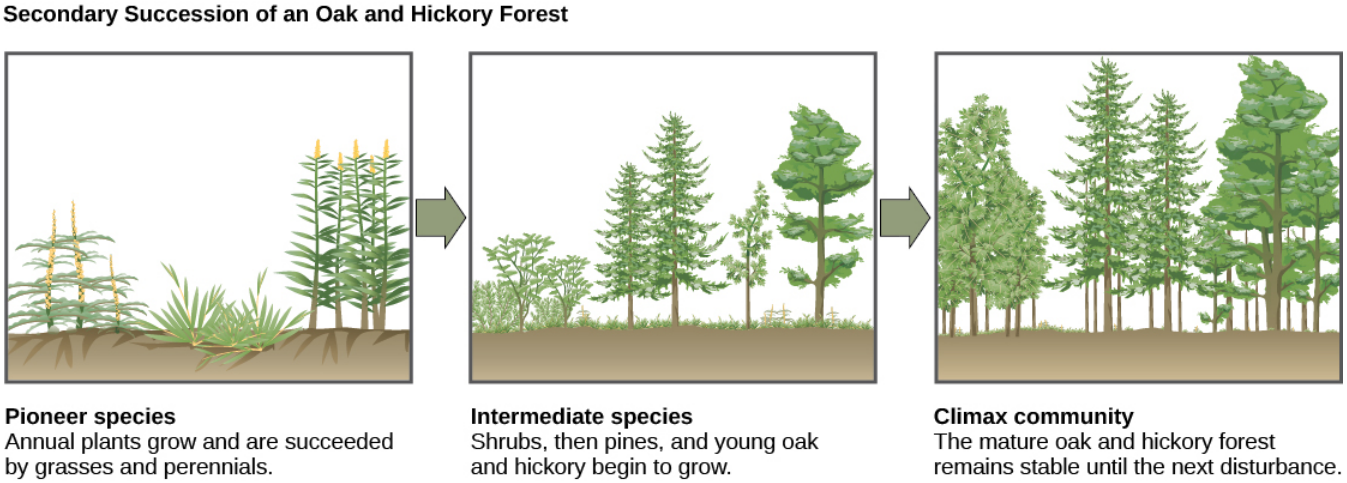


Figure **55.3.1.16**: Secondary succession is shown in an oak and hickory forest after a forest fire.

Summary

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism.

Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established.

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environmental disturbance
change in the environment caused by natural disasters or human activities

foundation species
species which often forms the major structural portion of the habitat

host
organism a parasite lives on

island biogeography
study of life on island chains and how their geography interacts with the diversity of species found there

keystone species
species whose presence is key to maintaining biodiversity in an ecosystem and to upholding an ecological community's structure

Müllerian mimicry
type of mimicry where species share warning coloration and all are harmful to predators

mutualism
symbiotic relationship between two species where both species benefit

parasite
organism that uses resources from another species, the host

pioneer species
first species to appear in primary and secondary succession

primary succession

succession on land that previously has had no life

relative species abundance

absolute population size of a particular species relative to the population sizes of other species within the community

secondary succession

succession in response to environmental disturbances that move a community away from its equilibrium

species richness

number of different species in a community

symbiosis

close interaction between individuals of different species over an extended period of time that impacts the abundance and distribution of the associating populations

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55.4: The Many Types of Species Interactions

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55.4.1: Community Ecology

Skills to Develop

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Describe community structure and succession

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations inhabiting a specific area at the same time. The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

Predation and Herbivory

Perhaps the classical example of species interaction is predation: the hunting of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests (Figure **55.4.1.1**). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.

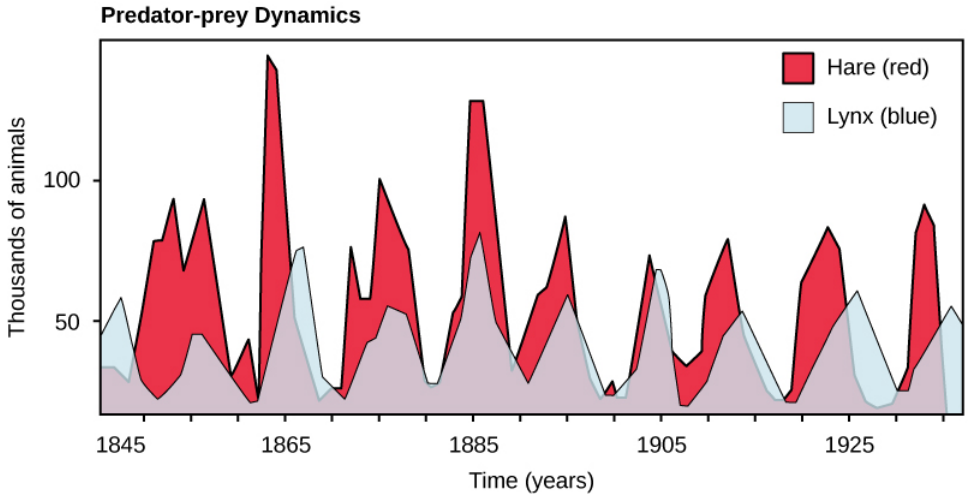


Figure **55.4.1.1**: The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

The idea that the population cycling of the two species is entirely controlled by predation models has come under question. More recent studies have pointed to undefined density-dependent factors as being important in the cycling, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. Figure **55.4.1.2** shows some organisms' defenses against predation and herbivory.



(a)



(b)



(c)



(d)

Figure **55.4.1.2**: The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni*) uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs (Figure **55.4.1.3**a). In another example, the chameleon can change its color to match its surroundings (Figure **55.4.1.3**b). Both of these are examples of camouflage, or avoiding detection by blending in with the background.



a b

Figure 55.4.1.3: (a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemical, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called aposematic coloration, or warning coloration (Figure 55.4.1.4).



(a) (b)

Figure 55.4.1.4: (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In Batesian mimicry, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation (Figure 55.4.1.5).



a b

Figure 55.4.1.5: Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)

In Müllerian mimicry, multiple species share the same warning coloration, but all of them actually have defenses. Figure 55.4.1.6 shows a variety of foul-tasting butterflies with similar coloration. In Emsleyan/Mertensian mimicry, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the non-venomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.



Figure 55.4.1.6: Several unpleasant-tasting *Heliconius* butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Link to Learning

Go to this website to view stunning examples of mimicry.

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The competitive exclusion principle states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in Figure **55.4.1.7**, with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

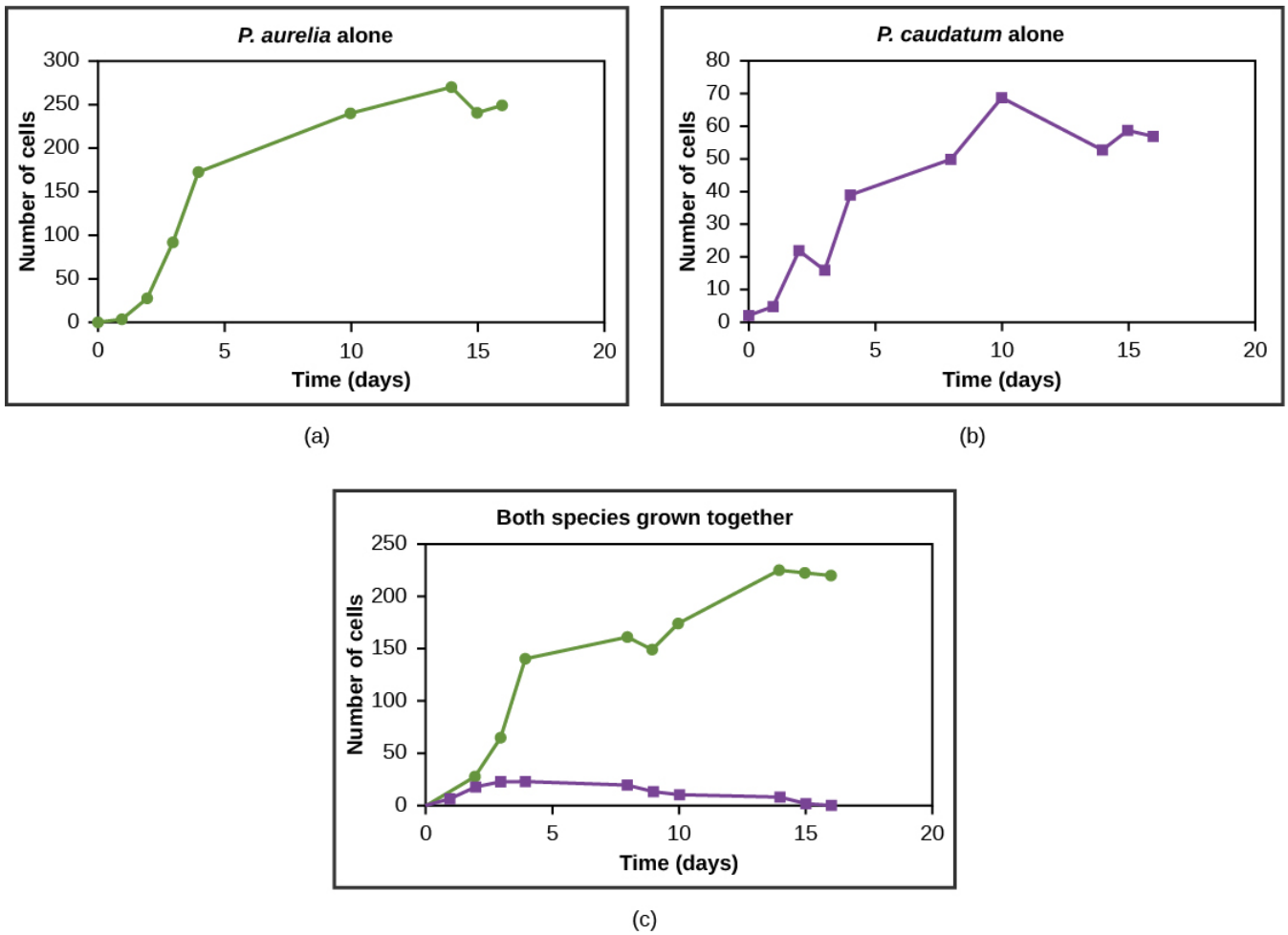


Figure **55.4.1.7**: *Paramecium aurelia* and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These

organisms coexist by minimizing direct competition.

Symbiosis

Symbiotic relationships, or symbioses (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

Commensalism

A commensal relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure **55.4.1.8**). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.



Figure **55.4.1.8**: The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: “Hanay”/Wikimedia Commons)

Mutualism

A second type of symbiotic relationship is called mutualism, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect’s gut (Figure **55.4.1.9**a). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria (Figure **55.4.1.9**b). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.



a b

Figure 55.4.1.9: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Parasitism

A parasite is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the organism being fed upon, the host, is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed (Figure 55.4.1.10). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle. Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.

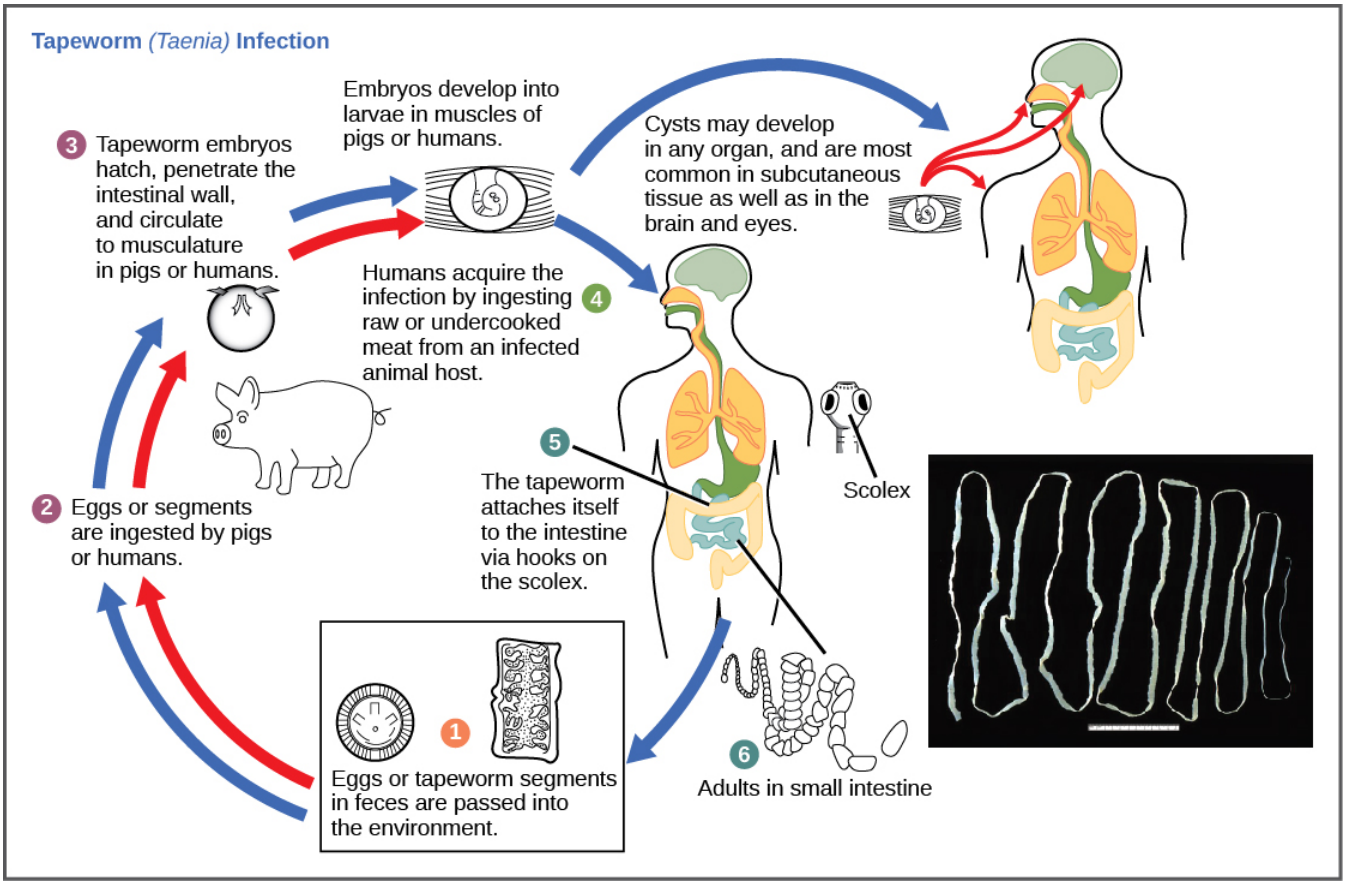


Figure 55.4.1.10: This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef (Figure 55.4.1.11). Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.

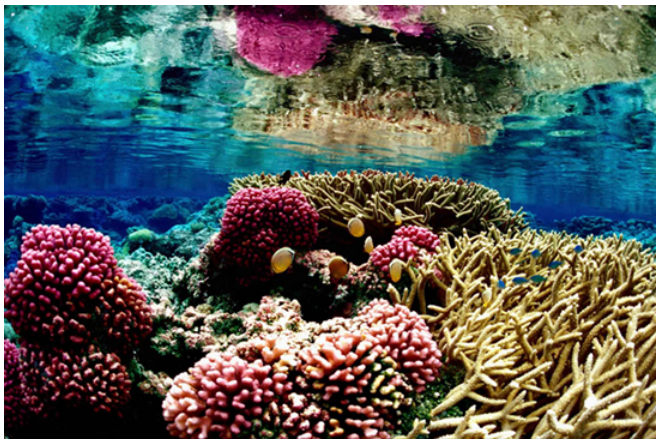


Figure 55.4.1.11: Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS)

Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. Species richness is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe (Figure 55.4.1.12). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of island biogeography attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. Relative species abundance is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.

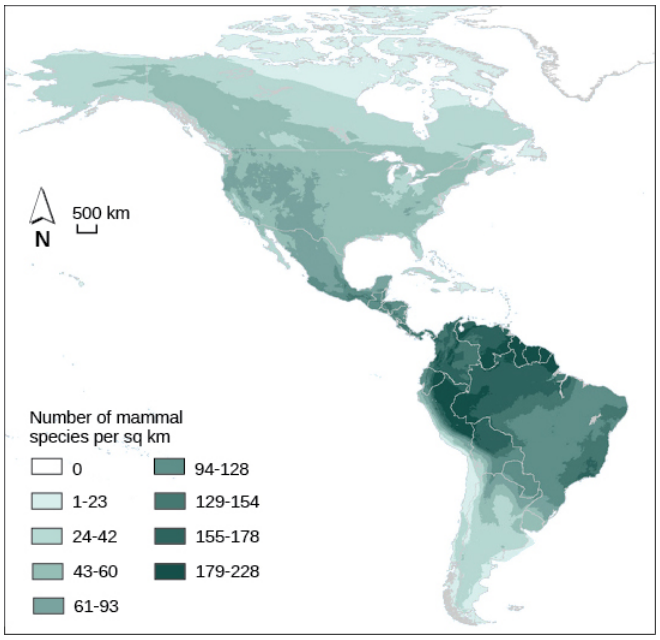


Figure 55.4.1.12: The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

Keystone Species

A keystone species is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species (Figure

55.4.1.13). Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.



Figure 55.4.1.13: The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

Everyday Connection: Invasive Species

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in Figure 55.4.1.14. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

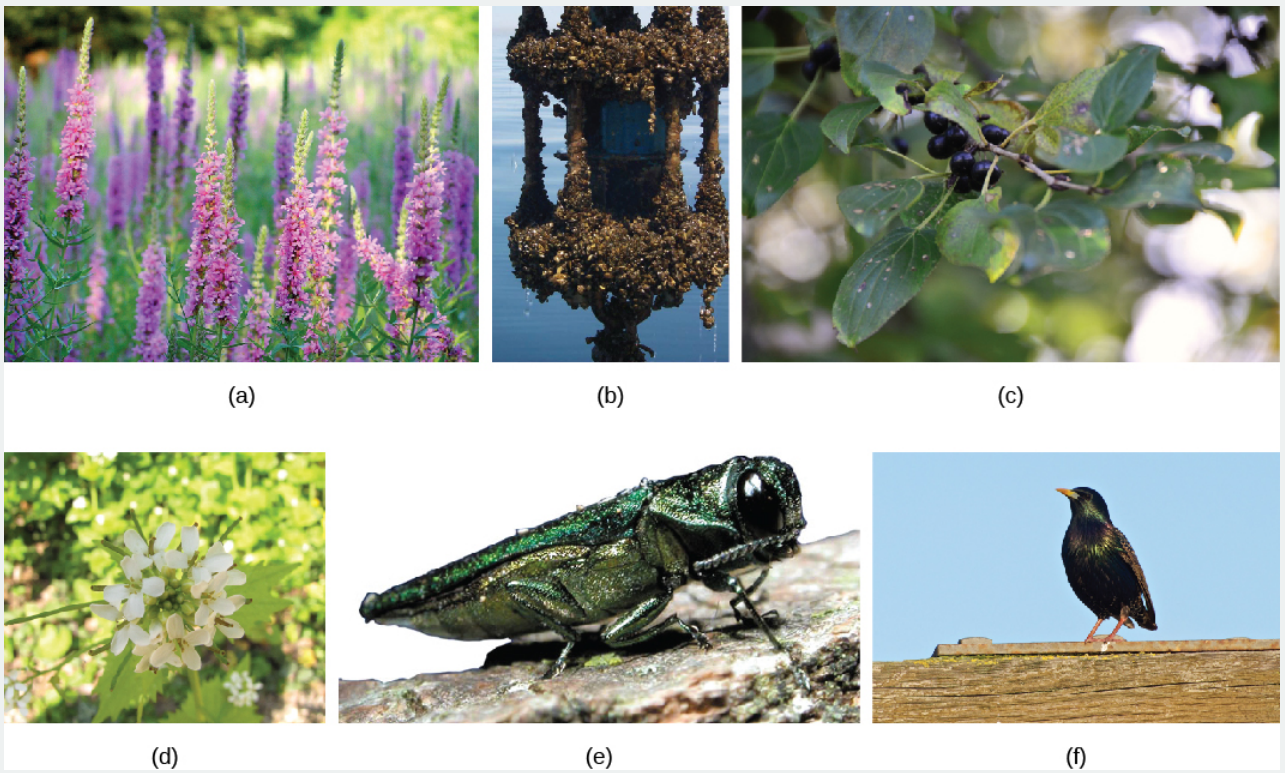


Figure 55.4.1.14: In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as pioneer species (Figure **55.4.1.15**). These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.



Figure **55.4.1.15**: During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire (Figure **55.4.1.16**). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the climax community, which will remain stable until the next disturbance.

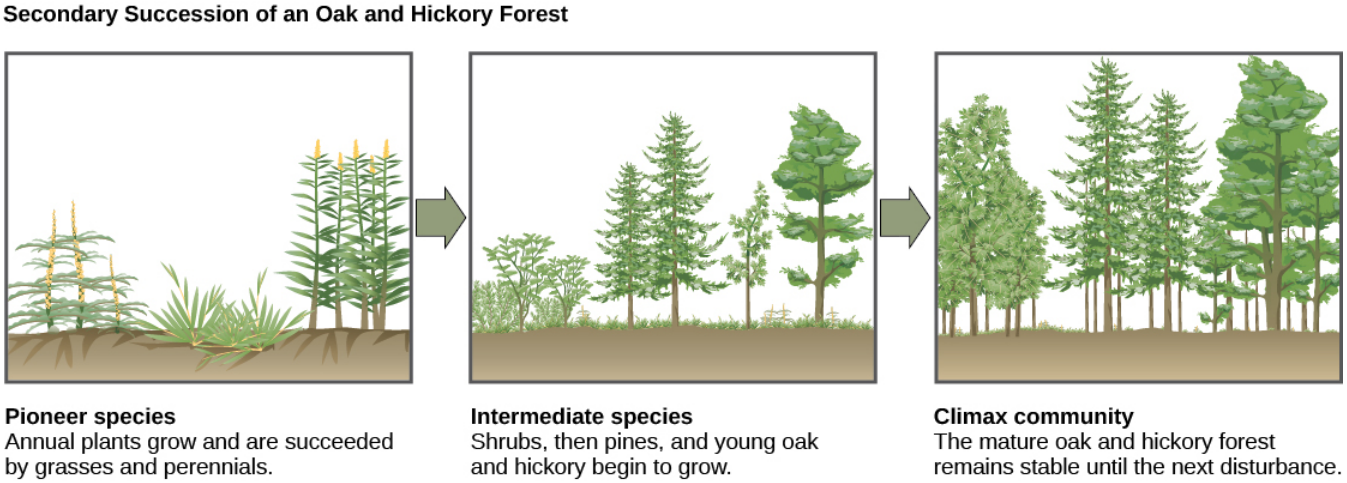


Figure **55.4.1.16**: Secondary succession is shown in an oak and hickory forest after a forest fire.

Summary

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism.

Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established.

Glossary

aposematic coloration
warning coloration used as a defensive mechanism against predation

Batesian mimicry
type of mimicry where a non-harmful species takes on the warning colorations of a harmful one

camouflage
avoid detection by blending in with the background.

climax community
final stage of succession, where a stable community is formed by a characteristic assortment of plant and animal species

commensalism
relationship between species wherein one species benefits from the close, prolonged interaction, while the other species neither benefits nor is harmed

competitive exclusion principle
no two species within a habitat can coexist when they compete for the same resources at the same place and time

Emsleyan/Mertensian mimicry
type of mimicry where a harmful species resembles a less harmful one

environmental disturbance
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55.5: Ecological Successions, Disturbance, and Species Richness

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55.5.1: Community Ecology

Skills to Develop

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- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Describe community structure and succession

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations inhabiting a specific area at the same time. The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

Predation and Herbivory

Perhaps the classical example of species interaction is predation: the hunting of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests (Figure **55.5.1.1**). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.

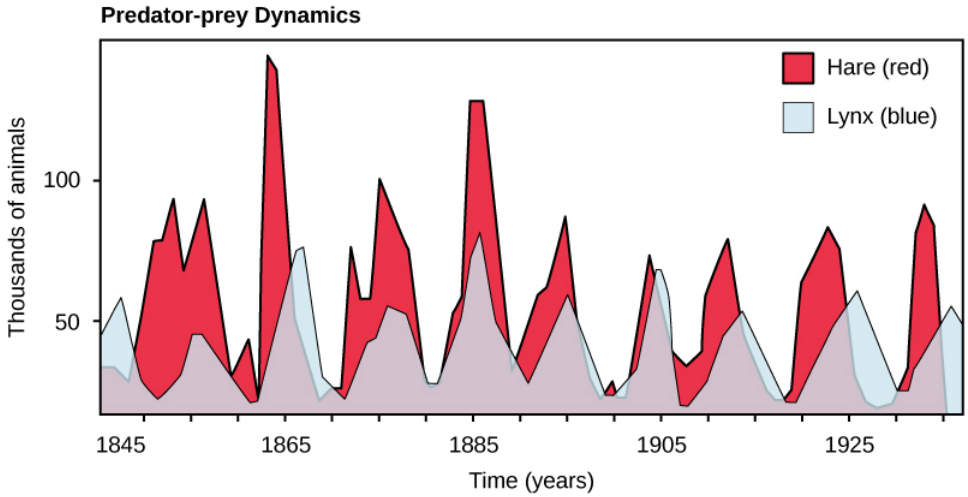


Figure **55.5.1.1**: The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

The idea that the population cycling of the two species is entirely controlled by predation models has come under question. More recent studies have pointed to undefined density-dependent factors as being important in the cycling, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. Figure **55.5.1.2** shows some organisms' defenses against predation and herbivory.



(a)



(b)



(c)



(d)

Figure **55.5.1.2**: The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni*) uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs (Figure **55.5.1.3**a). In another example, the chameleon can change its color to match its surroundings (Figure **55.5.1.3**b). Both of these are examples of camouflage, or avoiding detection by blending in with the background.



a b

Figure 55.5.1.3: (a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemical, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called aposematic coloration, or warning coloration (Figure 55.5.1.4).



(a) (b)

Figure 55.5.1.4: (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In Batesian mimicry, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation (Figure 55.5.1.5).



a b

Figure 55.5.1.5: Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)

In Müllerian mimicry, multiple species share the same warning coloration, but all of them actually have defenses. Figure 55.5.1.6 shows a variety of foul-tasting butterflies with similar coloration. In Emsleyan/Mertensian mimicry, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the non-venomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.



Figure 55.5.1.6: Several unpleasant-tasting *Heliconius* butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Link to Learning

Go to this website to view stunning examples of mimicry.

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The competitive exclusion principle states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in Figure **55.5.1.7**, with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

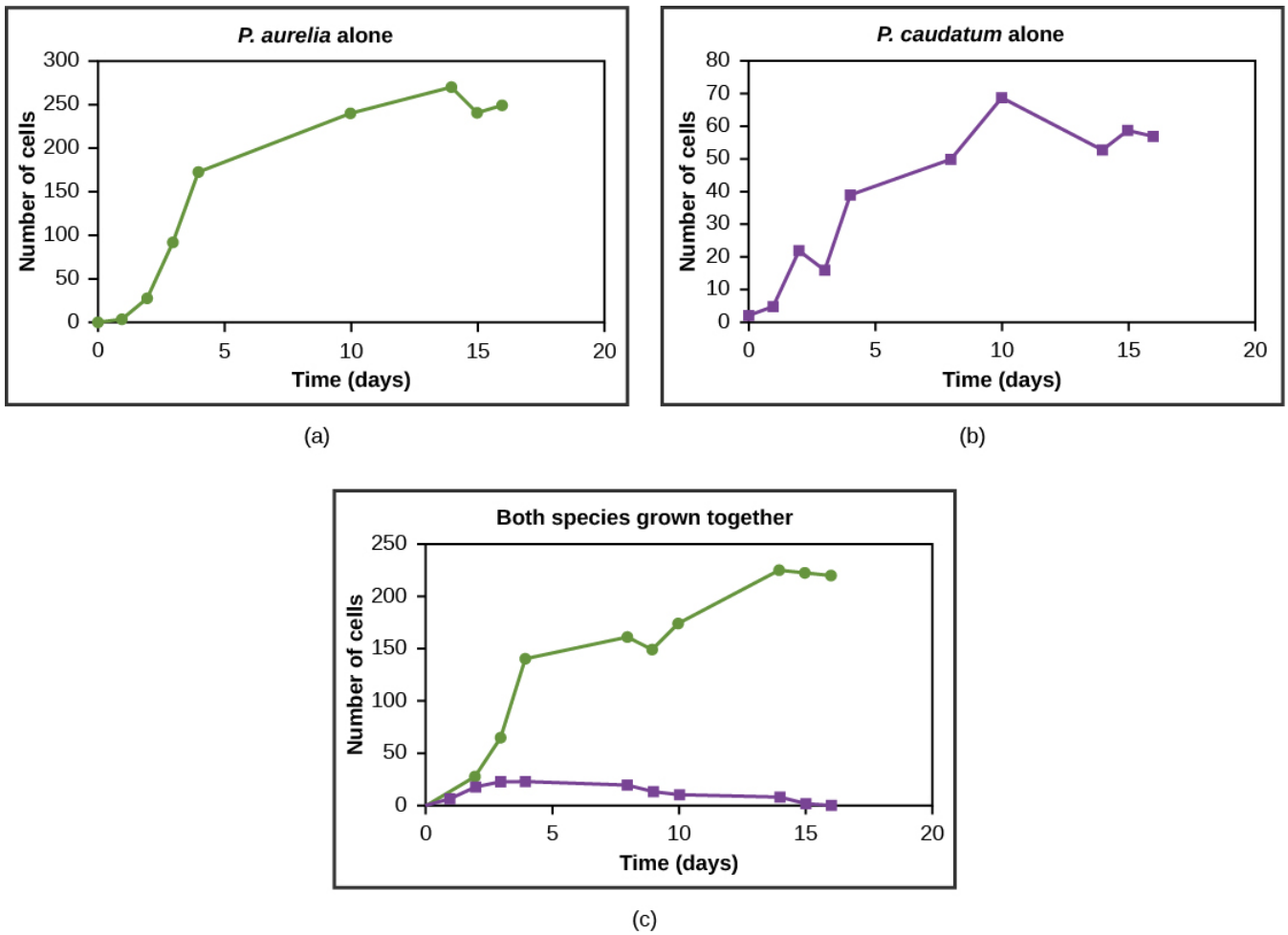


Figure **55.5.1.7**: *Paramecium aurelia* and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These

organisms coexist by minimizing direct competition.

Symbiosis

Symbiotic relationships, or symbioses (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

Commensalism

A commensal relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure **55.5.1.8**). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.



Figure **55.5.1.8**: The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: “Hanay”/Wikimedia Commons)

Mutualism

A second type of symbiotic relationship is called mutualism, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect’s gut (Figure **55.5.1.9**a). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria (Figure **55.5.1.9**b). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.



a b

Figure 55.5.1.9: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Parasitism

A parasite is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the organism being fed upon, the host, is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed (Figure 55.5.1.10). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle. Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.

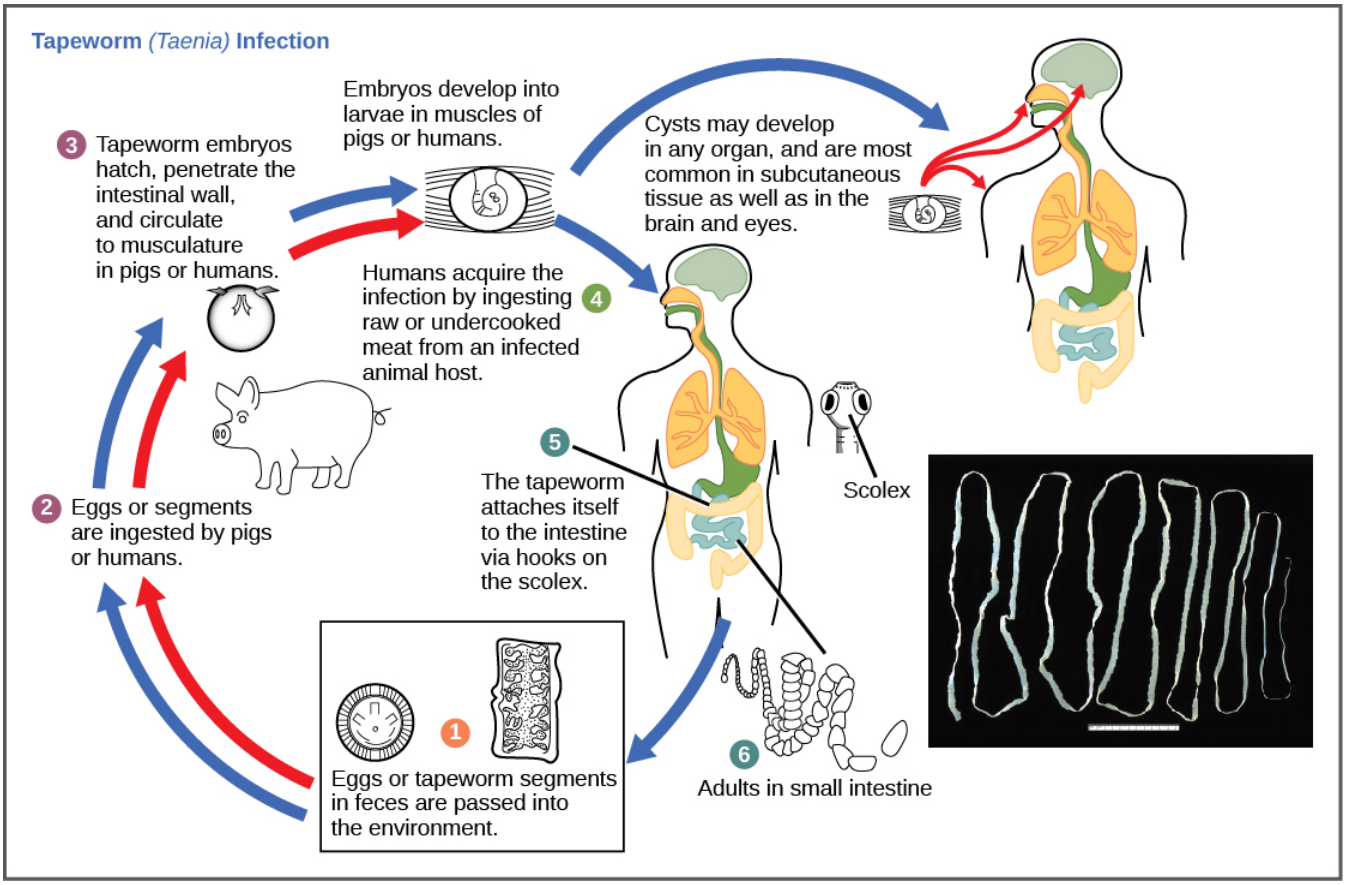


Figure 55.5.1.10: This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef (Figure 55.5.1.11). Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.

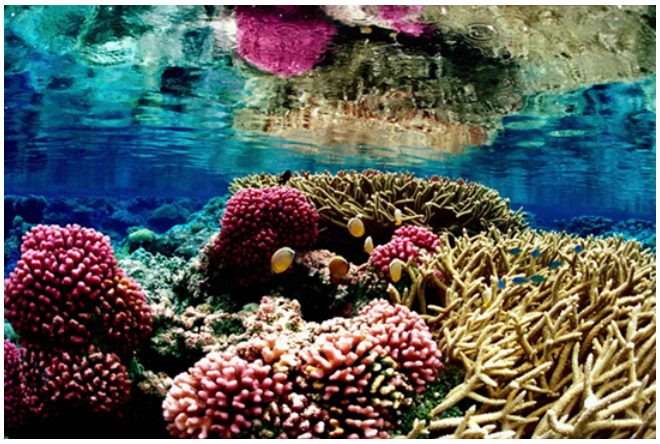


Figure 55.5.1.11: Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS)

Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. Species richness is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe (Figure 55.5.1.12). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of island biogeography attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. Relative species abundance is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.

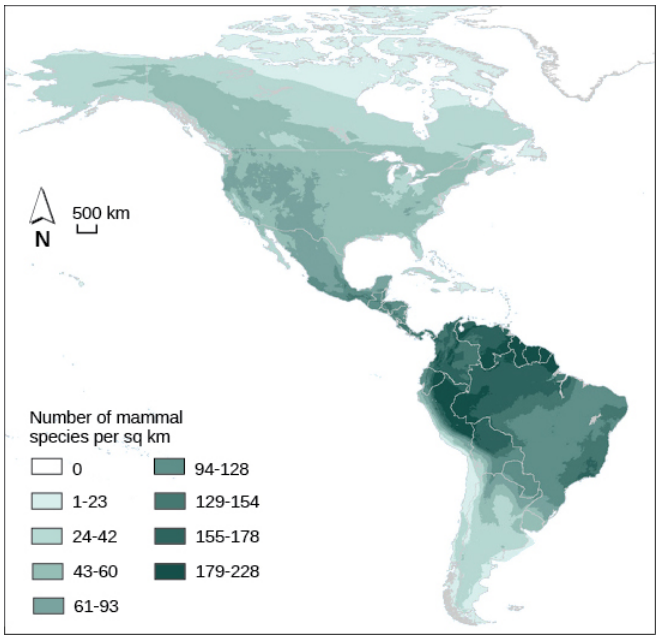


Figure 55.5.1.12: The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

Keystone Species

A keystone species is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species (Figure

55.5.1.13). Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.



Figure 55.5.1.13: The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

Everyday Connection: Invasive Species

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in Figure 55.5.1.14. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

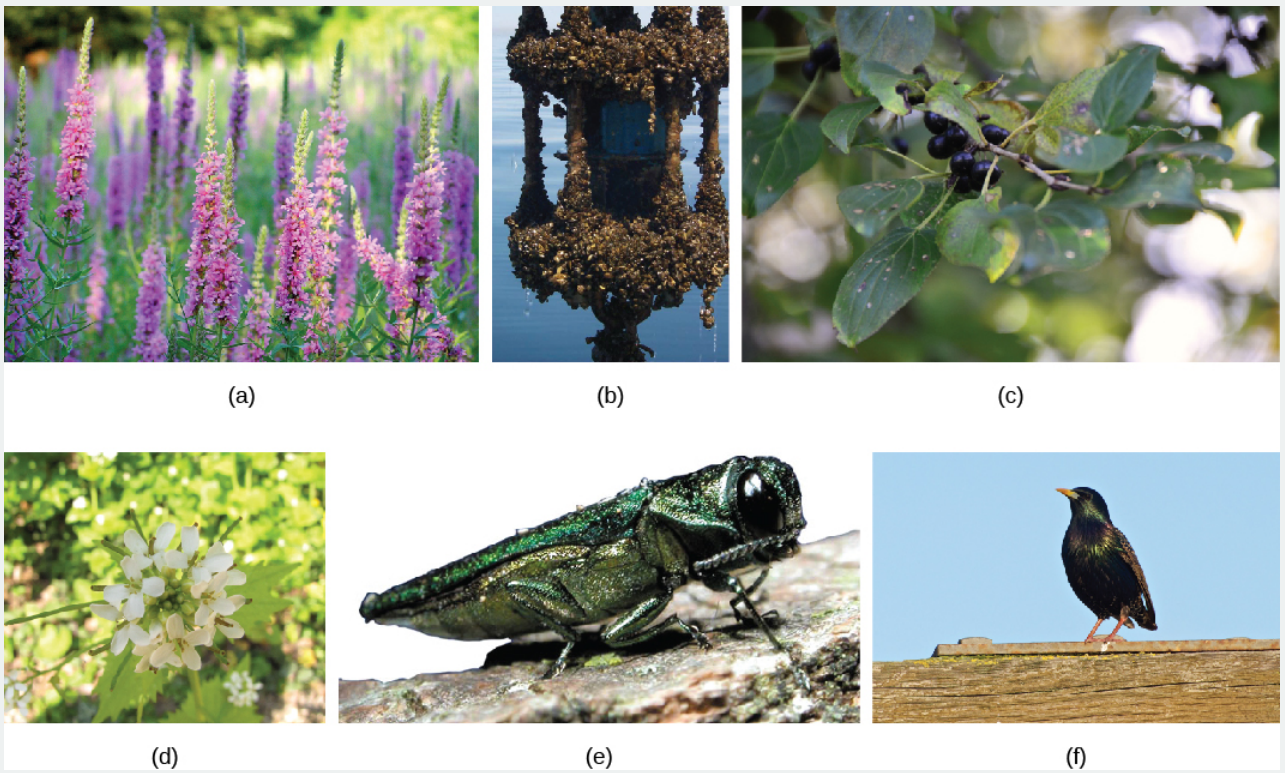


Figure 55.5.1.14: In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as pioneer species (Figure **55.5.1.15**). These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.



Figure 55.5.1.15: During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire (Figure 55.5.1.16). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the climax community, which will remain stable until the next disturbance.

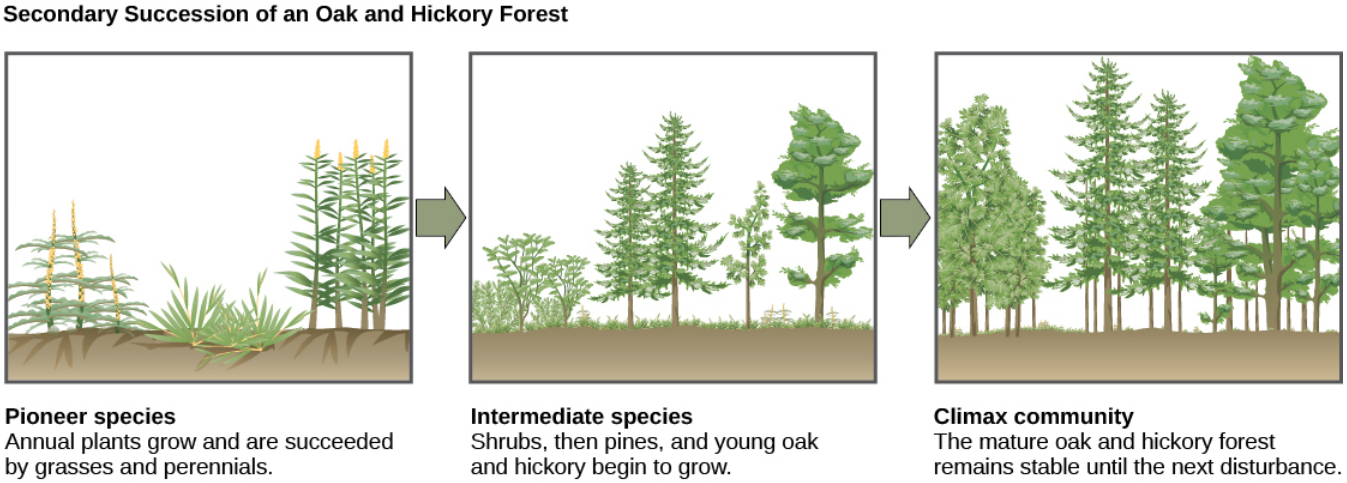


Figure 55.5.1.16: Secondary succession is shown in an oak and hickory forest after a forest fire.

Summary

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism.

Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established.

Glossary

aposematic coloration
warning coloration used as a defensive mechanism against predation

Batesian mimicry
type of mimicry where a non-harmful species takes on the warning colorations of a harmful one

camouflage
avoid detection by blending in with the background.

climax community
final stage of succession, where a stable community is formed by a characteristic assortment of plant and animal species

commensalism
relationship between species wherein one species benefits from the close, prolonged interaction, while the other species neither benefits nor is harmed

competitive exclusion principle
no two species within a habitat can coexist when they compete for the same resources at the same place and time

Emsleyan/Mertensian mimicry
type of mimicry where a harmful species resembles a less harmful one

environmental disturbance
change in the environment caused by natural disasters or human activities

foundation species
species which often forms the major structural portion of the habitat

host
organism a parasite lives on

island biogeography
study of life on island chains and how their geography interacts with the diversity of species found there

keystone species
species whose presence is key to maintaining biodiversity in an ecosystem and to upholding an ecological community's structure

Müllerian mimicry
type of mimicry where species share warning coloration and all are harmful to predators

mutualism
symbiotic relationship between two species where both species benefit

parasite
organism that uses resources from another species, the host

pioneer species
first species to appear in primary and secondary succession

primary succession

succession on land that previously has had no life

relative species abundance

absolute population size of a particular species relative to the population sizes of other species within the community

secondary succession

succession in response to environmental disturbances that move a community away from its equilibrium

species richness

number of different species in a community

symbiosis

close interaction between individuals of different species over an extended period of time that impacts the abundance and distribution of the associating populations

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CHAPTER OVERVIEW

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- 56.1: Biogeochemical Cycles
- 56.2: The Flow of Energy in Ecosystems
- 56.3: Trophic Level Interactions
  - 56.3.1: Predation
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56.1: Biogeochemical Cycles

Skills to Develop

- Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur
- Explain how human activities have impacted these cycles and the potential consequences for Earth

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules—carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur—take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the Earth's surface. Geologic processes, such as weathering, erosion, water drainage, and the subduction of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a biogeochemical cycle.

Water contains hydrogen and oxygen, which is essential to all living processes. The hydrosphere is the area of the Earth where water movement and storage occurs: as liquid water on the surface and beneath the surface or frozen (rivers, lakes, oceans, groundwater, polar ice caps, and glaciers), and as water vapor in the atmosphere. Carbon is found in all organic macromolecules and is an important constituent of fossil fuels. Nitrogen is a major component of our nucleic acids and proteins and is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur, critical to the 3–D folding of proteins (as in disulfide binding), is released into the atmosphere by the burning of fossil fuels, such as coal.

The cycling of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

The Water (Hydrologic) Cycle

Water is the basis of all living processes. The human body is more than 1/2 water and human cells are more than 70 percent water. Thus, most land animals need a supply of fresh water to survive. However, when examining the stores of water on Earth, 97.5 percent of it is non-potable salt water (Figure **56.1.1**). Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1 percent of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on the small amount of fresh surface water supply, a lack of which can have massive effects on ecosystem dynamics. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean. Although this pursuit of drinkable water has been ongoing throughout human history, the supply of fresh water is still a major issue in modern times.

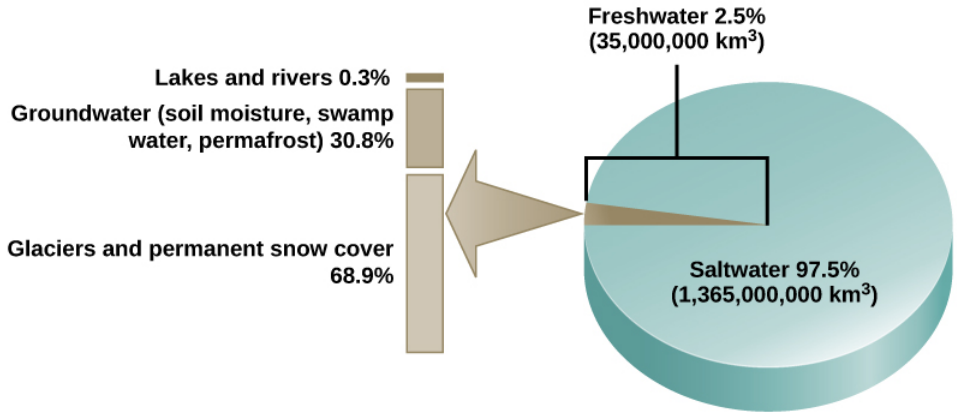


Figure **56.1.1**: Only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things.

Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems, some located on distant parts of the Earth. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. Figure **56.1.2** illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. Residence time is a measure of the average time an individual water molecule stays in a particular reservoir. A large amount of the Earth's water is locked in place in these reservoirs as ice, beneath the ground, and in the ocean, and, thus, is unavailable for short-term cycling (only surface water can evaporate).

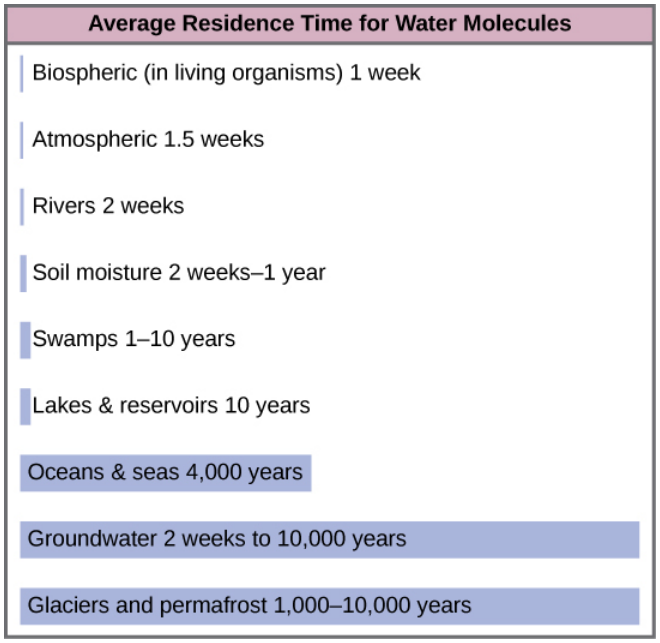


Figure **56.1.2**: This graph shows the average residence time for water molecules in the Earth's water reservoirs.

There are various processes that occur during the cycling of water, shown in Figure **56.1.3**. These processes include the following:

- evaporation/sublimation
- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

The water cycle is driven by the sun's energy as it warms the oceans and other surface waters. This leads to the evaporation (water to water vapor) of liquid surface water and the sublimation (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets and is eventually followed by precipitation (rain or snow), which returns water to the Earth's surface. Rain eventually permeates into the ground, where it may evaporate again if it is near the surface, flow beneath the surface, or be stored for long periods. More easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

Link to Learning

Head to this website to learn more about the world's fresh water supply.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. The environmental effects of runoff will be discussed later as these cycles are described.

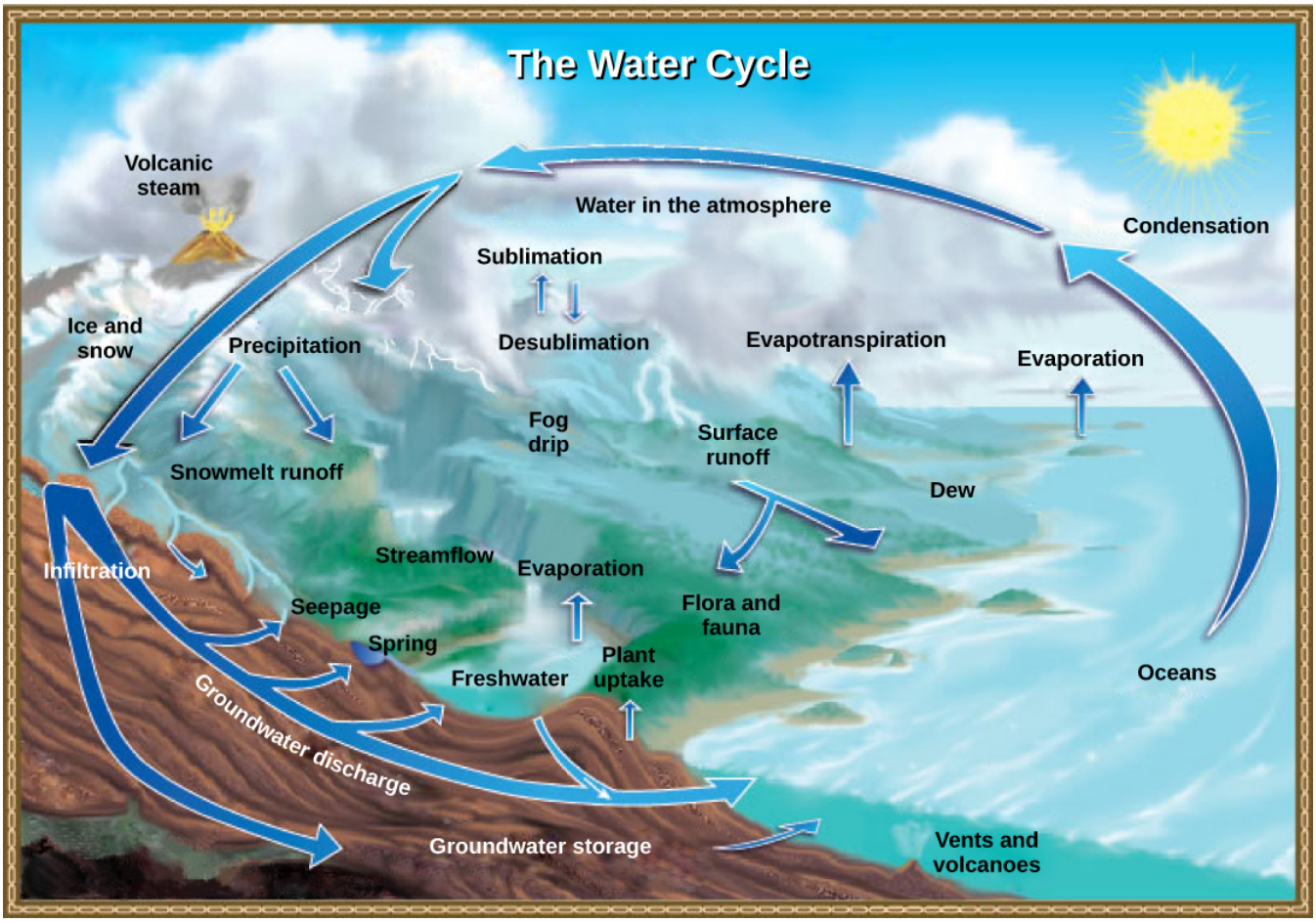


Figure **56.1.3**: Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Carbon Cycle

Carbon is the second most abundant element in living organisms. Carbon is present in all organic molecules, and its role in the structure of macromolecules is of primary importance to living organisms. Carbon compounds contain especially high energy, particularly those derived from fossilized organisms, mainly plants, which humans use as fuel. Since the 1800s, the number of countries using massive amounts of fossil fuels has increased. Since the beginning of the Industrial Revolution, global demand for the Earth's limited fossil fuel supplies has risen; therefore, the amount of carbon dioxide in our atmosphere has increased. This increase in carbon dioxide has been associated with climate change and other disturbances of the Earth's ecosystems and is a major environmental concern worldwide. Thus, the "carbon footprint" is based on how much carbon dioxide is produced and how much fossil fuel countries consume.

The carbon cycle is most easily studied as two interconnected sub-cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes. The entire carbon cycle is shown in Figure **56.1.4**.

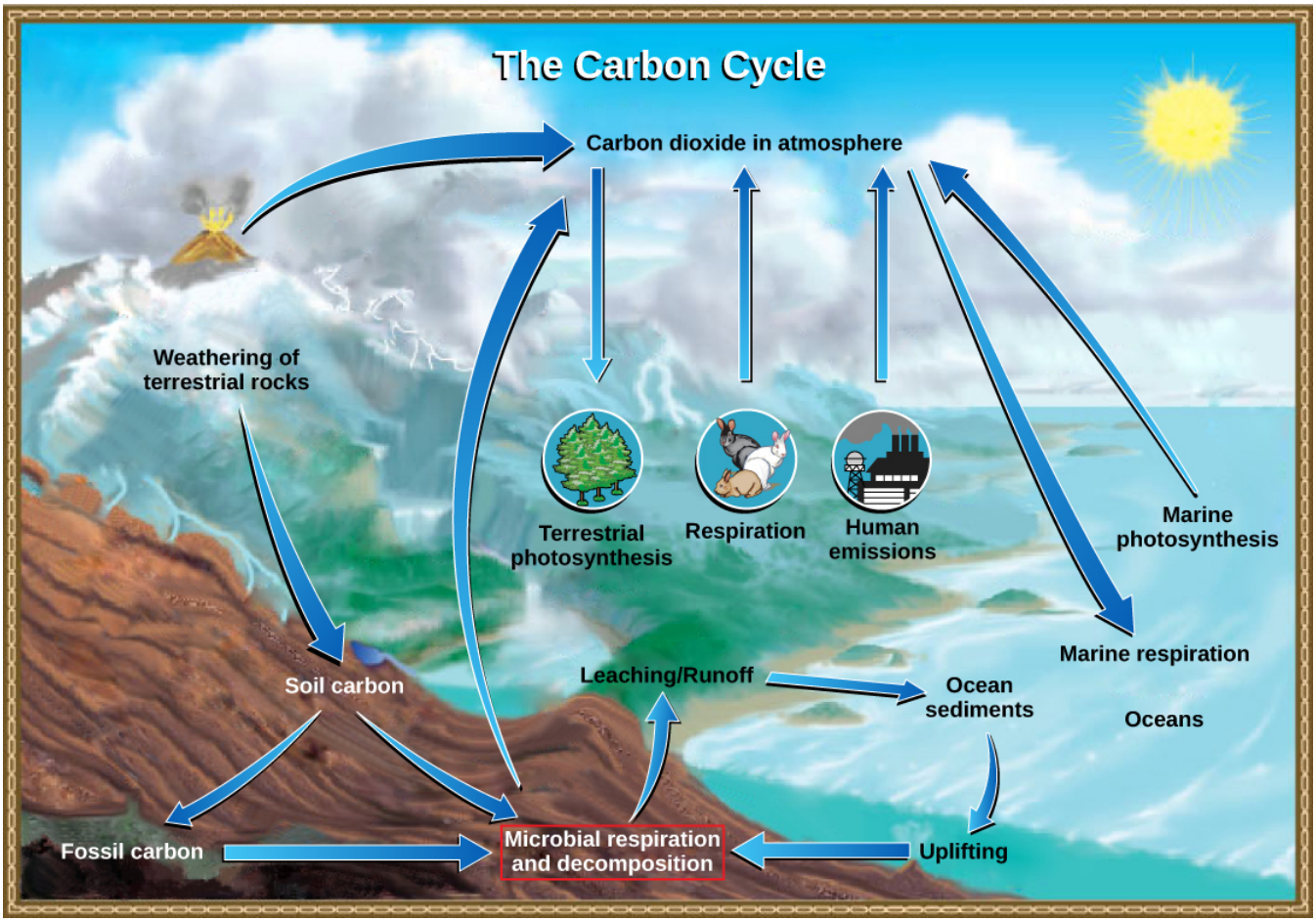


Figure **56.1.4**: Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions, bring this stored carbon back into the carbon cycle. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Link to Learning

Click this link to read information about the United States Carbon Cycle Science Program.

The Biological Carbon Cycle

Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs within and between ecosystems by way of atmospheric carbon dioxide. Carbon dioxide is the basic building block that most autotrophs use to build multi-carbon, high energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds thereby store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (carbonic acid, $H_2CO_3^-$). However

carbon dioxide is acquired, a by-product of the process is oxygen. The photosynthetic organisms are responsible for depositing approximately 21 percent oxygen content of the atmosphere that we observe today.

Heterotrophs and autotrophs are partners in biological carbon exchange (especially the primary consumers, largely herbivores). Heterotrophs acquire the high-energy carbon compounds from the autotrophs by consuming them, and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Gas exchange through the atmosphere and water is one way that the carbon cycle connects all living organisms on Earth.

The Biogeochemical Carbon Cycle

The movement of carbon through the land, water, and air is complex, and in many cases, it occurs much more slowly geologically than as seen between living organisms. Carbon is stored for long periods in what are known as carbon reservoirs, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, land sediments (including fossil fuels), and the Earth's interior.

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide and is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each location, and each one affects the other reciprocally. Carbon dioxide (CO_2) from the atmosphere dissolves in water and combines with water molecules to form carbonic acid, and then it ionizes to carbonate and bicarbonate ions (Figure **56.1.5**)

Step 1: CO_2 (atmospheric) $\rightleftharpoons$ CO_2 (dissolved)
Step 2: CO_2 (dissolved) + H_2O $\rightleftharpoons$ H_2CO_3 (carbonic acid)
Step 3: H_2CO_3 $\rightleftharpoons$ + H^+ + HCO_3^- (biocarbonate ion)
Step 4: HCO_3^- $\rightleftharpoons$ H^+ + CO_3^{2-} (carbonate ion)

Figure **56.1.5**: Carbon dioxide reacts with water to form bicarbonate and carbonate ions.

The equilibrium coefficients are such that more than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate ($CaCO_3$), a major component of marine organism shells. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

On land, carbon is stored in soil as a result of the decomposition of living organisms (by decomposers) or from weathering of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Deeper underground, on land and at sea, are fossil fuels: the anaerobically decomposed remains of plants that take millions of years to form. Fossil fuels are considered a non-renewable resource because their use far exceeds their rate of formation. A non-renewable resource, such as fossil fuel, is either regenerated very slowly or not at all. Another way for carbon to enter the atmosphere is from land (including land beneath the surface of the ocean) by the eruption of volcanoes and other geothermal systems. Carbon sediments from the ocean floor are taken deep within the Earth by the process of subduction: the movement of one tectonic plate beneath another. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.

Carbon dioxide is also added to the atmosphere by the animal husbandry practices of humans. The large numbers of land animals raised to feed the Earth's growing population results in increased carbon dioxide levels in the atmosphere due to farming practices and the respiration and methane production. This is another example of how human activity indirectly affects biogeochemical cycles in a significant way. Although much of the debate about the future effects of increasing atmospheric carbon on climate change focuses on fossils fuels, scientists take natural processes, such as volcanoes and respiration, into account as they model and predict the future impact of this increase.

The Nitrogen Cycle

Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly bonded, triple covalent N_2) even though this molecule comprises approximately 78 percent of

the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through nitrogen fixation (conversion of N_2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to "fix" nitrogen. *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. As shown in Figure **56.1.6**, the nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the ammonification process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by nitrifying bacteria, such as *Nitrosomonas*, through nitrification. Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of denitrification occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to re-enter the atmosphere.

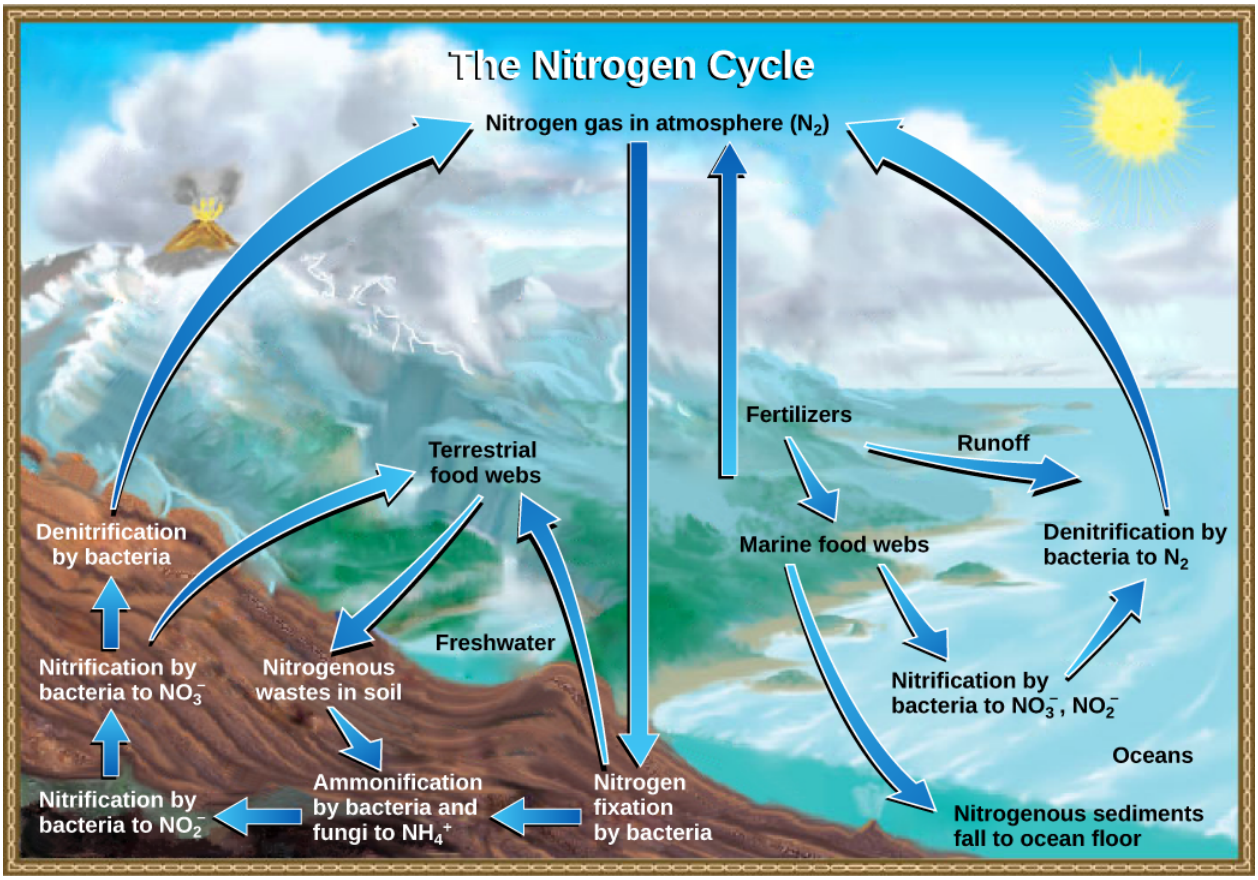


Figure **56.1.6**: Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Exercise

Which of the following statements about the nitrogen cycle is false?

A. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
B. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
C. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
D. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

Answer

C: Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers in agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on Earth's ecosystems including the production of acid rain (as nitric acid, HNO_3) and greenhouse gas (as nitrous oxide, N_2O) potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater eutrophication, a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the Earth's surface and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle.[1]

The Phosphorus Cycle

Phosphorus is an essential nutrient for living processes; it is a major component of nucleic acid and phospholipids, and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems (Figure **56.1.7**).

Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is moved to land over geologic time by the uplifting of areas of the Earth's surface.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.

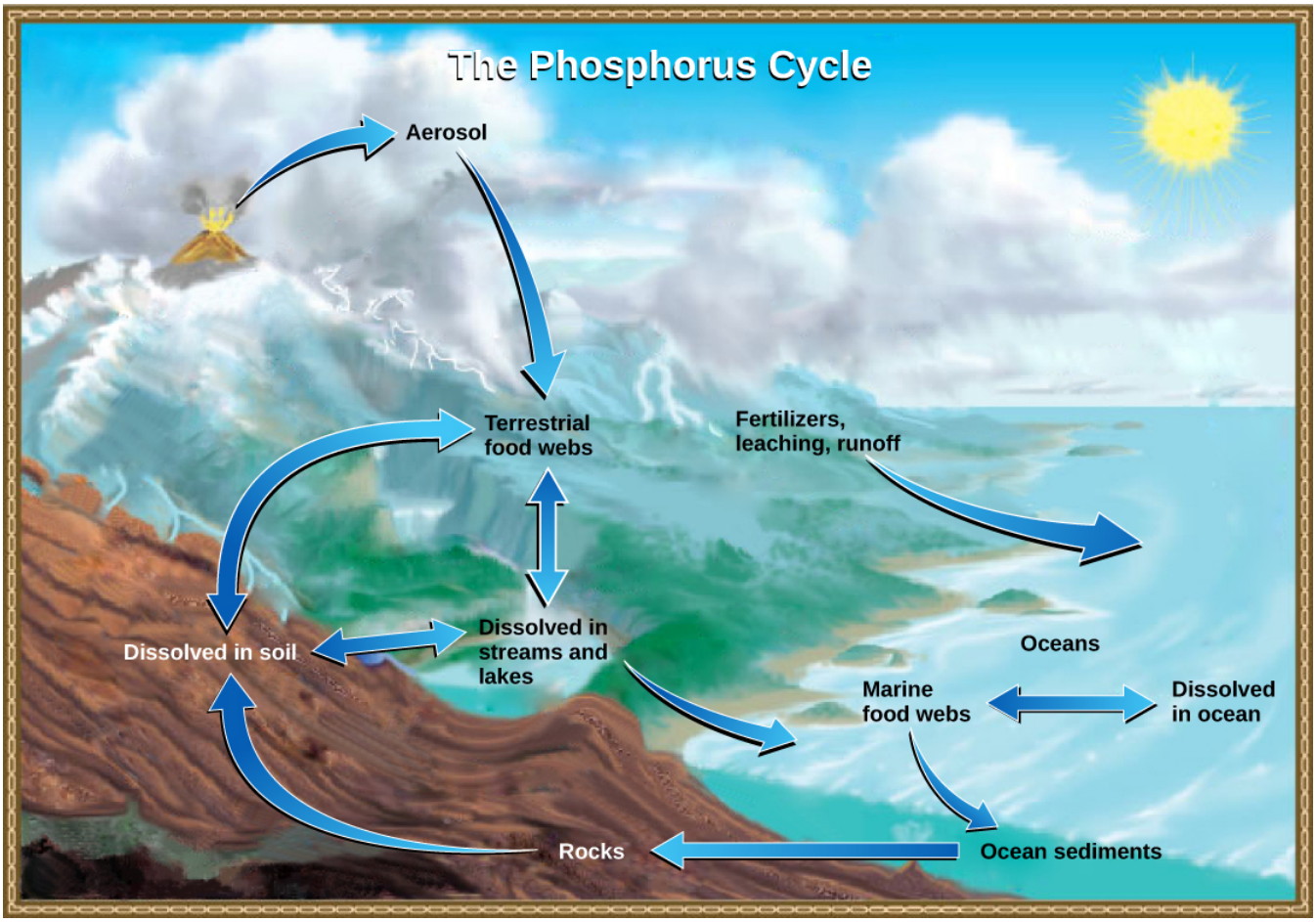


Figure **56.1.7**: In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers (Figure **56.1.8**).

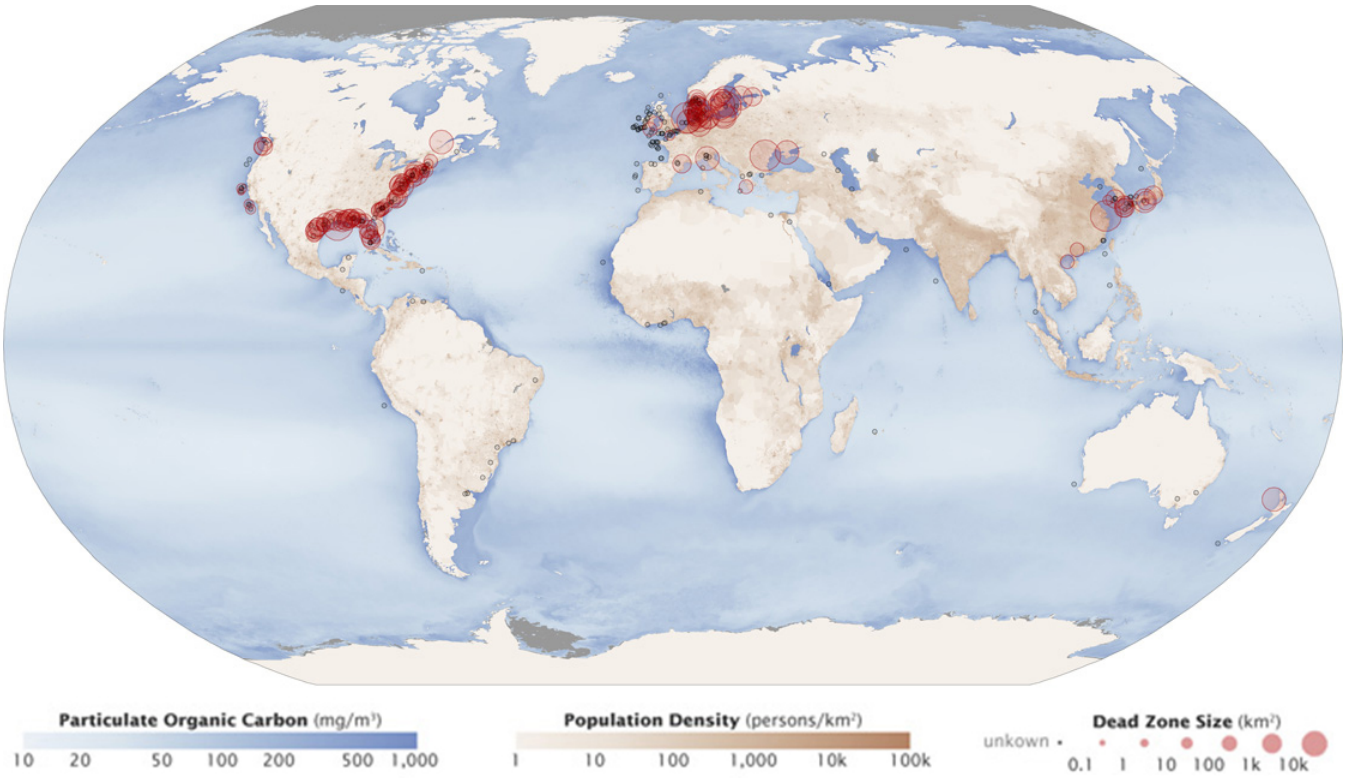
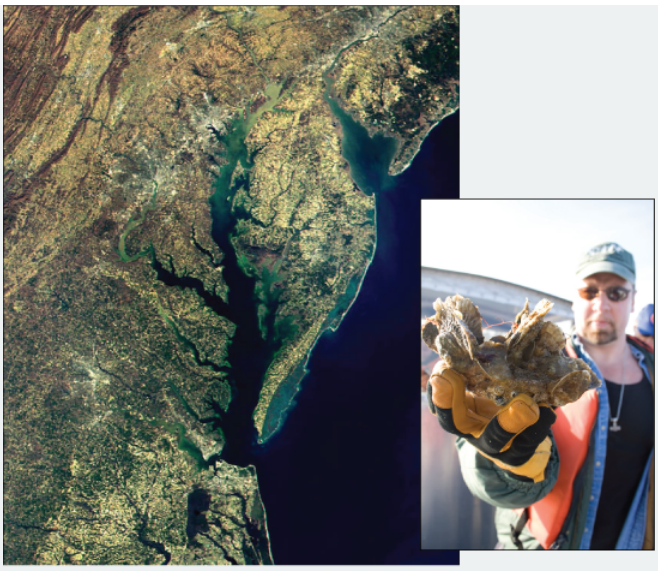


Figure 56.1.8: Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

A dead zone is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years, and more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 8463 square miles. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States.

Everyday Connection: Chesapeake Bay



(a) (b)

Figure **56.1.9**: This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay. (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army)

The Chesapeake Bay has long been valued as one of the most scenic areas on Earth; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms. Several species have declined in the Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overharvesting. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by non-profit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for inter-state cooperation to gain successful restoration.

The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

The Sulfur Cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns, and hence their functions. As shown in Figure **56.1.10**, sulfur cycles between the oceans, land, and atmosphere. Atmospheric sulfur is found in the form of sulfur dioxide (SO_2) and enters the atmosphere in three ways: from the decomposition of organic molecules, from volcanic activity and geothermal vents, and from the burning of fossil fuels by humans.

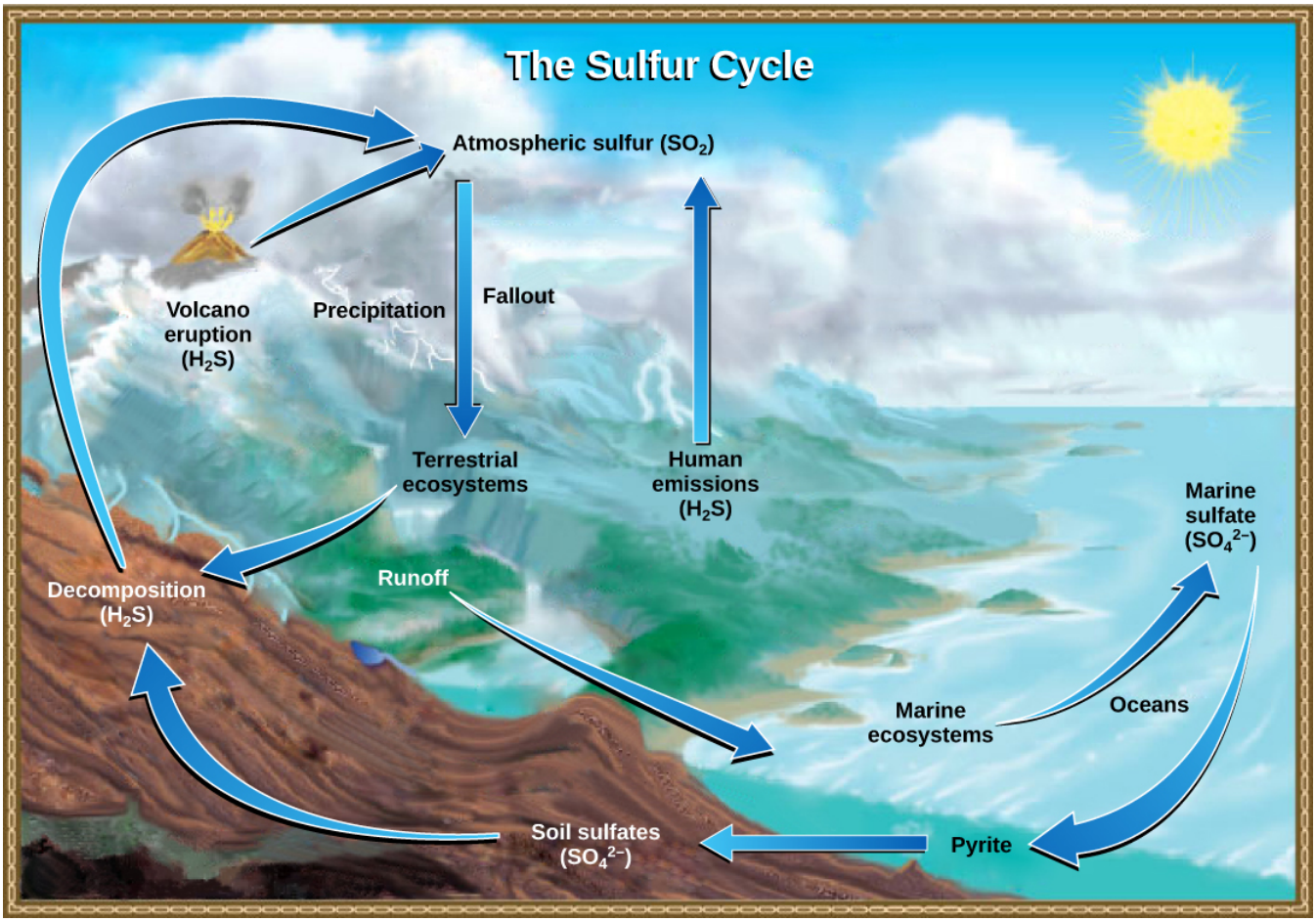


Figure **56.1.10**: Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the Earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil and atmosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and geothermal vents (Figure **56.1.11**). Atmospheric sulfur is found in the form of sulfur dioxide (SO_2), and as rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfuric acid (H_2SO_4). Sulfur can also fall directly from the atmosphere in a process called fallout. Also, the weathering of sulfur-containing rocks releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplifting of ocean sediments. Terrestrial ecosystems can then make use of these soil sulfates ($\mathbf{SO_4^{2-}}$), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide (H_2S) gas.



Figure 56.1.11: At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially from coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. As rain falls through this gas, it creates the phenomenon known as acid rain. Acid rain is corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid, which causes damage to aquatic ecosystems. Acid rain damages the natural environment by lowering the pH of lakes, which kills many of the resident fauna; it also affects the man-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years. These examples show the wide-ranging effects of human activities on our environment and the challenges that remain for our future.

Link to Learning

Click this link to learn more about global climate change.

Summary

Mineral nutrients are cycled through ecosystems and their environment. Of particular importance are water, carbon, nitrogen, phosphorus, and sulfur. All of these cycles have major impacts on ecosystem structure and function. As human activities have caused major disturbances to these cycles, their study and modeling is especially important. A variety of human activities, such as pollution, oil spills, and other events have damaged ecosystems, potentially causing global climate change. The health of Earth depends on understanding these cycles and how to protect the environment from irreversible damage.

Footnotes

1. 1 Scott L. Morford, Benjamin Z. Houlton, and Randy A. Dahlgren, “Increased Forest Ecosystem Carbon and Nitrogen Storage from Nitrogen Rich Bedrock,” *Nature* 477, no. 7362 (2011): 78–81.

Glossary

acid rain
corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid; can damage structures and ecosystems

biogeochemical cycle
cycling of mineral nutrients through ecosystems and through the non-living world

dead zone
area within an ecosystem in lakes and near the mouths of rivers where large areas of ecosystems are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities

eutrophication
process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna

fallout
direct deposit of solid minerals on land or in the ocean from the atmosphere

hydrosphere
area of the Earth where water movement and storage occurs

non-renewable resource
resource, such as fossil fuel, that is either regenerated very slowly or not at all

residence time
measure of the average time an individual water molecule stays in a particular reservoir

subduction
movement of one tectonic plate beneath another

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56.2: The Flow of Energy in Ecosystems

Learning Objectives

- Describe how organisms acquire energy in a food web and in associated food chains
- Explain how the efficiency of energy transfers between trophic levels affects ecosystem structure and dynamics
- Discuss trophic levels and how ecological pyramids are used to model them

All living things require energy in one form or another. Energy is required by most complex metabolic pathways (often in the form of adenosine triphosphate, ATP), especially those responsible for building large molecules from smaller compounds, and life itself is an energy-driven process. Living organisms would not be able to assemble macromolecules (proteins, lipids, nucleic acids, and complex carbohydrates) from their monomeric subunits without a constant energy input.

It is important to understand how organisms acquire energy and how that energy is passed from one organism to another through food webs and their constituent food chains. Food webs illustrate how energy flows directionally through ecosystems, including how efficiently organisms acquire it, use it, and how much remains for use by other organisms of the food web.

How Organisms Acquire Energy in a Food Web

Energy is acquired by living things in three ways: photosynthesis, chemosynthesis, and the consumption and digestion of other living or previously living organisms by heterotrophs.

Photosynthetic and chemosynthetic organisms are both grouped into a category known as autotrophs: organisms capable of synthesizing their own food (more specifically, capable of using inorganic carbon as a carbon source). Photosynthetic autotrophs (photoautotrophs) use sunlight as an energy source, whereas chemosynthetic autotrophs (chemoautotrophs) use inorganic molecules as an energy source. Autotrophs are critical for all ecosystems. Without these organisms, energy would not be available to other living organisms and life itself would not be possible.

Photoautotrophs, such as plants, algae, and photosynthetic bacteria, serve as the energy source for a majority of the world's ecosystems. These ecosystems are often described by grazing food webs. Photoautotrophs harness the solar energy of the sun by converting it to chemical energy in the form of ATP (and NADP). The energy stored in ATP is used to synthesize complex organic molecules, such as glucose.

Chemoautotrophs are primarily bacteria that are found in rare ecosystems where sunlight is not available, such as in those associated with dark caves or hydrothermal vents at the bottom of the ocean (Figure **56.2.1**). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H_2S), which is released from the vents as a source of chemical energy. This allows chemoautotrophs to synthesize complex organic molecules, such as glucose, for their own energy and in turn supplies energy to the rest of the ecosystem.

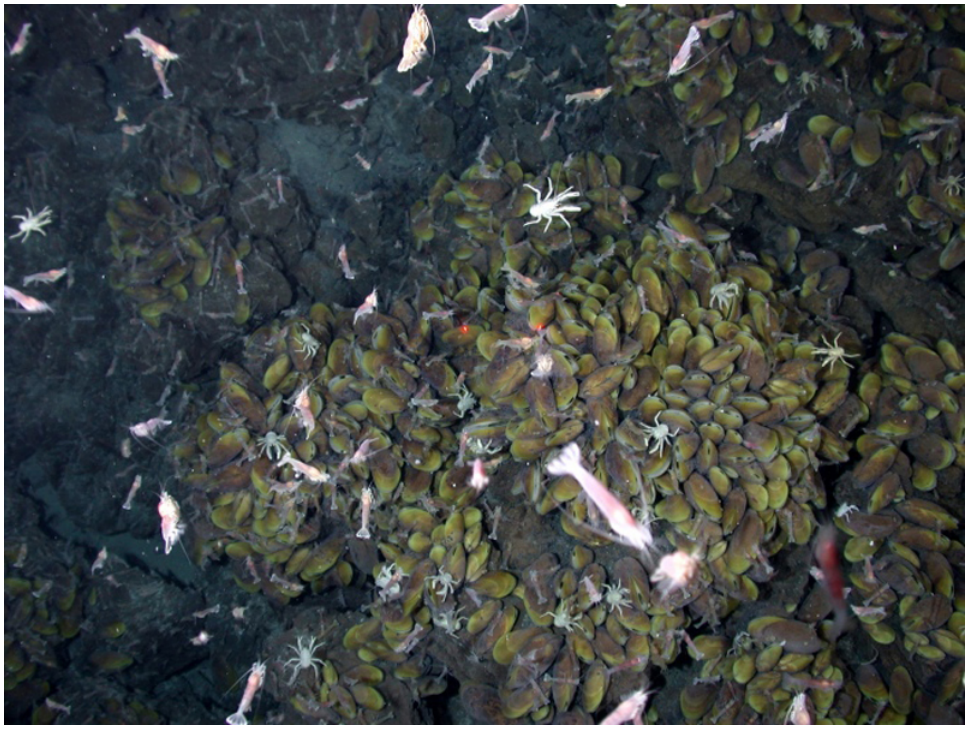


Figure 56.2.1: Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture was taken in 2006 at the submerged NW Eifuku volcano off the coast of Japan by the National Oceanic and Atmospheric Administration (NOAA). The summit of this highly active volcano lies 1535 m below the surface.

Productivity within Trophic Levels

Productivity within an ecosystem can be defined as the percentage of energy entering the ecosystem incorporated into biomass in a particular trophic level. Biomass is the total mass, in a unit area at the time of measurement, of living or previously living organisms within a trophic level. Ecosystems have characteristic amounts of biomass at each trophic level. For example, in the English Channel ecosystem the primary producers account for a biomass of 4 g/m^2 (grams per meter squared), while the primary consumers exhibit a biomass of 21 g/m^2.

The productivity of the primary producers is especially important in any ecosystem because these organisms bring energy to other living organisms by photoautotrophy or chemoautotrophy. The rate at which photosynthetic primary producers incorporate energy from the sun is called gross primary productivity. An example of gross primary productivity is shown in the compartment diagram of energy flow within the Silver Springs aquatic ecosystem as shown (Figure 46.1.7). In this ecosystem, the total energy accumulated by the primary producers (gross primary productivity) was shown to be 20,810 $kcal/m^2/yr$.

Because all organisms need to use some of this energy for their own functions (like respiration and resulting metabolic heat loss) scientists often refer to the net primary productivity of an ecosystem. Net primary productivity is the energy that remains in the primary producers after accounting for the organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level. In our Silver Spring example, 13,187 of the 20,810 $kcal/m^2/yr$ were used for respiration or were lost as heat, leaving 7,632 $kcal/m^2/yr$ of energy for use by the primary consumers.

Ecological Efficiency: The Transfer of Energy between Trophic Levels

As illustrated in Figure 46.1.7, large amounts of energy are lost from the ecosystem from one trophic level to the next level as energy flows from the primary producers through the various trophic levels of consumers and decomposers. The main reason for this loss is the second law of thermodynamics, which states that whenever energy is converted from one form to another, there is a tendency toward disorder (entropy) in the system. In biologic systems, this means a great deal of energy is lost as metabolic heat when the organisms from one trophic level consume the next level. In the Silver Springs ecosystem example (Figure 46.1.7), we see that the primary consumers produced 1103 $kcal/m^2/yr$ from the 7618 $kcal/m^2/yr$ of energy available to them from the primary

producers. The measurement of energy transfer efficiency between two successive trophic levels is termed the trophic level transfer efficiency (TLTE) and is defined by the formula:

$$\text{TLTE} = \frac{\text{production at present trophic level}}{\text{production at previous trophic level}} * 100$$

In Silver Springs, the TLTE between the first two trophic levels was approximately 14.8 percent. The low efficiency of energy transfer between trophic levels is usually the major factor that limits the length of food chains observed in a food web. The fact is, after four to six energy transfers, there is not enough energy left to support another trophic level. In the Lake Ontario example shown in Figure 46.1.5, only three energy transfers occurred between the primary producer, (green algae), and the apex consumer (Chinook salmon).

Ecologists have many different methods of measuring energy transfers within ecosystems. Some transfers are easier or more difficult to measure depending on the complexity of the ecosystem and how much access scientists have to observe the ecosystem. In other words, some ecosystems are more difficult to study than others, and sometimes the quantification of energy transfers has to be estimated.

Another main parameter that is important in characterizing energy flow within an ecosystem is the net production efficiency. Net production efficiency (NPE) allows ecologists to quantify how efficiently organisms of a particular trophic level incorporate the energy they receive into biomass; it is calculated using the following formula:

$$\text{NPE} = \frac{\text{net consumer productivity}}{\text{assimilation}} * 100$$

Net consumer productivity is the energy content available to the organisms of the next trophic level. Assimilation is the biomass (energy content generated per unit area) of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste. Incomplete ingestion refers to the fact that some consumers eat only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide.

Thus, NPE measures how efficiently each trophic level uses and incorporates the energy from its food into biomass to fuel the next trophic level. In general, cold-blooded animals (ectotherms), such as invertebrates, fish, amphibians, and reptiles, use less of the energy they obtain for respiration and heat than warm-blooded animals (endotherms), such as birds and mammals. The extra heat generated in endotherms, although an advantage in terms of the activity of these organisms in colder environments, is a major disadvantage in terms of NPE. Therefore, many endotherms have to eat more often than ectotherms to get the energy they need for survival. In general, NPE for ectotherms is an order of magnitude (10x) higher than for endotherms. For example, the NPE for a caterpillar eating leaves has been measured at 18 percent, whereas the NPE for a squirrel eating acorns may be as low as 1.6 percent.

The inefficiency of energy use by warm-blooded animals has broad implications for the world's food supply. It is widely accepted that the meat industry uses large amounts of crops to feed livestock, and because the NPE is low, much of the energy from animal feed is lost. For example, it costs about 1¢ to produce 1000 dietary calories (kcal) of corn or soybeans, but approximately $0.19 to produce a similar number of calories growing cattle for beef consumption. The same energy content of milk from cattle is also costly, at approximately $0.16 per 1000 kcal. Much of this difference is due to the low NPE of cattle. Thus, there has been a growing movement worldwide to promote the consumption of non-meat and non-dairy foods so that less energy is wasted feeding animals for the meat industry.

Modeling Ecosystems Energy Flow: Ecological Pyramids

The structure of ecosystems can be visualized with ecological pyramids, which were first described by the pioneering studies of Charles Elton in the 1920s. Ecological pyramids show the relative amounts of various parameters (such as number of organisms, energy, and biomass) across trophic levels.

Pyramids of numbers can be either upright or inverted, depending on the ecosystem. As shown in Figure **56.2.2**, typical grassland during the summer has a base of many plants and the numbers of organisms decrease at each trophic level. However, during the summer in a temperate forest, the base of the pyramid consists of few trees compared with the number of primary consumers,

mostly insects. Because trees are large, they have great photosynthetic capability, and dominate other plants in this ecosystem to obtain sunlight. Even in smaller numbers, primary producers in forests are still capable of supporting other trophic levels.

Another way to visualize ecosystem structure is with pyramids of biomass. This pyramid measures the amount of energy converted into living tissue at the different trophic levels. Using the Silver Springs ecosystem example, this data exhibits an upright biomass pyramid (Figure **56.2.2**), whereas the pyramid from the English Channel example is inverted. The plants (primary producers) of the Silver Springs ecosystem make up a large percentage of the biomass found there. However, the phytoplankton in the English Channel example make up less biomass than the primary consumers, the zooplankton. As with inverted pyramids of numbers, this inverted pyramid is not due to a lack of productivity from the primary producers, but results from the high turnover rate of the phytoplankton. The phytoplankton are consumed rapidly by the primary consumers, thus, minimizing their biomass at any particular point in time. However, phytoplankton reproduce quickly, thus they are able to support the rest of the ecosystem.

Pyramid ecosystem modeling can also be used to show energy flow through the trophic levels. Notice that these numbers are the same as those used in the energy flow compartment diagram in Figure 46.1.7. Pyramids of energy are always upright, and an ecosystem without sufficient primary productivity cannot be supported. All types of ecological pyramids are useful for characterizing ecosystem structure. However, in the study of energy flow through the ecosystem, pyramids of energy are the most consistent and representative models of ecosystem structure (Figure **56.2.2**).

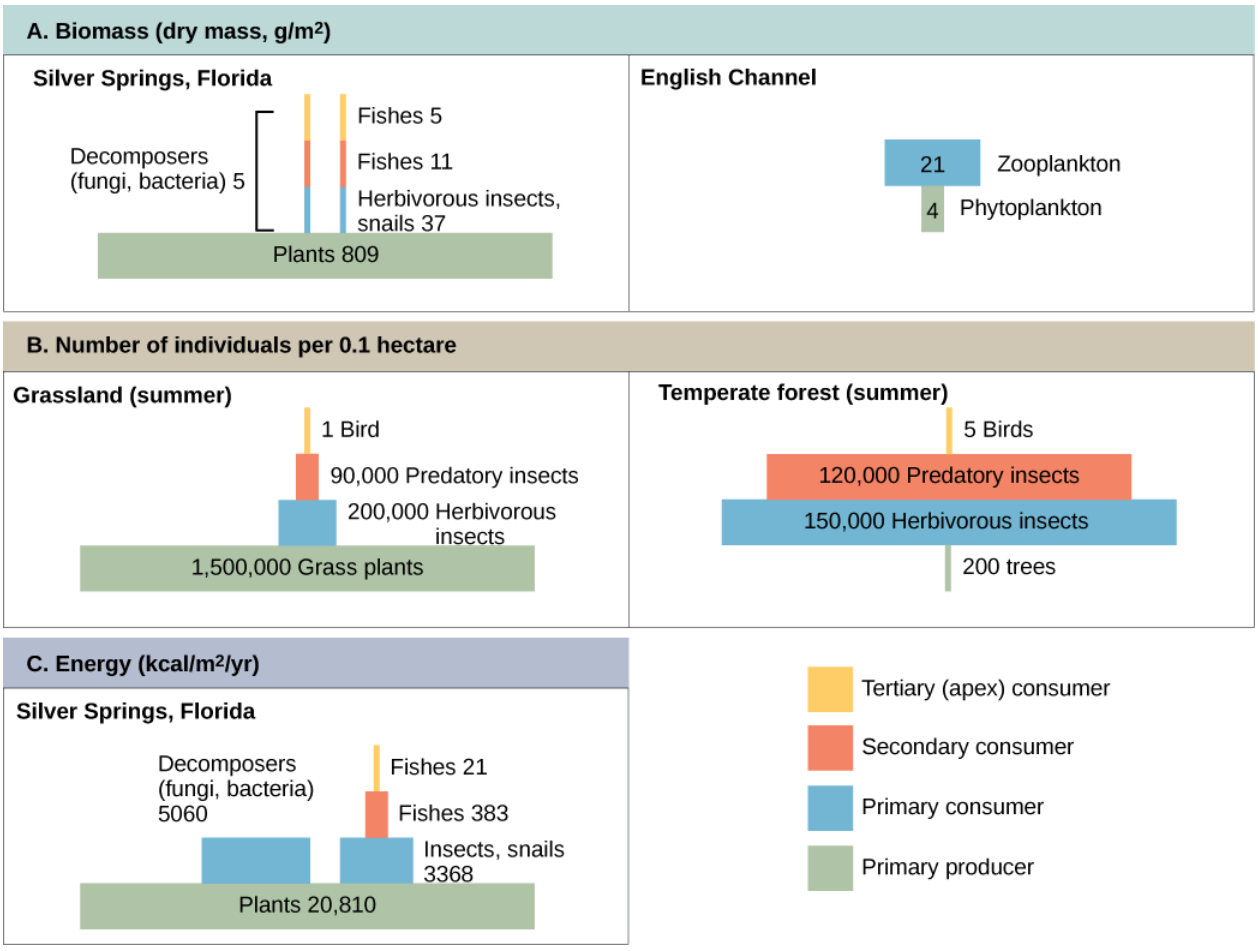


Figure **56.2.2**: Ecological pyramids depict the (a) biomass, (b) number of organisms, and (c) energy in each trophic level.

Exercise

Pyramids depicting the number of organisms or biomass may be inverted, upright, or even diamond-shaped. Energy pyramids, however, are always upright. Why?

Answer

Pyramids of organisms may be inverted or diamond-shaped because a large organism, such as a tree, can sustain many smaller organisms. Likewise, a low biomass of organisms can sustain a larger biomass at the next trophic level because the organisms reproduce rapidly and thus supply continuous nourishment. Energy pyramids, however, must always be upright because of the laws of thermodynamics. The first law of thermodynamics states that energy can neither be created nor destroyed; thus, each trophic level must acquire energy from the trophic level below. The second law of thermodynamics states that, during the transfer of energy, some energy is always lost as heat; thus, less energy is available at each higher trophic level.

Consequences of Food Webs: Biological Magnification

One of the most important environmental consequences of ecosystem dynamics is biomagnification. Biomagnification is the increasing concentration of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers. Many substances have been shown to bioaccumulate, including classical studies with the pesticide **d**ichloro**d**iphenyl**t**richloroethane (DDT), which was published in the 1960s bestseller, *Silent Spring*, by Rachel Carson. DDT was a commonly used pesticide before its dangers became known. In some aquatic ecosystems, organisms from each trophic level consumed many organisms of the lower level, which caused DDT to increase in birds (apex consumers) that ate fish. Thus, the birds accumulated sufficient amounts of DDT to cause fragility in their eggshells. This effect increased egg breakage during nesting and was shown to have adverse effects on these bird populations. The use of DDT was banned in the United States in the 1970s.

Other substances that biomagnify are polychlorinated biphenyls (PCBs), which were used in coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances were best studied in aquatic ecosystems, where fish species at different trophic levels accumulate toxic substances brought through the ecosystem by the primary producers. As illustrated in a study performed by the National Oceanic and Atmospheric Administration (NOAA) in the Saginaw Bay of Lake Huron (Figure **56.2.3**), PCB concentrations increased from the ecosystem's primary producers (phytoplankton) through the different trophic levels of fish species. The apex consumer (walleye) has more than four times the amount of PCBs compared to phytoplankton. Also, based on results from other studies, birds that eat these fish may have PCB levels at least one order of magnitude higher than those found in the lake fish.

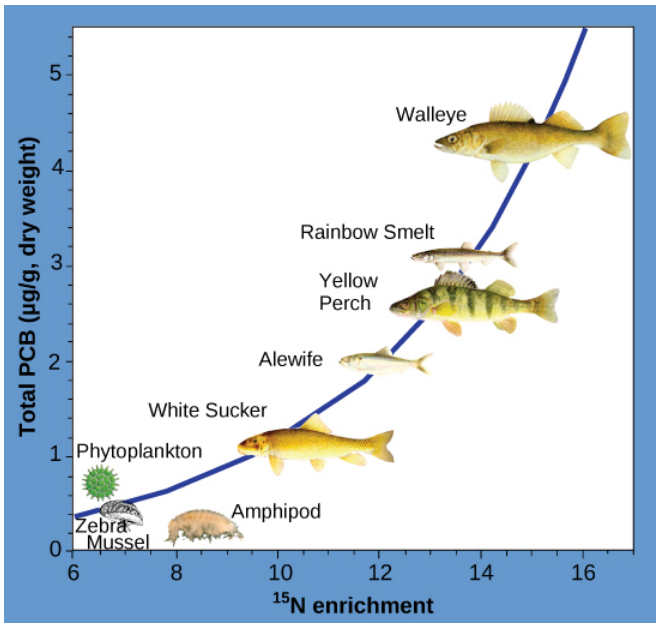


Figure **56.2.3**: This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Numbers on the x-axis reflect enrichment with heavy isotopes of nitrogen (^{15}N), which is a marker for increasing trophic level. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels. (credit: Patricia Van Hoof, NOAA, GLERL)

Other concerns have been raised by the accumulation of heavy metals, such as mercury and cadmium, in certain types of seafood. The United States Environmental Protection Agency (EPA) recommends that pregnant women and young children should not

consume any swordfish, shark, king mackerel, or tilefish because of their high mercury content. These individuals are advised to eat fish low in mercury: salmon, tilapia, shrimp, pollock, and catfish. Biomagnification is a good example of how ecosystem dynamics can affect our everyday lives, even influencing the food we eat.

Summary

Organisms in an ecosystem acquire energy in a variety of ways, which is transferred between trophic levels as the energy flows from the bottom to the top of the food web, with energy being lost at each transfer. The efficiency of these transfers is important for understanding the different behaviors and eating habits of warm-blooded versus cold-blooded animals. Modeling of ecosystem energy is best done with ecological pyramids of energy, although other ecological pyramids provide other vital information about ecosystem structure.

Glossary

assimilation
: biomass consumed and assimilated from the previous trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste

biomagnification
: increasing concentrations of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers

biomass
: total weight, at the time of measurement, of living or previously living organisms in a unit area within a trophic level

chemoautotroph
: organism capable of synthesizing its own food using energy from inorganic molecules

ecological pyramid
: (also, Eltonian pyramid) graphical representation of different trophic levels in an ecosystem based of organism numbers, biomass, or energy content

gross primary productivity
: rate at which photosynthetic primary producers incorporate energy from the sun

net consumer productivity
: energy content available to the organisms of the next trophic level

net primary productivity
: energy that remains in the primary producers after accounting for the organisms' respiration and heat loss

net production efficiency (NPE)
: measure of the ability of a trophic level to convert the energy it receives from the previous trophic level into biomass

trophic level transfer efficiency (TLTE)
: energy transfer efficiency between two successive trophic levels

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CHAPTER OVERVIEW

56.3: Trophic Level Interactions

Trophic interactions occur when one organism feeds on another. The three main types of trophic interactions are **predation** (figure 6.1.1.a6.1.1.), **herbivory**, or **parasitism**. During these interactions, one species benefits by gaining food at the expense of the other, which either dies or loses nutrients, tissues, or organs (such as leaves). Trophic interactions involve the flow of energy, and the trophic interactions in a community can be represented by **food chains** and **food webs**.

56.3.1: Predation

56.3.2: Herbivory

56.3.3: Parasitism

56.3.4: Food Chains and Food Webs

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56.3.1: Predation

Perhaps the classical example of a biotic interaction is the predator-prey relationship. **Predation** occurs when one species (the **predator**) kills and eats multiple **prey** over its lifetime.

Predator-Prey Dynamics

Population sizes of predators and prey in a community are not constant over time, and they may vary in cycles that appear to be related. For example, 100 years of trapping data from North America shows how population dynamics of the lynx (predator) and the snowshoe hare (prey) cycle (figure **56.3.1.*a***-b).



Figure **56.3.1.*a***: The Canada lynx is an example of a predator. Image by Michael Zahra (CC-BY-SA).



Figure **56.3.1.*b***: The snowshoe hare is the prey of the Canada lynx. Image by the National Park Service (public domain).

This cycling of predator and prey population sizes has a period of approximately ten years, with the predator population lagging one to two years behind the prey population (figure **56.3.1.*a***-c). An apparent explanation for this pattern is that as the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare numbers begin to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, in part, to low predation pressure, starting the cycle anew.

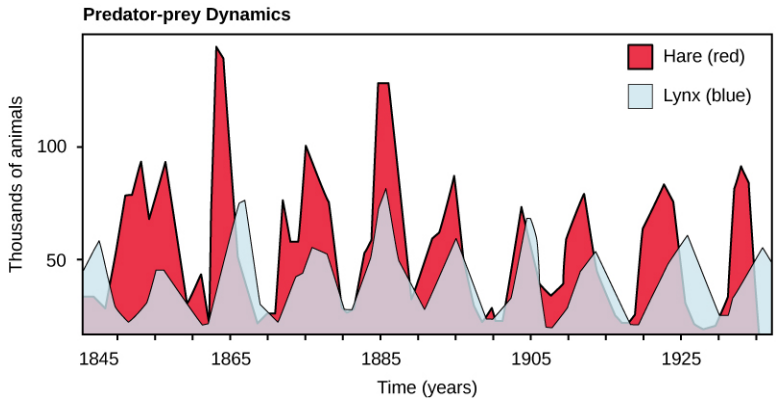


Figure **56.3.1.*c***: The cycling of Canada lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics. The x-axis shows time in years, and the y-axis shows population size in thousands of animals. The lynx population is represented in blue (shorter peaks), and the hare population is represented in red (taller peaks). Both populations increase and decrease in 10-year cycles, with changes in the lynx population lagging a few years behind that of hare.

The dynamic of closely matched population cycling occurs because the snowshoe hare is the primary food source for the lynx. When predators have generalists, feeding on a variety of prey species, and prey are consumed by a variety of predators species, their population dynamics are less likely to cycle together.

Adaptations of Predators

Predators have a variety of adaptations to catch and consume prey, and the specific adaptations depend on the predator. For example, raptors, such as owls and hawks, have hooked beaks for tearing flesh and talons for grabbing prey. Mammal predators often have sharp teeth and claws. Some predators can run quickly to chase prey, and others "sit and wait", lunging forward when prey pass them. Some predators, like rattlesnakes and tarantulas, subdue their prey by injecting them with venom (figure **56.3.1.*d***). Predators often have large eyes located forward (like a wolf) rather than eyes spaced far apart on the sides of the head (like a sheep). Forward-facing eyes allow for depth perception, which is key to tracking prey. In contrast, peripheral vision is expanded when eyes are located to the sides, and this helps prey identify threats.



Figure **56.3.1.*d***: This Asian birdeater tarantula uses its fangs to inject its prey with poisonous venom. Image by Matt Reinbold (CC-BY-SA).

Defensive Traits in Prey

Prey evolve mechanical, chemical, physical, or behavioral defenses against predators. Some prey have armor (such as a turtle shell or the bony plates protecting armadillos), a **mechanical defense** that reduces predation by discouraging physical contact. Many animals produce or obtain **chemical defenses** from plants and store them to prevent predation. Other species use their body shape and coloration as **camouflage** to avoid being detected by predators, an example of a **physical defense**. The tropical walking stick is an insect with the coloration and body shape of a twig, which makes it very hard to see when it is stationary against a background

of real twigs (figure 56.3.1.*e*-a). In another example, the chameleon can change its color to match its surroundings (figure 56.3.1.*e*-b).



(a) (b)

Figure 56.3.1.*e*: (a) The tropical walking stick and (b) the chameleon use their body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are distasteful or poisonous. For example, the monarch butterfly caterpillar sequesters poisons from its food (plants and milkweeds) to make itself poisonous or distasteful to potential predators. The caterpillar is bright yellow and black to advertise its toxicity. The caterpillar is also able to pass the sequestered toxins on to the adult monarch, which is also dramatically colored black and red as a warning to potential predators. Fire-bellied toads produce toxins that make them distasteful to their potential predators (figure 56.3.1.*f*). They have bright red or orange coloration on their bellies, which they display to a potential predator to advertise their poisonous nature and discourage an attack. Warning coloration only works if a predator uses eyesight to locate prey and can learn—a naïve predator must experience the negative consequences of eating one before it will avoid other similarly colored individuals.



Figure 56.3.1.*f*: The fire-bellied toad has bright coloration on its belly that serves to warn potential predators that it is toxic. (credit: modification of work by Roberto Verzo)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In some cases of **mimicry**, a harmless species imitates the warning coloration of a harmful species. Assuming they share the same predators, this coloration then protects the harmless ones. Many insect species mimic the coloration of wasps, which are stinging, venomous insects, thereby discouraging predation (figure 56.3.1.*g*). In other cases of mimicry, multiple species share the same warning coloration, but all of them actually have defenses. The commonness of the signal improves the compliance of all the potential predators.



(a) (b)

Figure **56.3.1.*g***: One form of mimicry is when a harmless species mimics the coloration of a harmful species, as is seen with the (a) wasp (*Polistes* sp.) and the (b) hoverfly (*Syrphus* sp.). (credit: modification of work by Tom Ings)

Running from predators, hiding, and playing dead are examples of **behavioral defenses**. Some prey also exhibit behaviors that threaten predators. For example, snapping turtles stretch their legs to appear larger and snap aggressively at predators.

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56.3.2: Herbivory

When an animal feed on parts of another organism (usually a plant), **herbivory** occurs. For example, the koala eats the eucalyptus leaves (figure **56.3.2.*a***) or a cicada feeds a plant's sap (figure **56.3.2.*b***). Like predators, herbivores may feed on multiple individuals over their lives; however, herbivores do not necessarily kill the plants that they eat.



Figure **56.3.2.*a***: Koalas are herbivores that feed exclusively on eucalyptus leaves. They are thus considered specialists because the specialize on just one type of food. Image by Dr. Umesh Behari Mathur (CC-BY).



Figure **56.3.2.*b***: This floury baker cicada feeds on plant sap by piercing the tree with needle-like mouth parts. Image by Toby Hudson (CC-BY-SA).

Plant species have evolved numerous defenses that reduce herbivory. Thorns are an example of a mechanical defense that discourages large herbivores from feeding on a plant (Figure **56.3.2.*c***-a). Many plant species produce secondary plant compounds that serve no function for the plant except that they are toxic to animals and discourage consumption, acting as a chemical defense. For example, the foxglove produces several compounds, including digitalis, that are extremely toxic when eaten (Figure **56.3.2.*c***-b). (Biomedical scientists have repurposed the chemical produced by foxglove as a heart medication, which has saved lives for many decades.)



(a) (b)

Figure **56.3.2.c**: The (a) honey locust tree uses thorns, a mechanical defense, against herbivores, while the (b) foxglove uses a chemical defense: toxins produces by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (credit a: modification of work by Huw Williams; credit b: modification of work by Philip Jägenstedt)

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56.3.3: Parasitism

Parasitism occurs when one organism (the **parasite**) takes nutrients from another (the **host**). The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. Parasites do not necessarily kill their hosts. When they do, it is often a slow process, allowing the parasite time to complete its reproductive cycle before it or its offspring are able to spread to another host. A parasite may remain attached to the same host for its full lifespan, but some parasites have complex life cycles involving multiple host species. For example, a tapeworm causes disease in humans when contaminated and under-cooked meat such as pork, fish, or beef is consumed. Figure **56.3.3.*a*** illustrates the life cycle of the pork tapeworm. The tapeworm can live inside the intestine of the host for several years, benefiting from the host's food, and it may grow to be over 50 feet long by adding segments. The parasite moves from one host species to a second host species in order to complete its life cycle.

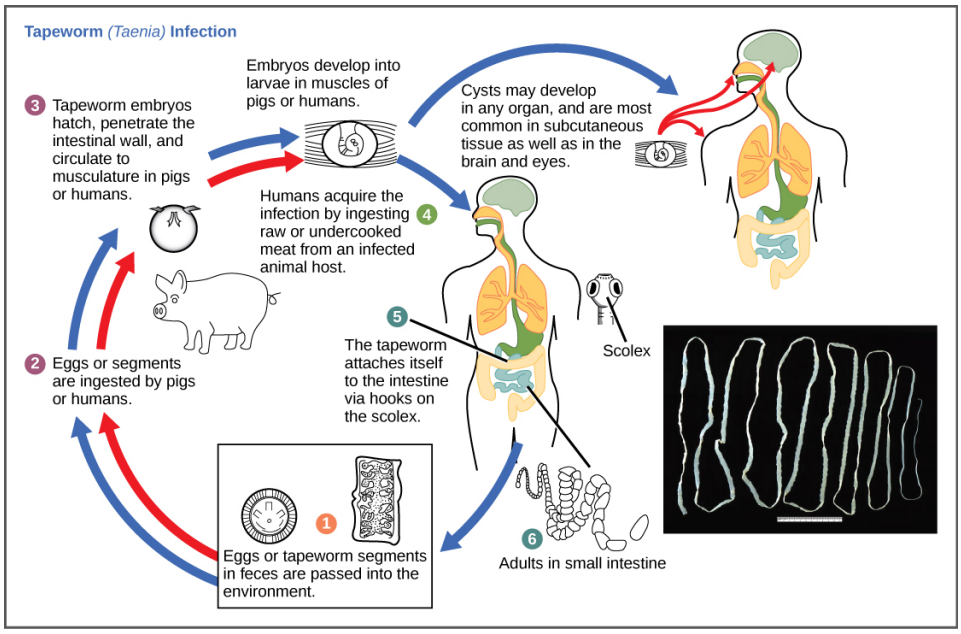


Figure **56.3.3.*a***: This diagram shows the life cycle of the tapeworm, a human worm parasite. In the first step, eggs or tapeworm segments from human feces contaminate the environment. Second, pigs ingest these eggs or segments. Third, the eggs mature into larvae, which encyst in the muscle tissue of the pig. It is also possible for humans to develop cysts if they ingest eggs. Fourth, humans become infected when they eat pork that is undercooked. Fifth, the larvae mature into adults, attaching themselves to the intestine wall. Sixth, adult tapeworms can grow many segments and become quite long. They produce the eggs or segments that continue the life cycle. (credit: modification of work by CDC)

Parasites infect many types of organisms, including other animals and plants. For example, fleas and roundworms are common dog parasites. Plants can be infected by fungi, bacteria, and viruses; there are also plants that parasitize other plants (figure **56.3.3.*b***). Even bacteria can be parasitized by viruses called bacteriophages.



Figure **56.3.3.*b***: Instead of conducting its own photosynthesis, the parasitic plant dodder siphons nutrients from its host plant. Image by Scot Nelson (public domain).

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56.3.4: Food Chains and Food Webs

Trophic interactions in a community can be represented by diagrams called **food chains** and **food webs**. Before discussing these representations in detail, we must first review the basics of energy. Energy flows through a community as a result of trophic interactions.

Energy

Virtually every task performed by living organisms requires energy. In general, **energy** is defined as the ability to do work, or to create some kind of change. Energy exists in different forms. Examples include light energy, kinetic energy, heat energy, potential energy, and chemical energy.

When an object is in motion, there is energy associated with that object. Think of a wrecking ball. Even a slow-moving wrecking ball can do a great deal of damage to other objects. Energy associated with objects in motion is called **kinetic energy**. **Heat energy** is the energy of motion in **matter** (anything that takes up space and has mass) and is considered a type of kinetic energy. The warmer the substance, the faster its molecules are moving. The rapid movement of molecules in the air, a speeding bullet, and a walking person all have kinetic energy. Now what if that same motionless wrecking ball is lifted two stories above ground with a crane? If the suspended wrecking ball is not moving, is there energy associated with it? The answer is yes. The energy that was required to lift the wrecking ball did not disappear, but is now stored in the wrecking ball by virtue of its position and the force of gravity acting on it. This type of energy is called **potential energy**. If the ball were to fall, the potential energy would be transformed into kinetic energy until all of the potential energy was exhausted when the ball rested on the ground. Wrecking balls also swing like a pendulum; through the swing, there is a constant change of potential energy (highest at the top of the swing) to kinetic energy (highest at the bottom of the swing). Other examples of potential energy include the energy of water held behind a dam or a person about to skydive out of an airplane (figure **56.3.4.*a***).



Figure **56.3.4.*a***: Still water has potential energy; moving water, such as in a waterfall or a rapidly flowing river, has kinetic energy. (credit “dam”: modification of work by “Pascal”/Flickr; credit “waterfall”: modification of work by Frank Gualtieri)

Potential energy is not only associated with the location of matter, but also with the structure of matter. **Chemical energy** is an example of potential energy that is stored in molecules. When molecules that are higher energy and less stable react to form products that are lower energy and more stable, this stored energy is released. Chemical energy is responsible for providing living cells with energy from food.

To appreciate the way energy flows into and out of biological systems, it is important to understand two of the physical laws that govern energy. The **first law of thermodynamics** states that the total amount of energy in the universe is constant and conserved. In other words, there has always been, and always will be, exactly the same amount of energy in the universe. Energy exists in many different forms. According to the first law of thermodynamics, energy may be transferred from place to place or transformed into different forms, but it cannot be created or destroyed. The transfers and transformations of energy take place around us all the time. Light bulbs transform electrical energy into light and heat energy. Gas stoves transform chemical energy from natural gas into heat energy. Plants perform one of the most biologically useful energy transformations on earth: that of converting the energy of sunlight to chemical energy stored within biological molecules, such as sugars (figure **56.3.4.*b***).

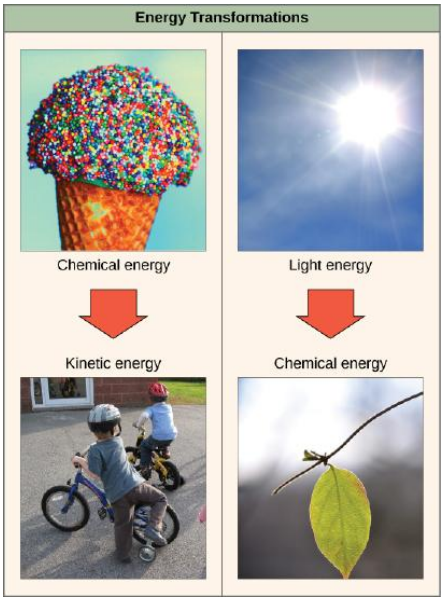


Figure 56.3.4.*b*: Shown are some examples of energy transferred and transformed from one system to another and from one form to another. The food we consume, represented by the ice cream cone, provides our cells with the chemical energy required to carry out bodily functions. This can be converted into kinetic energy (the energy of motion), which would be needed to ride a bike. Leaves conduct photosynthesis, converting light energy from the sun to chemical energy. (credit “ice cream”: modification of work by D. Sharon Pruitt; credit “kids”: modification of work by Max from Providence; credit “leaf”: modification of work by Cory Zanker)

The challenge for all living organisms is to obtain energy from their surroundings in forms that are usable to perform cellular work. A living cell’s primary tasks of obtaining, transforming, and using energy to do work may seem simple. However, the **second law of thermodynamics** explains why these tasks are harder than they appear. All energy transfers and transformations are never completely efficient. In every energy transfer, some amount of energy is lost in a form that is unusable. In most cases, this form is heat energy. For example, when a light bulb is turned on, some of the energy being converted from electrical energy into light energy is lost as heat energy. Likewise, some energy is lost as heat energy during the metabolic reactions that occur in organisms.

The concept of order and disorder relates to the second law of thermodynamics. The more energy that is lost by a system to its surroundings, the less ordered and more random the system is. Scientists refer to the measure of randomness or disorder within a system as **entropy**. High entropy means high disorder and low energy. Living things are highly ordered, requiring constant energy input to be maintained in a state of low entropy.

Energy Flow

Cells run on the chemical energy found mainly in carbohydrate molecules, and the majority of these molecules are produced by one process: **photosynthesis**. Through photosynthesis, certain organisms convert solar energy (sunlight) into chemical energy, which is then used to build carbohydrate molecules (figure 56.3.4.*c*). The energy that is harnessed from photosynthesis enters the communities continuously and is transferred from one organism to another. Therefore, directly or indirectly, the process of photosynthesis provides most of the energy required by living things on Earth. See the Carbon Cycle and Photosynthesis in OpenStax *Concepts of Biology* for more details about photosynthesis.

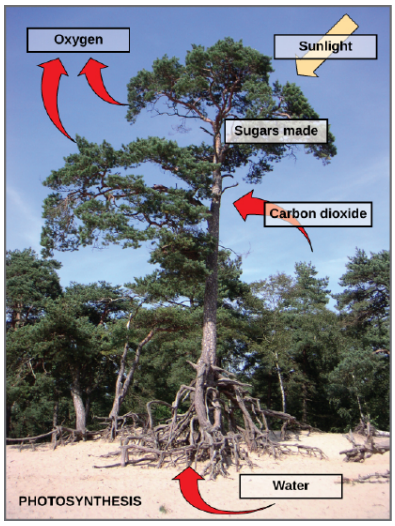


Figure **56.3.4.*c***: Photosynthesis uses solar energy, carbon dioxide, and water to release oxygen and to produce energy-storing sugar molecules. Image and caption by OpenStax (CC-BY). Access for free at openstax.org.

Organisms that conduct photosynthesis (such as plants, algae, and some bacteria), and organisms that synthesize sugars through other means are called **producers**. Without these organisms, energy would not be available to other living organisms, and life would not be possible. **Consumers**, like animals, fungi, and various microorganisms depend on producers, either directly or indirectly. For example, a deer obtains energy by eating plants. A wolf eating a deer obtains energy that originally came from the plants eaten by that deer (figure **56.3.4.*d***). Using this reasoning, all food eaten by humans can be traced back to producers that carry out photosynthesis (figure **56.3.4.*e***).



Figure **56.3.4.*d***: The energy stored in carbohydrate molecules from photosynthesis passes through the food chain. The predator that eats these deer is getting energy that originated in the photosynthetic vegetation that the deer consumed. (credit: Steve VanRiper, U.S. Fish and Wildlife Service)

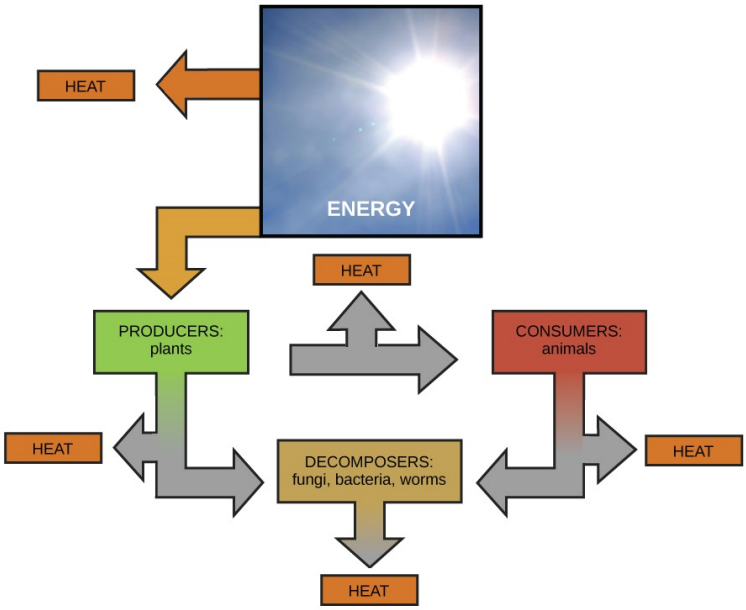


Figure **56.3.4.*e***: Ultimately, most life forms get their energy from the sun. This flow chart shows energy from the sun being captured by producers, such as plants, through photosynthesis. The energy is transferred to the consumers of the producers, such as animals. Energy can be obtained from producers directly (herbivores eat plants) or indirectly (carnivores eat herbivores). Decomposers eventually breakdown of dead organisms, including plant and animal material, and contribute to the nutrient pool. Fungi and bacteria are decomposers, and worms are detritivores (not shown). During each energy transfer, some of the energy in the system is lost as heat.

Consumers can be classified based on whether they eat animal or plant material (figure **56.3.4.*f***). Consumers that feed exclusively on animals are called **carnivores**. Lions, tigers, snakes, sharks, sea stars, spiders, and ladybugs are all carnivores. **Herbivores** are consumers that feed exclusively on plant material, and examples include deer, koalas, some bird species, crickets, and caterpillars. Herbivores can be further classified into **frugivores** (fruit-eaters), **granivores** (seed eaters), **nectivores** (nectar feeders), and **folivores** (leaf eaters). Consumers that eat both plant and animal material are considered **omnivores**. Humans, bears, chickens, cockroaches, and crayfish are examples of omnivores.



Figure 56.3.4.*f*: Carnivores like the lion (top left) eat primarily meat. The ladybug (lower left) is also a carnivore that consumes small insects called aphids. Herbivores, like the mule deer (middle) eat primarily plant material. Omnivores like the bear (top right) and crayfish (bottom right) eat both plant and animal based food. Lion by Kevin Pluck; ladybug by Jon Sullivan; mule deer by Bill Ebbesen; bear by Dave Menke; crayfish by Jon Sullivan. All from OpenStax (CC-BY). Access for free at openstax.org.

Dead producers and consumers are eaten by **detritivores** (which ingest dead tissues) and **decomposers** (which further break down these tissues into simple molecules by secreting digestive enzymes). Invertebrate animals, such as worms and millipedes, are examples of detritivores, whereas fungi and certain bacteria are examples decomposers.

Food Chains

A **food chain** is a linear sequence of organisms through which nutrients and energy pass as one organism eats another. Each organism in a food chain occupies a specific **trophic level** (energy level), its position in the food chain. The first trophic level in the food chain is the producers. The **primary consumers** (the herbivores that eat producers) are the second trophic level. Next are higher-level consumers. Higher-level consumers include **secondary consumers** (third trophic level), which are usually carnivores that eat the primary consumers, and **tertiary consumers** (fourth trophic level), which are carnivores that eat other carnivores. In the Lake Ontario food chain, shown in figure 56.3.4.*g*, the Chinook salmon is the apex consumer at the top of this food chain. Some communities have additional trophic levels (quaternary consumers, fifth order consumers, etc.). Finally, detritivores and decomposers break down dead and decaying organisms from any trophic level. There is a single path through a food chain.

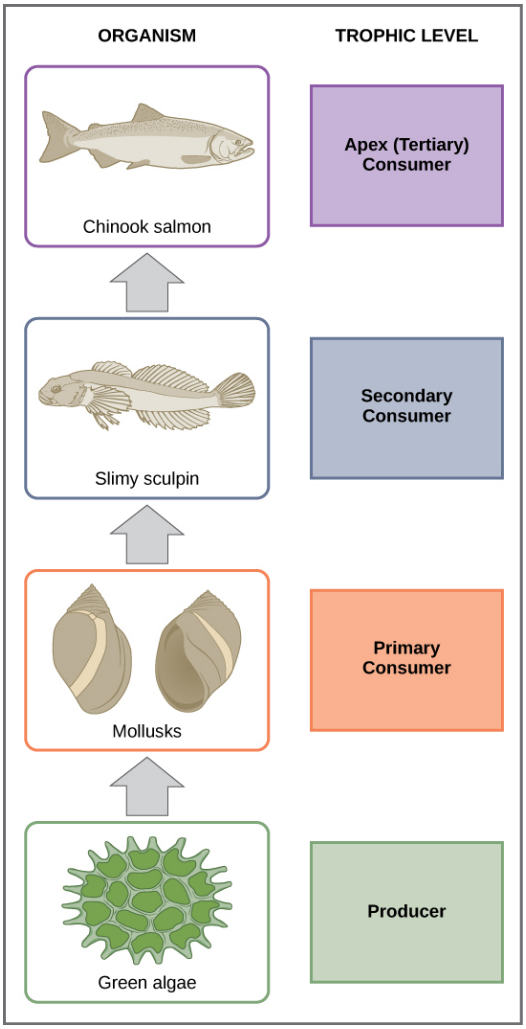


Figure **56.3.4.*g***: These are the trophic levels of a food chain in Lake Ontario at the United States–Canada border. Energy and nutrients flow from photosynthetic green algae (producers) at the base to the primary consumers, which are mollusks, or snails. The secondary consumers are small fish called slimy sculpin. The tertiary and apex consumer is Chinook salmon. Detritivores and decomposers are not shown. (credit: modification of work by National Oceanic and Atmospheric Administration/NOAA)

One major factor that limits the number of steps in a food chain is energy. Only about 10% of the energy in one trophic level is transferred to the next trophic level. This is because much energy is lost as heat during transfers between trophic levels or to decomposers due to the second law of thermodynamics. Thus, after four to six trophic energy transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at higher trophic levels (also see Community Productivity and Transfer Efficiency).

Certain environmental toxins can become more concentrated as they move up the food chain, with the highest concentrations occurring in the top consumers, a process called **biomagnification**. Essentially, a top consumer ingests all the toxins that had previously accumulated in the bodies of the organisms at the lower trophic levels. This explains why frequently eating certain fish, like tuna or swordfish, increases your exposure to mercury, a toxic heavy metal.

Food Webs

While food chains are simple and easy to analyze, there is a one problem when using food chains to describe most communities. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed at more than one trophic level. In addition, species feed on and are eaten by more than one species. In other words, the linear model of trophic interactions, the food chain, is a hypothetical and overly simplistic representation of community structure. A holistic model—which includes all the interactions between different species and their complex interconnected relationships with each other and with the environment

—is a more accurate and descriptive model. A **food web** is a concept that accounts for the multiple trophic interactions between each species (figure 56.3.4.*h* and i).

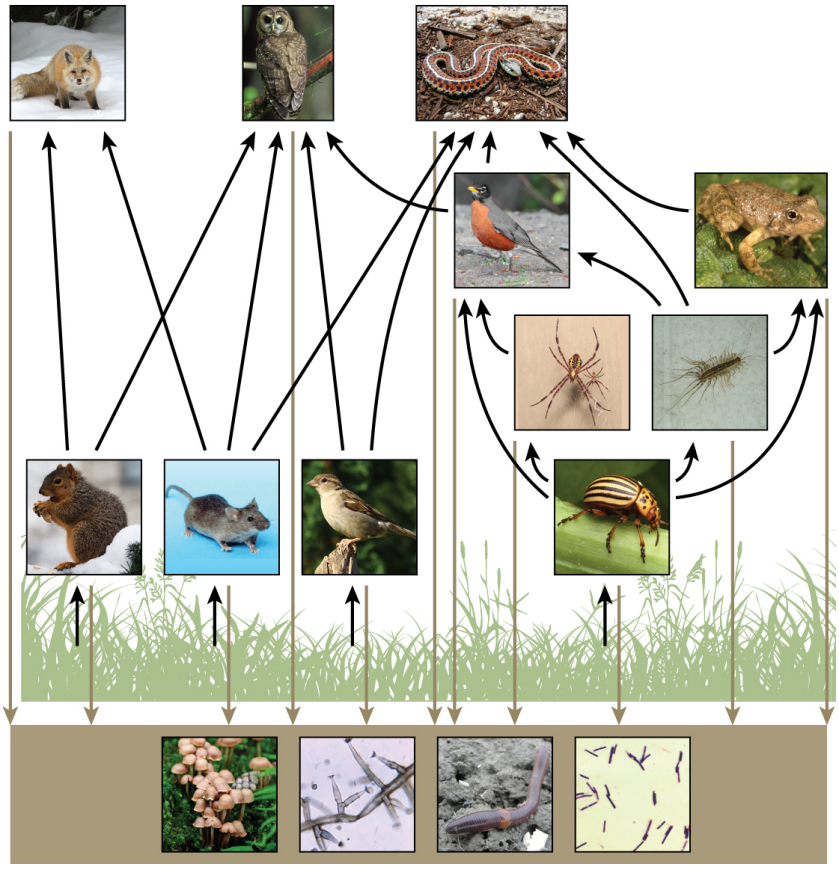


Figure 56.3.4.*h*: This food web shows the interactions among organisms across trophic levels. Arrows point from an organism that is consumed to the organism that consumes it and represent energy transfer. The producers (plants) capture energy from the sun. The level above the producers shows the primary consumers that eat the producers. Some examples are squirrels, mice, seed-eating birds, and beetles. Spiders and centipedes eat beetles. Robins eat beetles, spiders, and centipedes, and toads eat beetles and centipedes. Foxes eat squirrels and mice; owls eat squirrels, mice, seed-eating birds, and robins; and snakes eat mice, seed-eating birds, robins, centipedes, and toads. Some consumers are in between trophic levels because they eat a combination of primary, secondary, and/or tertiary consumers. All the producers and consumers eventually become nourishment for the decomposers (mushrooms, mold, and bacteria) and detritivores (earthworms) in the soil, which are depicted at the bottom of the illustration. (credit "fox": modification of work by Kevin Bacher, NPS; credit "owl": modification of work by John and Karen Hollingsworth, USFWS; credit "snake": modification of work by Steve Jurvetson; credit "robin": modification of work by Alan Vernon; credit "frog": modification of work by Alessandro Catenazzi; credit "spider": modification of work by "Sanba38″/Wikimedia Commons; credit "centipede": modification of work by "Bauerph"/Wikimedia Commons; credit "squirrel": modification of work by Dawn Huczek; credit "mouse": modification of work by NIGMS, NIH; credit "sparrow": modification of work by David Friel; credit "beetle": modification of work by Scott Bauer, USDA Agricultural Research Service; credit "mushrooms": modification of work by Chris Wee; credit "mold": modification of work by Dr. Lucille Georg, CDC; credit "earthworm": modification of work by Rob Hille; credit "bacteria": modification of work by Don Stalons, CDC)

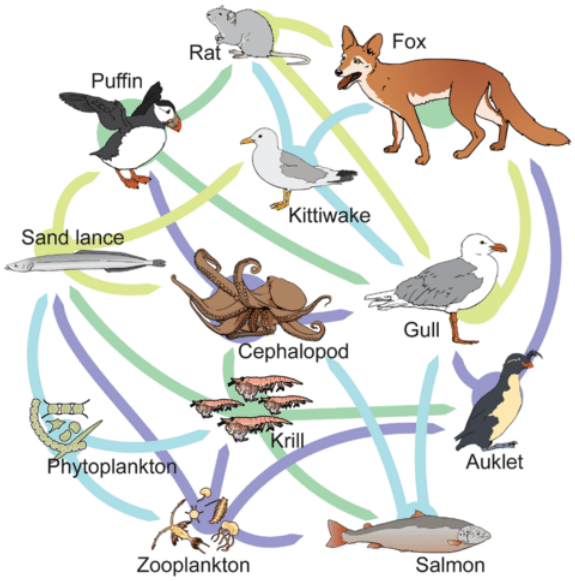


Figure **56.3.4.*i***: In this food web, each organism may have multiple food sources or be eaten by multiple species. Phytoplankton are the primary producers. They are consumed by sand lances, krill, and zooplankton. Sand lances are consumed by puffins, kittiwake, and cephalopods. Krill are consumed by the sand lance, cephalopods, auklets, and salmon. Zooplankton are consumed by the sand lance, krill, auklets, and salmon. Puffins are eaten by rats and gulls. Kittiwakes are eaten by rats, foxes, and gulls. Cephalopods are consumed by puffins and gulls. Auklets are consumed by gulls and foxes. Salmon are consumed by cephalopods and gulls. Rats are consumed by foxes and gulls. Gulls are consumed by foxes. Detritivores and decomposers are not shown. Image by Mariana Ruiz Villarreal (LadyofHats) for CK-12 Foundation (CC-BY-NC).

The trophic level of each species in a food web is not necessarily a whole number. In figure **56.3.4.*i***, phytoplankton are the primary producers (trophic level 1). Zooplankton only feed on phytoplankton, making them primary consumers (trophic level 2). Determining the trophic level of the other species is more complex. For example, krill eat both phytoplankton and zooplankton. If krill only ate phytoplankton they would primary consumers (trophic level 2). If they ate only zooplankton, they would be secondary consumers (trophic level 3). Since, krill consume both, their trophic level is 2.5.

Community Productivity and Transfer Efficiency

The rate at which photosynthetic producers incorporate energy from the sun is called **gross primary productivity**. In a cattail marsh, plants only trap 2.2% of the energy from the sun that reaches them. Three percent of the energy is reflected, and another 94.8% is used to heat and evaporate water within and surrounding the plant. However, not all of the energy incorporated by producers is available to the other organisms in the food web because producers must also grow and reproduce, which consumes energy. At least half of the 2.2% trapped by cattail marsh plants is used to meet the plants own energy needs.

Net primary productivity is the energy that remains in the producers after accounting for the metabolic needs of the producers and heat loss. The net productivity is then available to the primary consumers at the next trophic level. One way to measure net primary productivity is to collect and weigh the plant material produced on a m^2 (about 10.7 ft^2) of land over a given interval. One gram of plant material (e.g., stems and leaves), which is largely the carbohydrate cellulose, yields about 4.25 kcal of energy when burned. Net primary productivity can range from 500 kcal/m^2/yr in the desert to 15,000 kcal/m^2/yr in a tropical rain forest.

In an aquatic community in Silver Springs, Florida, the gross primary productivity (total energy accumulated by the primary producers) was 20,810 kcal/m^2/yr (figure **56.3.4.*j***). The net primary productivity (energy available to consumers) was only 7,632 kcal/m^2/yr after accounting for energy lost as heat and energy require to meet the producer's metabolic needs.

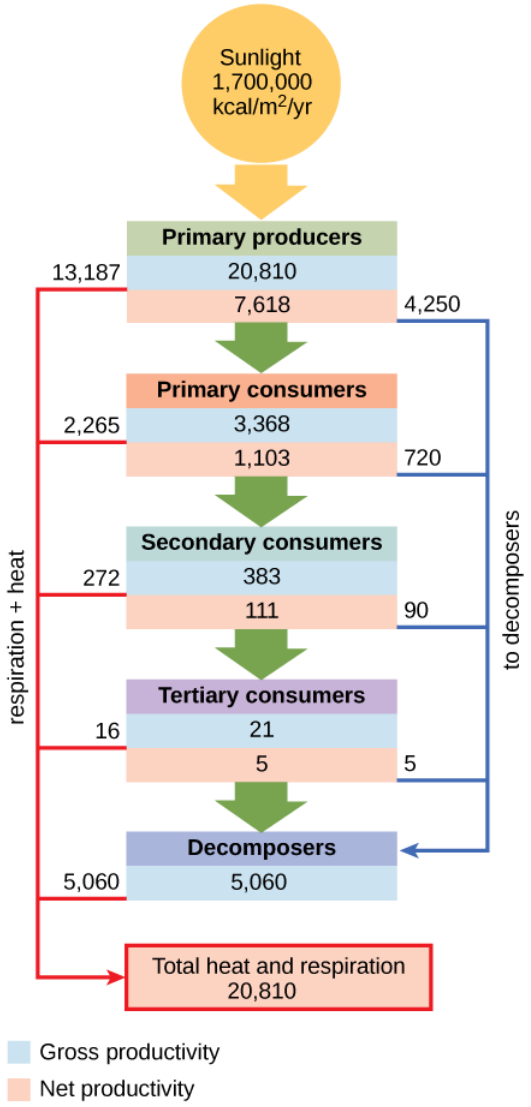


Figure **56.3.4.j**: The flow of energy through a spring ecosystem in Silver Springs, Florida. The gross productivity (blue) for each trophic level is listed just above the net productivity (red). Notice that the energy decreases with each increase in trophic level. The energy content of primary producers (gross productivity) is 20,810 kcal/m^2/yr. The gross productivity of primary consumers is much smaller, about 3,368 kcal/m^2/yr. The gross productivity of secondary consumers is 383 kcal/m^2/yr, and the gross productivity of tertiary consumers is only 21 kcal/m^2/yr. The net productivity of each trophic level is less than the gross productivity because some energy is used to meet metabolic needs (respiration), and some energy is lost as heat. For example, the net productivity of primary consumers was 1,103 kcal/m^2/yr, only about a third of the gross productivity. Some of the energy in each trophic level (a total of 5,060 kcal/m^2/yr) is transferred to decomposers. All of the energy initially captured by primary producers (20,810 kcal/m^2/yr) is eventually released from the system.

Only a fraction of the energy captured by one trophic level is assimilated into biomass, which makes it available to the next trophic level. Assimilation is the biomass of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used to conduct work by that trophic level, and energy lost as waste. Incomplete ingestion refers to the fact that some consumers eat only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide. In Silver Springs, only 1103 kcal/m^2/yr from the 7618 kcal/m^2/yr of energy available to primary consumers was assimilated into their biomass. (The **trophic level transfer efficiency** between the first two trophic levels was approximately 14.8 percent.)

An animal's source of heat influences its energy needs. **Ectotherms**, such as invertebrates, fish, amphibians, and reptiles, rely on external sources for body heat, and **endotherms**, such as birds and mammals, rely on internally generated heat. Generally,

ectotherms require less of the energy to meet their metabolic needs and than endotherms do, and therefore, many endotherms have to eat more often than ectotherms.

The inefficiency of energy use by endotherms has broad implications for the world's food supply. It is widely accepted that the meat industry uses large amounts of crops to feed livestock, and because a low percentage of this is assimilated into biomass, much of the energy from animal feed is lost. For example, it costs about 1¢ to produce 1000 dietary calories (kcal) of corn or soybeans, but approximately $0.19 to produce a similar number of calories growing cattle for beef consumption. The same energy content of milk from cattle is also costly, at approximately $0.16 per 1000 kcal. Thus, there has been a growing movement worldwide to promote the consumption of non-meat and non-dairy foods so that less energy is wasted feeding animals for the meat industry.

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56.4: Biodiversity and Ecosystem Stability

Stability

An ecosystem is said to possess ecological **stability** (or equilibrium) if it is capable of returning to its equilibrium state after a perturbation (a capacity known as resilience) or does not experience unexpected large changes in its characteristics across time. Although the terms community stability and ecological stability are sometimes used interchangeably, community stability refers only to the characteristics of communities. It is possible for an ecosystem or a community to be stable in some of their properties and unstable in others.

The relation between diversity and stability has been widely studied. **Diversity** can operate to enhance the stability of ecosystem functions at various ecological scales. For example, genetic diversity can enhance resistance to environmental perturbations. At the community level, the structure of food webs can affect stability. At the level of landscapes, environmental heterogeneity across locations has been shown to increase the stability of ecosystem functions

Resistance and Resilience

Resistance is the ability for an ecosystem to remain unchanged when being subjected to a disturbance or disturbances. Some ecosystems are better at resisting change than others, and therefore have high resistance.

Resilience is the ability and rate of an ecosystem to recover from a disturbance and return to its pre-disturbed state. Some ecosystems can shift greatly from their previous state and still return to pre-disturbance conditions. The measure for how far an ecosystem can be shifted from its previous state and still return to normal is called its amplitude.

Both resistance and resilience are components of determining **ecosystem stability**. Both can also occur at the community, population, and individual level. An ecosystem can have high resistance to disturbance, but low resilience, and vice versa. Low resistance can sometimes be advantageous, such as in ecosystems that rely on natural disturbances to temporarily change their conditions in order to remain stable over the long term.

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56.5: Island Biogeography

Biogeography is the study of the distribution of species and ecosystems in geographic space and through geological time. Organisms and biological communities often vary in a regular fashion along geographic gradients of latitude, elevation, isolation, and habitat area. The latter pattern, often called the **species-area relationship**, has long been a fascination for biogeographers. Figure **56.5.1** demonstrates this species-area relationship for amphibians and reptiles in the West Indies. A study from around 1957 was included in Robert H. MacArthur and Edward O. Wilson's famous book "The Theory of Island Biogeography", and showed that among seven islands studied, the largest, Cuba, had the most species, and the smallest, Redonda, had the fewest. This general pattern has been found in many different islands groups, and across various different taxa.

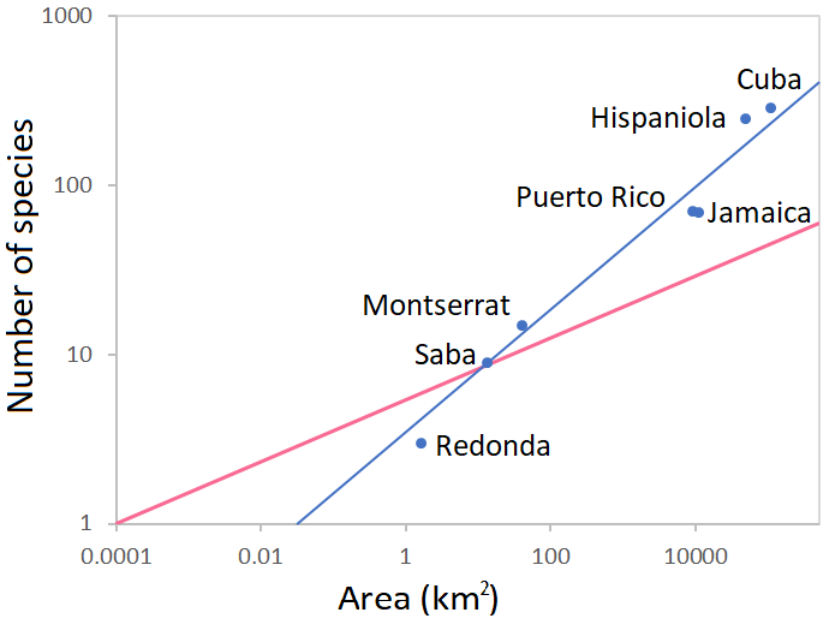


Figure 56.5.1: Species-area relationship for amphibians and reptilians on seven different islands in the West Indies. An original study (Darlington c. 1957), published in "The Theory of Island biogeography", showed a strong positive correlation between island size and number of species (blue line). A more recent study by Gao and Perry (2016) included data for many additional small islands (smaller than Redonda) and found that while the pattern holds, the relationship is flatter than in the original study--indicated by the pink line. Figure drawn by Andy Wilson, based on Figure 4 in Gao and Perry (2016).

While studying these species-area relationships for their seminal book, MacArthur and Wilson were drawn to another of the four geographic gradients--that of isolation. They observed that some large Islands had fewer species than would be expected for their size, while conversely, some small islands had more species than expected.

While studying patterns of species richness on islands, two ecologists, Robert H. MacArthur and Edward O. Wilson, noted some exceptions to the **species-area relationship**. For example, some large islands had fewer species than expected due to their size, while some small islands had more species than expected. These patterns were explained by MacArthur and Wilson's **Equilibrium Theory of Island Biogeography**, which takes into account the fact that islands are colonized by species from elsewhere, and natural extinctions will occur on those islands, over long periods of time.

Imagine there are two islands (**a** and **b**) located off the coast of the mainland. Although the two islands are about the same size, island **a** is located much farther away than island **b**. If you are a bird that lives on the mainland, which island are you most likely to find? The answer is generally island **b**. This means immigration (or colonization) is influenced by the distance of an island from the mainland (a source of colonists). Therefore, islands that are closer to the island are more likely to receive immigrants than islands that are further away.

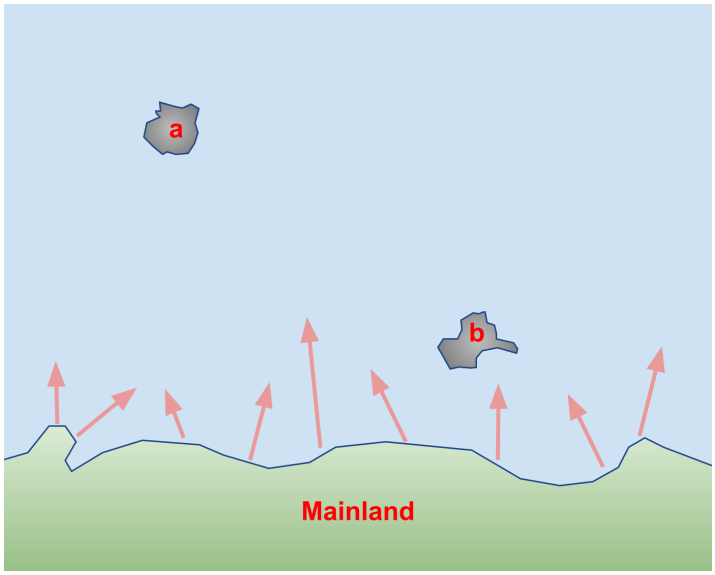


Figure 56.5.2: Two offshore islands--the Theory of Island Biogeography suggests that fewer species will colonize the more distant island **a**, in comparison to island **b** (credit: Andy Wilson, redrawn from Hdelucalowell15 (CC BY-SA 4.0)).

Once a species manages to reach and colonize an island, the rate of extinction is largely influenced by size of the island. This is because smaller islands tend to hold smaller populations (which are more likely to experience extinction due to stochastic effects like genetic drift). Larger habitat size reduces the probability of extinction of the colonized species due to chance events. Smaller islands are also likely to hold fewer populations in general because they have fewer resources and less diversity of resources. Larger islands have larger and more habitat areas, which typically leads to more differences in habitat or *habitat heterogeneity*. Higher heterogeneity means that there are more opportunities for a variety of species to find their suitable niches. Habitat heterogeneity also helps increase the number of species to successfully colonize after immigration.

Now let's consider the situation if we had two different islands sizes in our offshore archipelago, with **c** and **d**, much bigger than **a** and **b** Figure **56.5.3**. We would expect extinction rates to be much lower on islands **c** and **d** than on the two smaller islands.

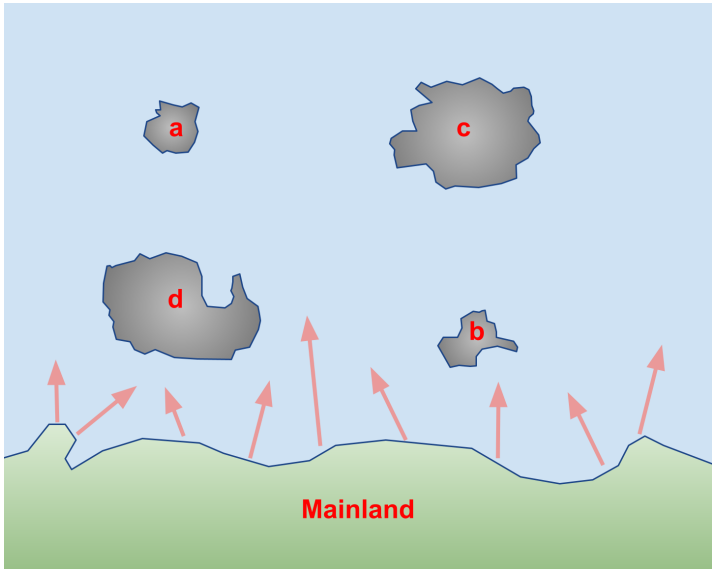


Figure 56.5.3: Four offshore islands--the Theory of Island Biogeography suggests that fewer species will go extinct on the larger islands **c** and **d**, in comparison to islands **a** and **b** (credit: Andy Wilson, redrawn from Wikipedia (CC BY-SA 4.0)).

We could plot both immigration and extinction relationships on a single image, as in Figure **56.5.4**. Note the y-axis is the number of species (either colonizing or going extinct). Now we see that of the four islands in Figure **56.5.3**, island **a** (small and far) would

likely have the fewest species, island **d** (large and close), would have the most, and islands **b** and **c** would fall between the two extremes.

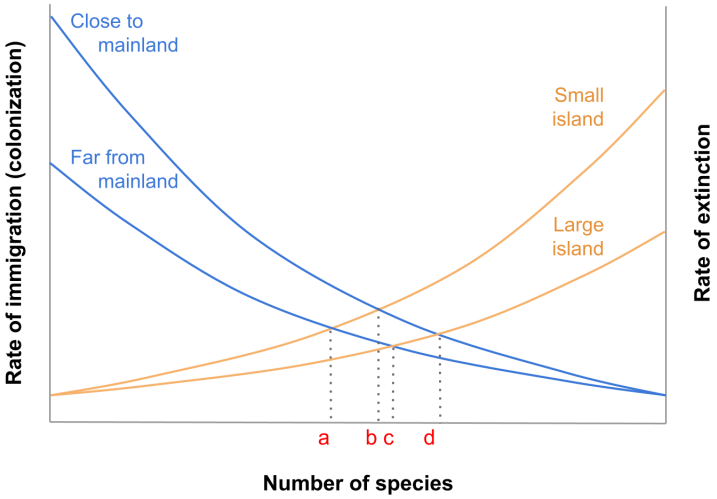


Figure 56.5.4: Equilibrium Theory of Island Biogeogaphy (credit: Andy Wilson, redrawn from Wikipedia (CC BY-SA 4.0)).

This basic graph makes a lot of assumptions but also offers a lot of insight. In this graph, immigration rates (blue lines) depend on proximity to mainland. Immigration rates also decline with species richness. That's becasuse its' easiest to immigrate to an island when it is empty because all the resources on the island are available. As the islands get more and more full, colonizing the island becomes more difficult.

Extinction rates (orange lines), as noted above, depend on island size. We also see that extinction rates tend to increase with the number of species. This should make sense: If there are no species on an island, extinction is impossible, but as more and more species arrive (and compete!) extinction becomes more likely.

Figure **56.5.4** shows the basic Equilibrium Theory of Island Biogeography. It suggests that islands will reach an equilibrium, or stable, number of species when immigration and extinction rates are equal! Note this model could be modified in multiple ways. Size of an island, for example, likely also impacts immigration rate (larger islands are easier to hit!), and islands that are close together may also share individuals (the Rescue effect!), but even this simple conceptualization has proven useful for understanding global species richness patterns.

One interesting point to note is that an equilibrium number of species is reached when immigration and extinction rates are equal, not when those processes stop! This means islands may consistently be changing species composition but should maintain fairly consistent levels of species richness. As odd as this sounds, early tests of the Equilibrium Theory of Island Biogeography supported these assumptions. When mangrove islands off the coast of Florida were fully cleared of their invertebrate (insect and arachnid) communities and allowed to recolonize, islands eventually stabilized with communities of about the same richness as they had before disturbance.

Conservation in Preserves as an application of Island Biogeography

The island biogeography model has crucial applications for wildlife management because wildlife reserves or patches of habitat can be considered “islands” of habitat in “an ocean” of an inhabitable area. For this reason, the Theory Island Biogeography has become central to our understanding of how habitat fragmentation leads to biodiversity loss. For a more detailed description of how habitat fragmentation leads to biodiversity loss, see the section on "Threats to Biodiversity" in the chapter on Conservation Biology from this book or see the section on "The Scramble for Space" in Conservation Biology in Sub-Saharan Africa (Wilson and Primack 2019).

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts (Figure 56.5.5). A **preserve** is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. There has been extensive research into optimal preserve designs for maintaining biodiversity. Conservation preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. In general, large preserves are better because they support more species, including species with large home ranges; they have more core area of optimal habitat for individual species; they have more niches to support more species; and they attract more species because they can be found and reached more easily. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by less hospitable ecosystems outside the preserve boundary. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing **wildlife corridors** (narrow strips of protected land) between two preserves is important so that species and their genes can move between them. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.



Figure 56.5.5: Mequon Nature Preserve in Wisconsin. Image by Jennifer Tomaloff (CC-BY-NC-SA).

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57.1.1: The annual solar cycle

Solar radiation drives the Earth system and makes life possible. Solar radiation is absorbed and then put to use to increase the surface temperature, to change the phase of water, and to fuel atmospheric chemistry. The uneven distribution of solar radiation on Earth's surface drives atmospheric dynamics.

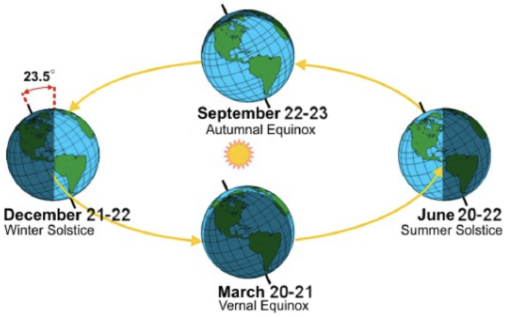


Figure 57.1.1.1: Earth's orbit around the sun. *Credit: National Weather Service*

The total amount of solar energy per unit time and unit area, also called the solar irradiance, is 1361 W m^{-2} at the top of the atmosphere (Stephens et al., 2012, Nature Geoscience 5, p. 691). It is distributed unevenly over Earth's surface. That distribution changes over the course of the seasons (see next two figures). The seasons result primarily from the Earth's rotation axis not being perpendicular to the plane of the Earth's orbit around the Sun.

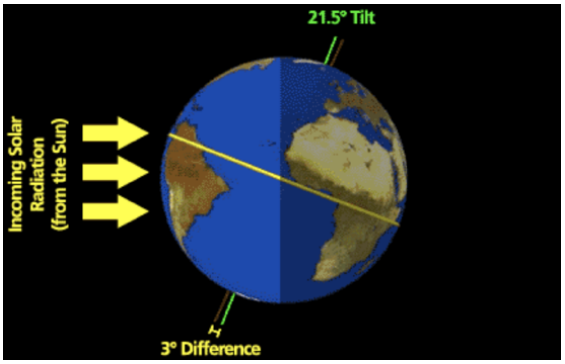


Figure 57.1.1.2: The current tilt of Earth's orbit. More solar radiation is absorbed by Earth's surface near the equator than at high latitudes as a result of the curvature of the Earth. Credit: National Park Service

Earth's spin and its orbit around the sun are not constant, but instead, change with time, like a spinning top. The orbit's eccentricity (i.e., how different it is from circular) varies with a 100,000-year period. The tilt of Earth's rotation axis with respect to the perpendicular from its orbit, which is called its obliquity, varies from 22.1° to 24.5° during a 41,000-year cycle. It is currently 23.4° and decreasing. Finally, the precession of Earth's orbit, which is the orientation of the rotation axis with respect to Earth's orbital position, also varies with a period of about 26,000 years, although the eccentricity of the orbit is also rotating around the sun, so that the effective period of precession is about 21,000 years. These motions, when taken together, slowly and periodically change the distribution of solar irradiance on Earth's surface and are described by the **Milankovitch Theory** (see next two figures).

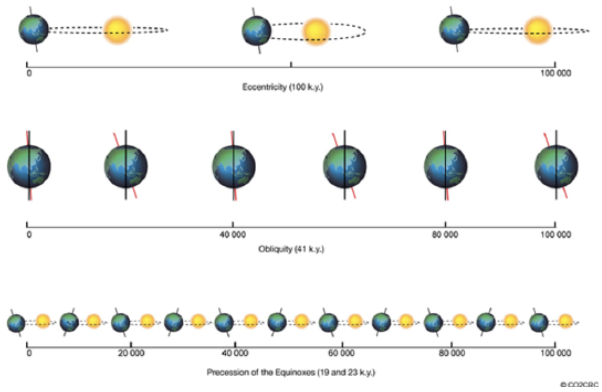


Figure **57.1.1.3**: Changes in Earth's orbit that occur over time (top). Eccentricity (non-circular shape) varies over 100,000 years (middle). Obliquity (tilt of Earth's rotation axis) varies every 41,000 years (bottom). Precession (obliquity relative to position in Earth's orbit) varies over a cycle with a period of approximately 20,000 years. Credit: CO2CRC

Changes in Earth's orbit and spin are not the only ways that solar irradiance changes—the Sun's energy output also changes. It has been increasing slightly (0.05–0.10%) over the past 300 years and varies by another ~0.1% over the course of the 11-year solar cycle. The ultraviolet (200–300 nm) irradiance has increased about 3% in the past 300 years and varies by ~1.5% between solar maximum and solar minimum. This increased UV leads to greater stratospheric ozone production, which increases stratospheric heating, leading to poleward displacement of the stratospheric meridional wind.

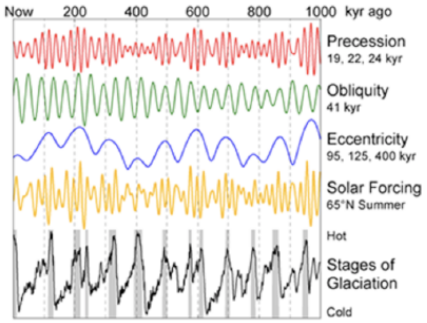


Figure **57.1.1.4**: Variation of solar irradiance (i.e., forcing) observed as a result of the changes in eccentricity, obliquity, and precession. Links to glaciation are complex but the distribution of solar irradiance on Earth is important for climate. Credit: The Azimuth Project Template:TranscludeAutoNumTitle

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57.1.2: Radiative Differential Heating

The general circulation is driven by differential heating. Incoming solar radiation (**insolation**) nearly balances the outgoing infrared (IR) radiation when averaged over the whole globe. However, at different latitudes are significant imbalances (Fig. 57.1.2.1), which cause the differential heating.

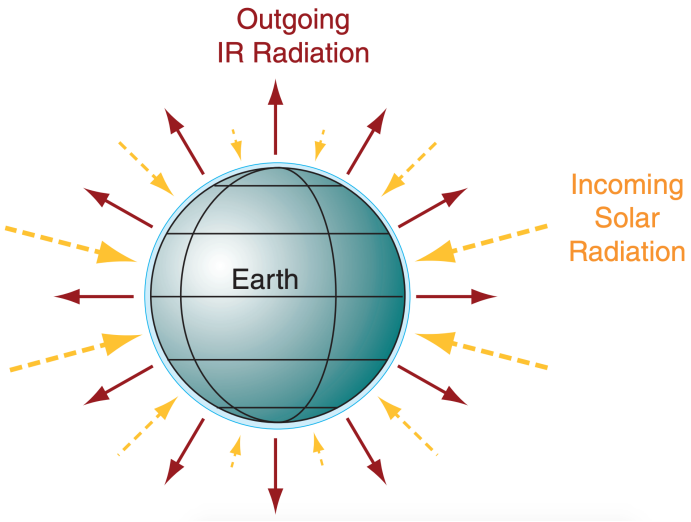


Figure 57.1.2.1: Annual average incoming solar radiation (yellow dashed arrows) and outgoing infrared (IR) radiation (solid dark red arrows), where arrow length indicates relative magnitude. [Because the Earth rotates and exposes all locations to the sun at one time or another during the year, the incoming solar radiation is sketched as approaching all locations on the Earth's surface.]

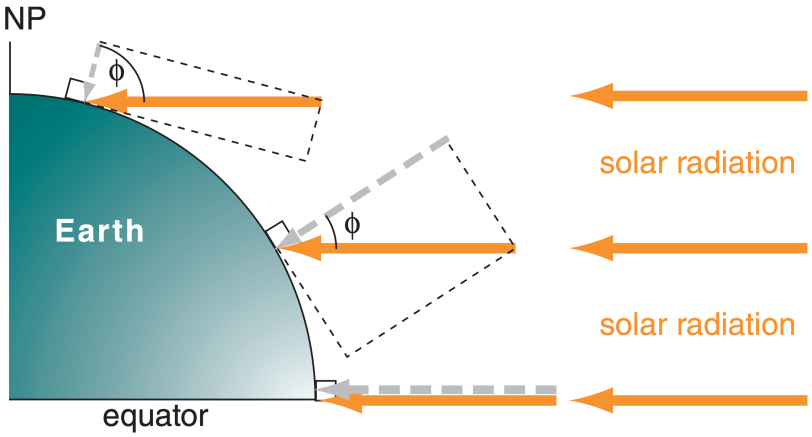


Figure 57.1.2.2: Of the solar radiation approaching the Earth (thick solid yellow arrows), the component (dashed grey arrow) that is perpendicular to the top of the atmosphere is proportional to the cosine of the latitude ϕ (during the equinox).

Recall from the Solar & Infrared Radiation chapter that the flux of solar radiation incident on the top of the atmosphere depends more or less on the cosine of the latitude, as shown in Fig. 57.1.2.2. The component of the incident ray of sunlight that is perpendicular to the Earth's surface is small in polar regions, but larger toward the equator (grey dashed arrows in Figs. 57.1.2.1 and 57.1.2.2). The incoming energy adds heat to the Earth-atmosphere-ocean system.

Heat is lost due to infrared (IR) radiation emitted from the Earth-ocean-atmosphere system to space. Since all locations near the surface in the Earthocean-atmosphere system are relatively warm compared to absolute zero, the Stefan-Boltzmann law from the Solar & Infrared Radiation chapter tells us that the emission rates are also more or less uniform around the Earth. This is sketched by the solid red arrows in Fig. 57.1.2.1.

Thus, at low latitudes, more solar radiation is absorbed than leaves as IR, causing net warming. At high latitudes, the opposite is true: IR radiative losses exceed solar heating, causing net cooling. This differential heating drives the global circulation.

The general circulation can't instantly eliminate all the global north-south temperature differences. What remains is a meridional temperature gradient — the focus of the next subsection.

North-South Temperature Gradient

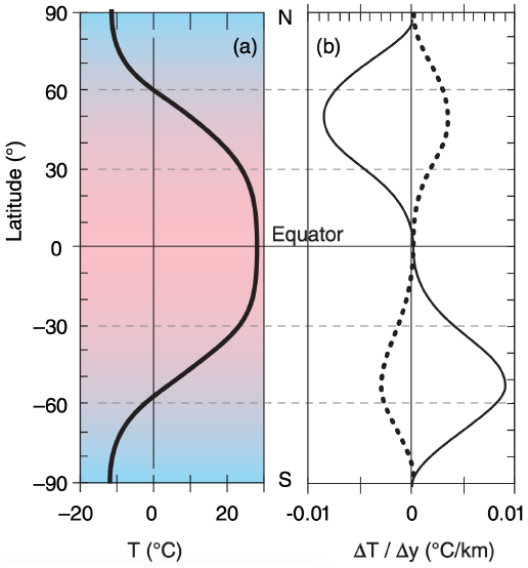


Figure **57.1.2.3**: Idealized variation of annual-average temperature (a) and meridional temperature gradient (b) with latitude, averaged around latitude belts (i.e., zonal averages). Solid curve represents Earth's surface (= sea-level because the toy model neglects terrain) and dotted curve is for 15 km altitude above sea level.

To create a first-order toy model, neglect monthly variations, monsoonal variations and mountains. Instead, focus on surface temperatures averaged around separate latitude belts and over one year. Those latitude belts near the equator are warmer, and those near the poles are colder (Fig. **57.1.2.3**).

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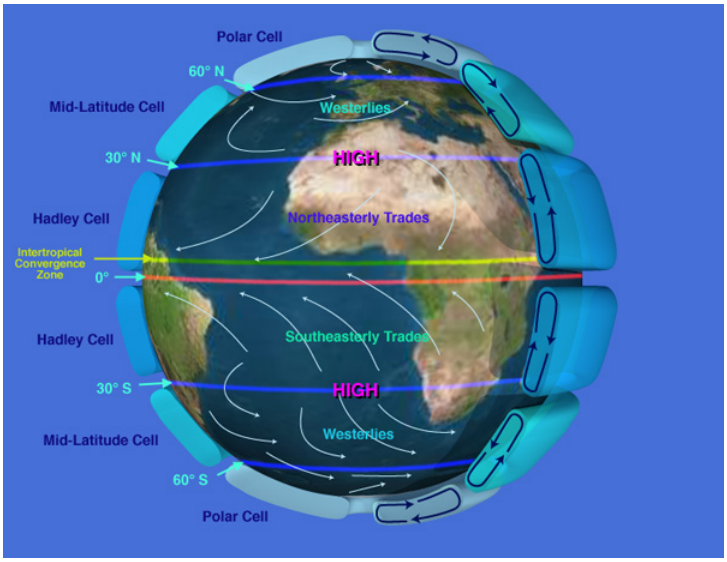
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57.1.3: Overview, Solar Energy, Pressure, and Wind Belts

The connections between atmospheric circulation, ocean currents and Earth's climate are both simple and wonderfully complex. We could easily spend the whole semester studying these topics and developing the background for ocean circulation, but we won't. Instead, we'll hit the high points and build a background for understanding ocean currents and thermo-haline circulation. It makes sense to start with atmospheric circulation because ocean surface currents are driven by wind. The basic pattern of surface ocean circulation, including the large-scale gyres, is caused by wind and the factors that produce large-scale wind patterns. We need to start by seeing how solar energy input on Earth and poleward transport of heat by winds sets up large-scale atmospheric cells that produce Easterly and Westerly winds in three main bands from the equator to the poles. The Coriolis effect, produced by Earth's rotation and conservation of momentum, plays an important role here. Ocean structure also plays an important role and we need to look at density driven circulation in the ocean as produced by temperature and salinity: so-called thermohaline circulation. Ocean circulation is three-dimensional and both surface currents and deep water currents play an important role in heat transport. Large-scale ocean currents are impacted by the Coriolis effect, and depth-variations in coupling between surface flow and wind stress produce another important effect, known as Ekman transport, which we will discuss. Ultimately, when we put all the pieces together, the goal is to arrive at a coherent picture of how solar energy, winds, and ocean circulation combine to produce a global thermostat for Earth.

It's all about Blowing Hot Air

This image shows large-scale atmospheric circulation on Earth. Note the three-dimensionality of the circulation. On the right-hand side of the image the arrows show vertical and horizontal air flow as part of six convection cells, three in each of the Northern and Southern hemispheres. The central part of the image shows surface winds blowing from the east (the Trade winds) or the west (The Westerlies) --note that the Polar Easterlies are not easily seen in this image.



Atmospheric Circulation and the Trade Winds

Source: NASA

Hadley circulation

One of the most important things to understand from this image is that everything is driven by unequal solar heating as a function of latitude. The energy from our Sun is focused on the equatorial region and spread comparatively thinly over the polar regions. This is true on an average annual basis, Earth receives more solar energy at the equator than at the poles. As a result, the land, water, and air, over the equator are warm, and air rises over the equator. This warm air rises through the atmosphere and flows poleward as an upper atmosphere wind that is, essentially, an air-mail package of heat known as a Hadley Cell. The image here has arrows showing circulation in a vertical plane along a line of longitude (just to the east of the African continent) but, of course, this

circulation occurs at all longitudes. Hadley circulation is 3D; heat moves poleward in upper atmosphere winds and there is a return flow from north to south (in the Northern hemisphere) that sets up the Northeasterly Trade winds (with the help of the Coriolis effect, as we'll see below).

Pressure belts

The Hadley Cell is set up by rising air over the equator. It begins with warming of air surrounding the equator, which creates a large region of lower surface pressures (due in part to the fact that columns of warm air weigh less than columns of cold air). This belt of equatorial low pressure causes air to be drawn together in a region called the Intertropical Convergence Zone (ITCZ). The convergence of warm, moist air over the equator transports large volumes of air aloft, to the top of the troposphere. This air is confined vertically by the base of the stratosphere and thus spreads out north and south toward the poles.

Because of Earth's spherical shape, the poleward-flowing air is compressed into an increasingly smaller volume as it moves away from the equatorial region. The airmasses also cool as they move poleward. The buildup of cool air aloft causes surface pressures to rise because surface pressure depends on the weight of the entire atmospheric column. The mass convergence and cooling also cause air mass densification, which forces some of the air aloft to sink. At some point, normally ~ 30 deg. North/South, the increase in surface pressures reaches a maximum, marking a belt of subtropical high pressure. Sinking air is dry and characterized by a lack of clouds and precipitation. These regions of subtropical high pressure systems are known for their tranquil weather. Air masses flowing equatorward from these high pressure belts form the Trade Winds that feed the ITCZ, thus completing the Hadley Cell circulation. Similar thinking explains the existence and wind circulation in the Ferrel Cell (labeled the 'mid-latitude' cell in this image) and the Polar Cell.

Activity 1: Pressure Belts

Let's think about the global pattern of atmospheric pressure. Hadley circulation implies a systematic pattern of pressure variation as a function of latitute. One question we could ask involves differences in air masses within a Hadley cell. Referring to the figure above: how do air masses differ between the ascending limbs of a Hadley Cell, over the equator, compared to the descending limb at 30 deg. North?

- Atmospheric Pressure(link is external) Start by skimming this page. Look at Figures 7d-1 and 7d-4 and read the associated text. (Note: The animation for 7d-4 may open in a separate Quicktime window or be downloaded to your desktop)
- Using these data, let's calculate the average density for air at 30 deg. North compared to that at the equator. You can assume that the atmosphere extends to the 70 km, which is within the Mesosphere. A useful formula for the relationship between pressure, p, density, ρ, gravity, g, and height, h, is: $p = \rho g h$
  - Let's assume that the average air pressure over the equator at Earth's surface is roughly 101.3 kPa (recall: 1 Pa = 1 Newton per square-meter). Does this jive with what you see in figure 7d-4? In this case, what is the average density of air if the column is 70 km tall?
  - Now calculate the density at 30 deg. north, assuming an average surface pressure of 102.5 kPa.
- Comment on how air pressure varies as a function of time throughout the year (hint, look at the animation on the web page that you just read).
- Thinking back to what you know about heat capacity and latent heat, do these differences in density make sense relative to your expectations for heat transfer by large-scale winds? Is the air at 30 deg. north likely to be colder/warmer/denser compared to that at the equator?

Submitting your work

Save your document as either a Microsoft Word or PDF file in the following format:
L4_Activity1_AccessAccountID_LastName.doc (or .pages or .pdf)
For example, student Elvis Aaron Presley's file would be named "L4_Activity1_eap1_presley.doc".

Put the file in the DropBox under Lesson 4 on Canvas.

Grading Criteria

See the grading rubric for specifics on how this assignment will be graded.

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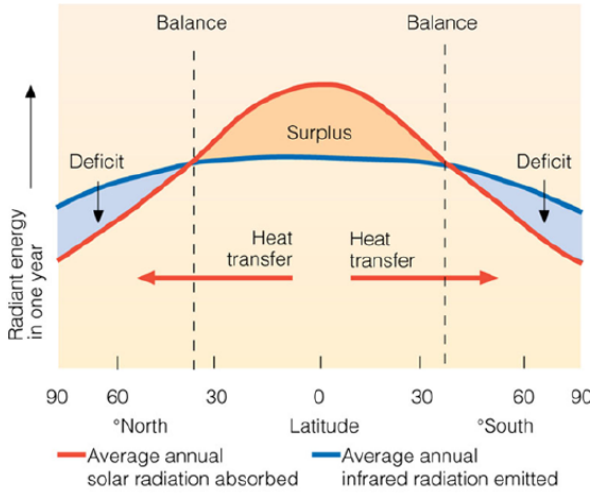
57.1.4: Redistributing Earth's Heat, Wind, and Currents

Heat redistribution

Earth's heat budget exhibits important variations with latitude. Heat input via solar radiation varies systematically with sun angle, and thus when averaged over a year, we find a simple relationship between latitude and heat absorbed, with more heat received in the equitorial region than in polar regions. The figure below shows this variation along with average annual radiation output from Earth. The dashed lines show the points at which input (heat absorbed at Earth's surface) is equal to output (heat lost via long-wavelength radiation).

Here's a useful animation for thinking about sun-angle variations throughout the year(link is external).

Now have a look at the figure below. This figure has important implications for wind generation and ocean currents because both are driven by temperature differences, and by heat input between the equatorial and polar regions. Winds and ocean currents play a major role in moving the surplus heat from the equatorial regions to the polar regions. Without this heat transfer, the polar regions of Earth would get colder every year and regions between ~ 35 N and 35 S would get warmer every year. Energy transfer occurs via sensible heat and via latent heat. As you'll recall from Lesson 3, latent heat of evaporation for water is very large compared to heat capacity, so it is no surprise that latent heat is the dominant process, with sensible heat transfer accounting for only a few percent of the heat flux, from ocean to atmosphere, associated with latent heat.

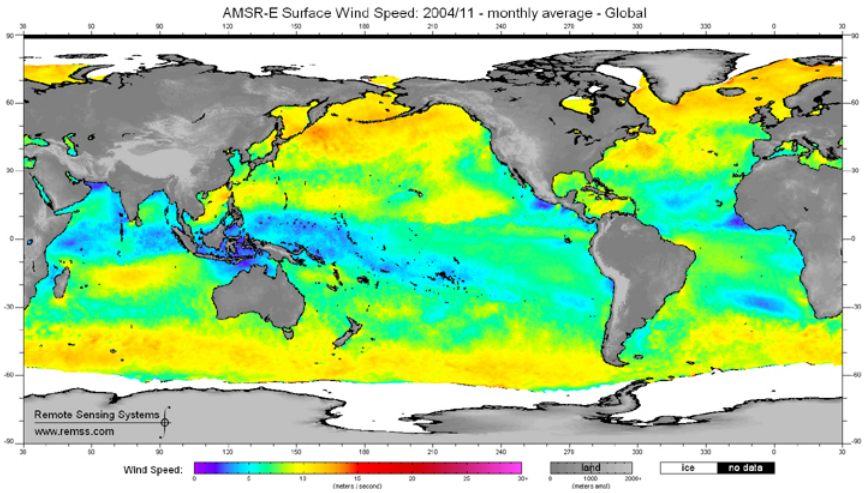


Credit: NASA

Wind and ocean currents

Winds and ocean currents play a big role in redistributing heat.

This figure shows sea surface wind speed, as derived from a NASA's satellite (Aqua) for the month of November, 2004. The large-scale pattern of surface ocean currents is set up by winds. Note the variations with latitude. Look back at the Hadley circulation and think about the location of the easterlies/westerlies compared to what you see here.



Sea surface wind speed, as derived from a NASA's satellite (Aqua) for the month of November, 2004.

Credit: NASA(link is external)

Reading assignment

Read the link below.

- The Atlantic heat conveyor slows(link is external) Are we heading toward *The Day After Tomorrow*?

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57.1.5: Coriolis and Ekman Transport

For large scale winds and ocean currents, the Coriolis effect is an important consideration because it changes the net direction of heat transport.

Coriolis Effect The Coriolis effect is due to an inertial force that is important in a rotating frame of reference. As you know from Newton's laws of motion, bodies in motion stay in motion unless acted upon by external forces. So, a wind blowing from north to south should go in a straight line, and in fact, it does. The problem is that this straight line does not look straight when referenced to a spinning Earth. There are many on-line resources for the Coriolis effect, so I won't try to duplicate visualizations here, but there are a few things to get straight before looking at a few of them.

1. The Coriolis force is given by the Coriolis acceleration times the mass of the object in motion. This is the familiar F = m a.
2. The Coriolis acceleration is proportional to the cross product between the (linear) velocity of the moving object and the angular velocity of the rotating frame of reference. On Earth, the angular velocity is given by 360 deg/24 Hr. or 2 π (radians) per 24 Hrs, which is equal to 1.454e-4 radians per sec. The formula is: $a_c = - 2\omega \times v$
3. As you recall from plate tectonics and spherical trigonometry, the magnitude of a cross product like this can be obtained from the magnitude of each vector ($\boldsymbol{\omega}$ and $\boldsymbol{v}$) times the sin of the angle between them.

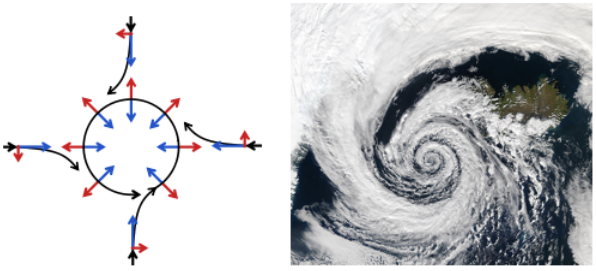
Thus, the magnitude of $a_c = \boldsymbol{\omega}\ \boldsymbol{v}\ \sin\Delta$ where **bold** indicates magnitude and Δ is the solid angle between the vectors. For a three-dimensional body, this angle is a solid angle, and we can use the formulas developed from plate tectonics and spherical trigonometry to determine the solid angle. But fortunately, we don't need to use these, because the rotation axis corresponds to Earth's north pole, thus, we can just use the latitude.

If you want more background and examples, I can recommend the Wikipedia page(link is external) which is very well done.

I can also recommend: Coriolis explained(link is external)

The left panel of the figure below is is an excellent summary of how the Coriolis effect (red arrows) combines with pressure driven wind (blue arrows) to produce the anticlockwise rotation (black arrows) around a low pressure system in the Northern Hemisphere What is the wind pattern, and sense of rotation, around a low pressure system in the Southern Hemisphere?

The right panel is a wonderful image of the wind pattern around a Low Pressure system over Iceland. Note the counterclockwise nature of the coiling pattern of the clouds. Does this look familiar from images that you've seen for hurricanes?



Sources: Left panel: Wikipedia(link is external) Right panel: NASA(link is external)

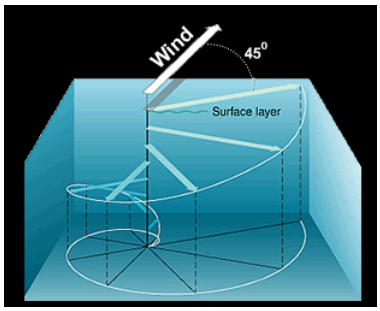
Reading

Read the link below.

- Coriolis Effect.(link is external) Thinking about Hadley circulation (and the image above), why does a north wind (i.e., a wind from the north) in the Northern hemisphere, such as in a Hadley Cell, blow toward the southwest?

Ekman Transport Water in the ocean can be divided roughly into three regions based on density: surface water, the pycnocline, and deep water. The pycnocline (also called the thermocline or halocline: recall that seawater density (pycno) is determined by temperature (thermo) and salinity (halo). Winds drive surface currents in the ocean, and these currents are effected by the Coriolis effect. But surface flow causes motion in the water below, so things get a bit more complicated. The physical properties of Surface Waters vary smoothly from the ocean surface to the pycnocline, but for the purposes of this discussion, it's useful to imagine that

the surface zone is composed of several layers of water. The top-most layer is driven by wind. Motion in this layer drives flow in the layer below, and so on, such that wind driven motion at the top, ultimately, drives flow in all of the layers below. Now here's the complication: each one of our 'layers' is influenced by the Coriolis effect. This sets up a spiral, with motion in each successively deeper layer bent somewhat to the right (in the Northern Hemisphere) relative to the forcing from above.



Sources: NOAA

Read more about Ekman Transport here

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57.1.6: Ocean Circulation: Surface Water and Deep Water

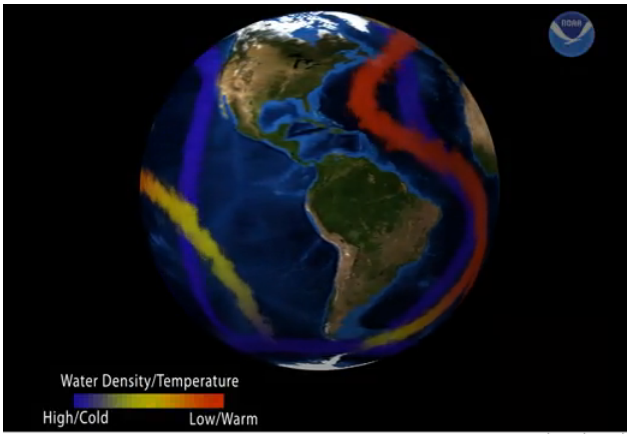
Global ocean currents and thermohaline circulation

Reading assignment

Read the link below.

- Broecker, GSA today(link is external) What If the Conveyor Were to Shut Down? Reflections on a Possible Outcome of the Great Global Experiment

Recall from Lesson 3 that water density increases with increasing salinity and decreasing temperature. Water density varies throughout the ocean and the water at the bottom of the ocean is densest, of course. Ocean-atmosphere interactions have important implications for global ocean currents. For example, think about what would happen if a large scale surface current continually lost heat. The colder it got the denser the water would be, and eventually that water would become dense enough to sink, and become deep water. Now lets add in evaporation. Imagine that water was continually evaporated from our surface current. This would make it saltier, which would increase the density. Eventually, the density would increase enough for the water to sink and become deep water.



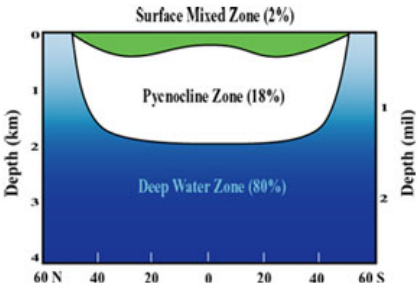
Source: NOAA

This is exactly what happens in the North Atlantic. But, if deep water forms in one place, then surface water has to form somewhere else; we can't push water into the deep ocean without something coming back to the surface, and in fact, surface water forms in various places in the ocean.

Look at the image above, and then back at the figure at the top of page 1 of this lesson. On page 1, the arrows are red for surface currents and blue for deep currents. The colors are a bit hard for me to see, but note that in the North Atlantic, a surface current flows north and a deep current flows south. This means that deep water forms in the North Atlantic.

It's important to appreciate that any Figure drawn at this scale, the entire ocean, is approximate. Don't take everything you see in these figures as the gospel. For a different perspective, have a look at this animation.(link is external)

The figure below shows the general structure of water masses as a function of depth in the ocean.



Source: Office of Naval Research(link is external)

Activity 2

Why does surface water sink in the North Atlantic? Let's calculate the density differences between surface waters in the tropics vs. where deep water forms in the north.

Go to the **Windows to the Universe**(link is external) is web site and read the information there (under: Density of Ocean Water)

Then click on the links in the second paragraph for ("the temperature(link is external) of the water and the salinity of the water(link is external)....")

Use those images to determine Temperature and Salinity in the North Atlantic off the coast of Florida and off the coast of Ireland.

For temperature, you'll need to click on the link for "Sea Surface Temperature Image(link is external)," which is under the heading "Related Links." If you have trouble finding it, click here(link is external)

For salinity, you can just click on "the salinity of the water" and then on the map at the top of the page.

The colors are a bit tricky to distinguish, but do your best and report the values you chose.

- Calculate the density of the water masses off the coast of Florida and off the coast of Ireland. Make sure to record your values for temperature and salinity. You can use the Ocean Water Density Calculator(link is external) for the density calculation
- Comment. Is this about what you expected? How are water densities normally determined in the ocean?

Submitting your work

Please put your answers in a file and drop that in the dropbox for Lesson 4, Activity 2 on Canvas.

Save your document as either a Microsoft Word or PDF file in the following format:
L4_Activity2_AccessAccountID_LastName.doc (or .pages or .pdf)
For example, student Elvis Aaron Presley's file would be named "L4_Activity2_eap1_presley.doc".

Grading criteria

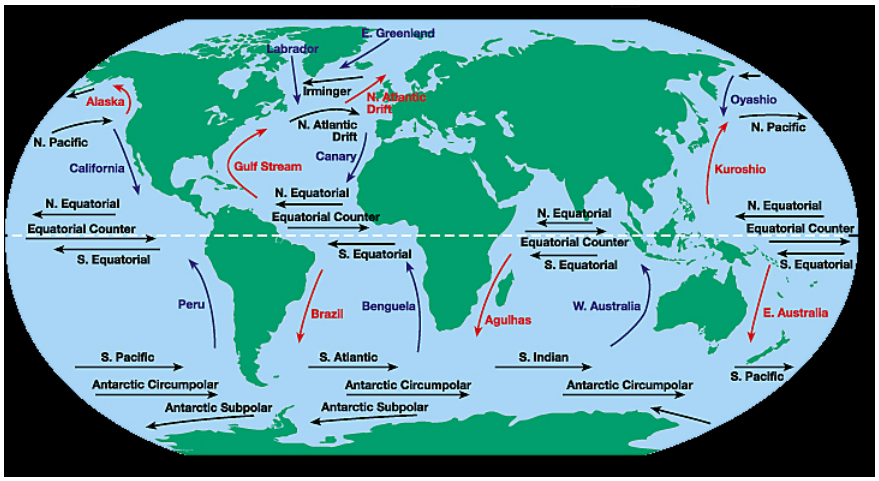
See the grading rubric for specifics on how this assignment will be graded.

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57.1.7: Gyres and Surface Currents

The global pattern of winds together with the Coriolis Effect and Ekman Transport produce large-scale currents in the world ocean. Ocean surface currents organize into Gyres that are characterized by circulation at the scale of the ocean basin. The figure below shows the basic pattern. Note that gyres circulate clockwise in the northern Hemisphere and counter-clockwise in the Southern Hemisphere.



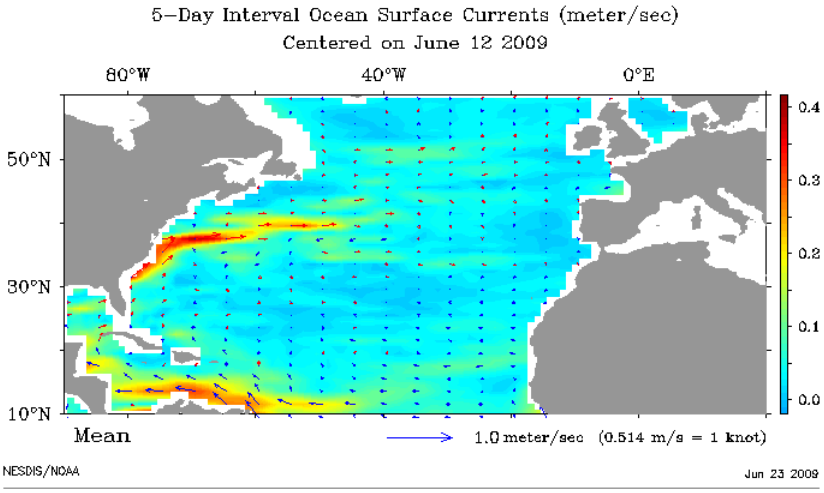
Source: UCAR

The influence of the Coriolis effect on ocean currents increases with increasing latitude, so the equatorial currents are similar in each ocean basin, although their flow direction (east to west) is consistent with the sense of flow in the large-scale gyres within each ocean basin. But the variation of Coriolis forcing as a function of latitude has a pronounced affect on surface currents. The poleward currents on the Western side of each ocean basin are distinctly different from those on the Eastern side of the ocean basin.

Western Boundary Currents are swift, narrow and deep relative to Eastern Boundary Currents, which are slower, broader and shallower than WBC's. Western Boundary Currents tend to carry heat from the equator poleward, so think back to where we started in this Lesson; everything is driven by differential solar heating. The excess heat received in the equatorial regions drives everything, including the strong Western Boundary Currents such as the familiar Gulf Stream and the East Australian Current (from *Finding Nemo fame*).

The figure below shows surface current information for the North Atlantic. The color scale is flow velocity in m/s, and the arrow along the bottom shows a 1 m/s scale bar (vector). Note the narrowness of the Gulf Stream.

Look here for more info on the Gulf Stream.(link is external)



Source: NOAA

Activity 3

Let's make our own maps and use them to calculate some things about heat transport. For this activity we will use ESR (Earth and Space Research) out of Seattle, WA. They have great research projects like OSCAR (Ocean Surface Current Analyses Real-Time) which suites our purposes nicely. Let's visit them HERE(link is external). There's some good background information about OSCAR there, but we will be using the link "OSCAR on SOTO", with SOTO standing for "State of the Ocean". Once you click on "OSCAR on SOTO", you will open up a really cool interactive map. I encourage you to play around with it for a bit to see what kind of data it is capable of conveying (we could have used this for our density calculations for Activity 2!) Once you're done playing, check out "Ocean Current Speed", but then settle on "Ocean Current Vectors".

->Note: This web site is mostly gone. Some of it is available here: https://www.esr.org/research/oscar/overview/(link is external)

1. Make and save (using "Grab" on a Mac or another print-screen application) a few maps of surface currents where you look at seasonal variations as well as flow directions and the basic pattern of ocean-basin scale gyres.
2. Choose your favorite map and tell me why you chose it in a few sentences. What did you learn from it? Put your map in a file, along with your comments.
3. And now for a couple of calculations.

- Calculate an estimate of the volume of water that flowed poleward in the Gulf Stream during all of June 2016.
- Calculate an estimate of how much heat was transported by the Gulf Stream in June 2016 (You can choose to estimate sensible heat and/or latent heat)

There are multiple ways one can do these, just make sure I can follow your train of thought through each/both. Your calculations should:

- *incorporate the max velocity of the Gulf Stream from June 2016*
- *assume that the depth of the current is 1 km*
- *estimate the width of the Gulf Stream from your map*
- *use OSCAR to find temperature estimates*

Submitting your work

Please put your answers in a file and drop that in the dropbox for Activity 3 on Canvas.

Save your document as either a Microsoft Word or PDF file in the following format:
L4_Activity3_AccessAccountID_LastName.doc (or .pages or .pdf)
For example, student Elvis Aaron Presley's file would be named "L4_Activity3_eap1_presley.doc".

Grading criteria

See the grading rubric for specifics on how this assignment will be graded.

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57.2: Earth's Biomes

Skills to Develop

- Identify the two major abiotic factors that determine terrestrial biomes
- Recognize distinguishing characteristics of each of the eight major terrestrial biomes

The Earth's biomes are categorized into two major groups: terrestrial and aquatic. Terrestrial biomes are based on land, while aquatic biomes include both ocean and freshwater biomes. The eight major terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation. Comparing the annual totals of precipitation and fluctuations in precipitation from one biome to another provides clues as to the importance of abiotic factors in the distribution of biomes. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of the biome and the vegetation type in the biome. The distribution of these biomes shows that the same biome can occur in geographically distinct areas with similar climates (Figure **57.2.1**).

Art Connection

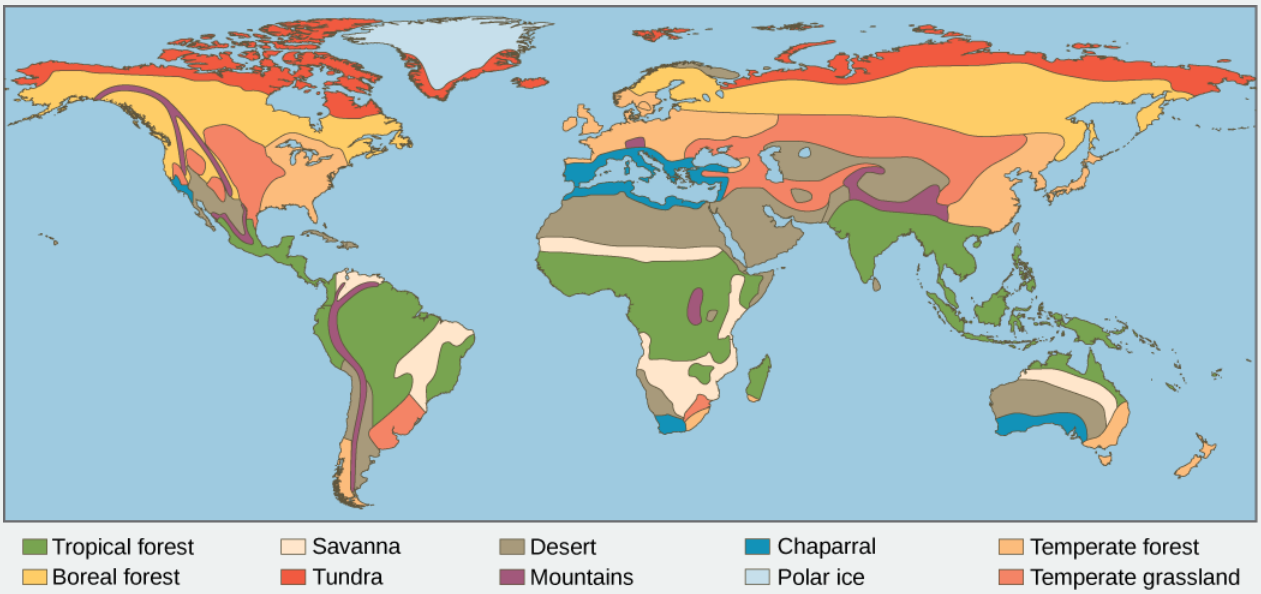


Figure **57.2.1**: Each of the world's major biomes is distinguished by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown.

Which of the following statements about biomes is false?

A. Chaparral is dominated by shrubs.
B. Savannas and temperate grasslands are dominated by grasses.
C. Boreal forests are dominated by deciduous trees.
D. Lichens are common in the arctic tundra.

Tropical Wet Forest

Tropical wet forests are also referred to as tropical rainforests. This biome is found in equatorial regions (Figure **57.2.1**). The vegetation is characterized by plants with broad leaves that fall off throughout the year. Unlike the trees of deciduous forests, the trees in this biome do not have a seasonal loss of leaves associated with variations in temperature and sunlight; these forests are "evergreen" year-round.

The temperature and sunlight profiles of tropical wet forests are very stable in comparison to that of other terrestrial biomes, with the temperatures ranging from 20 °C to 34 °C (68 °F to 93 °F). When one compares the annual temperature variation of tropical wet forests with that of other forest biomes, the lack of seasonal temperature variation in the tropical wet forest becomes apparent.

This lack of seasonality leads to year-round plant growth, rather than the seasonal (spring, summer, and fall) growth seen in other biomes. In contrast to other ecosystems, tropical ecosystems do not have long days and short days during the yearly cycle. Instead, a constant daily amount of sunlight (11–12 hrs per day) provides more solar radiation, thereby, a longer period of time for plant growth.

The annual rainfall in tropical wet forests ranges from 125 to 660 cm (50–200 in) with some monthly variation. While sunlight and temperature remain fairly consistent, annual rainfall is highly variable. Tropical wet forests have wet months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm (3.5 in) of rainfall. However, the driest month of a tropical wet forest still exceeds the *annual* rainfall of some other biomes, such as deserts.

Tropical wet forests have high net primary productivity because the annual temperatures and precipitation values in these areas are ideal for plant growth. Therefore, the extensive biomass present in the tropical wet forest leads to plant communities with very high species diversities (Figure **57.2.2**). Tropical wet forests have more species of trees than any other biome; on average between 100 and 300 species of trees are present in a single hectare (2.5 acres) of South America. One way to visualize this is to compare the distinctive horizontal layers within the tropical wet forest biome. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short shrubby foliage. A layer of trees rises above this understory and is topped by a closed upper canopy—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, fungi, animals, and other organisms within the tropical wet forests. For instance, epiphytes are plants that grow on other plants, which typically are not harmed. Epiphytes are found throughout tropical wet forest biomes. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground and have adapted to this arboreal lifestyle.



Figure **57.2.2**: Tropical wet forests, such as these forests of Madre de Dios, Peru, near the Amazon River, have high species diversity. (credit: Roosevelt Garcia)

Savannas

Savannas are grasslands with scattered trees, and they are located in Africa, South America, and northern Australia (Figure **57.2.3**). Savannas are hot, tropical areas with temperatures averaging from 24 °C to 29 °C (75 °F to 84 °F) and an annual rainfall of 10–40 cm (3.9–15.7 in). Savannas have an extensive dry season; for this reason, forest trees do not grow as well as they do in the tropical wet forest (or other forest biomes). As a result, within the grasses and forbs (herbaceous flowering plants) that dominate the savanna, there are relatively few trees (Figure **57.2.3**). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly re-sprout after a fire.



Figure 57.2.3: Savannas, like this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses. (credit: Christopher T. Cooper)

Subtropical Deserts

Subtropical deserts exist between 15 ° and 30 ° north and south latitude and are centered on the Tropics of Cancer and Capricorn (Figure 57.2.4). This biome is very dry; in some years, evaporation exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60 °C (140 °F) and nighttime temperatures approaching 0 °C (32 °F). In cold deserts, temperatures can be as high as 25 °C and can drop below -30 °C (-22 °F). Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in) with little monthly variation and lack of predictability in rainfall. In some cases, the annual rainfall can be as low as 2 cm (0.8 in) in subtropical deserts located in central Australia (“the Outback”) and northern Africa.

The vegetation and low animal diversity of this biome is closely related to this low and unpredictable precipitation. Very dry deserts lack perennial vegetation that lives from one year to the next; instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, then they die. Many other plants in these areas are characterized by having a number of adaptations that conserve water, such as deep roots, reduced foliage, and water-storing stems (Figure 57.2.4). Seed plants in the desert produce seeds that can be in dormancy for extended periods between rains. Adaptations in desert animals include nocturnal behavior and burrowing.



Figure **57.2.4**: To reduce water loss, many desert plants have tiny leaves or no leaves at all. The leaves of ocotillo (*Fouquieria splendens*), shown here in the Sonora Desert near Gila Bend, Arizona, appear only after rainfall, and then are shed.

Chaparral

The chaparral is also called the scrub forest and is found in California, along the Mediterranean Sea, and along the southern coast of Australia (Figure **57.2.5**). The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in), and the majority of the rain falls in the winter. Summers are very dry and many chaparral plants are dormant during the summertime. The chaparral vegetation, shown in Figure **57.2.5**, is dominated by shrubs and is adapted to periodic fires, with some plants producing seeds that only germinate after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote plant regrowth.



Figure 57.2.5: The chaparral is dominated by shrubs. (credit: Miguel Vieira)

Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as prairies; they are also in Eurasia, where they are known as steppes (Figure 57.2.6). Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth and when ample water is available, which occurs in the spring, summer, and fall. During much of the winter, temperatures are low, and water, which is stored in the form of ice, is not available for plant growth.

Annual precipitation ranges from 25 cm to 75 cm (9.8–29.5 in). Because of relatively lower annual precipitation in temperate grasslands, there are few trees except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses and some prairies sustain populations of grazing animals Figure 57.2.6. The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and rhizomes (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay.



Figure **57.2.6**: The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. (credit: Jack Dykinga, USDA Agricultural Research Service)

Fires, mainly caused by lightning, are a natural disturbance in temperate grasslands. When fire is suppressed in temperate grasslands, the vegetation eventually converts to scrub and dense forests. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.

Temperate Forests

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand (Figure **57.2.7**). This biome is found throughout mid-latitude regions. Temperatures range between -30 °C and 30 °C (-22 °F to 86 °F) and drop to below freezing on an annual basis. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm (29.5–59 in).

Because of the moderate annual rainfall and temperatures, deciduous trees are the dominant plant in this biome (Figure **57.2.7**). Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, no photosynthesis occurs in the deciduous trees during the dormant winter period. Each spring, new leaves appear as the temperature increases. Because of the dormant period, the net primary productivity of temperate forests is less than that of tropical wet forests. In addition, temperate forests show less diversity of tree species than tropical wet forest biomes.



Figure 57.2.7: Deciduous trees are the dominant plant in the temperate forest. (credit: Oliver Herold)

The trees of the temperate forests leaf out and shade much of the ground; however, this biome is more open than tropical wet forests because trees in the temperate forests do not grow as tall as the trees in tropical wet forests. The soils of the temperate forests are rich in inorganic and organic nutrients. This is due to the thick layer of leaf litter on forest floors. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, such as the red-backed salamander (*Plethodon cinereus*).

Boreal Forests

The boreal forest, also known as taiga or coniferous forest, is found south of the Arctic Circle and across most of Canada, Alaska, Russia, and northern Europe (Figure 57.2.8). This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm (15.7–39 in) and usually takes the form of snow. Little evaporation occurs because of the cold temperatures.

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the sun is required to warm a needle-like leaf than a broad leaf. This benefits evergreen trees, which grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles may have a competitive advantage over the broad-leafed deciduous trees.

The net primary productivity of boreal forests is lower than that of temperate forests and tropical wet forests. The aboveground biomass of boreal forests is high because these slow-growing tree species are long lived and accumulate standing biomass over time. Plant species diversity is less than that seen in temperate forests and tropical wet forests. Boreal forests lack the pronounced elements of the layered forest structure seen in tropical wet forests. The structure of a boreal forest is often only a tree layer and a ground layer (Figure 57.2.8). When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth.



Figure **57.2.8**: The boreal forest (taiga) has low lying plants and conifer trees. (credit: L.B. Brubaker)

Arctic Tundra

The Arctic tundra lies north of the subarctic boreal forest and is located throughout the Arctic regions of the northern hemisphere (Figure **57.2.9**). The average winter temperature is -34 °C (-34 °F) and the average summer temperature is from 3 °C to 12 °C (37 °F–52 °F). Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks. However, during this time, there are almost 24 hours of daylight and plant growth is rapid. The annual precipitation of the Arctic tundra is very low with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation due to the cold temperatures.

Plants in the Arctic tundra are generally low to the ground (Figure **57.2.9**). There is little species diversity, low net primary productivity, and low aboveground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as permafrost. The permafrost makes it impossible for roots to penetrate deep into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.



Figure **57.2.9:** Low-growing plants such as shrub willow dominate the tundra landscape, shown here in the Arctic National Wildlife Refuge. (credit: USFWS Arctic National Wildlife Refuge)

Link to Learning



Watch this *Assignment Discovery: Biomes* video for an overview of biomes. To explore further, select one of the biomes on the extended playlist: desert, savanna, temperate forest, temperate grassland, tropic, tundra.

Summary

The Earth has terrestrial biomes and aquatic biomes. Aquatic biomes include both freshwater and marine environments. There are eight major terrestrial biomes: tropical wet forests, savannas, subtropical deserts, chaparral, temperate grasslands, temperate forests, boreal forests, and Arctic tundra. The same biome can occur in different geographic locations with similar climates. Temperature and precipitation, and variations in both, are key abiotic factors that shape the composition of animal and plant communities in terrestrial biomes. Some biomes, such as temperate grasslands and temperate forests, have distinct seasons, with cold weather and hot weather alternating throughout the year. In warm, moist biomes, such as the tropical wet forest, net primary productivity is high, as warm temperatures, abundant water, and a year-round growing season fuel plant growth. Other biomes, such as deserts and tundra, have low primary productivity due to extreme temperatures and a shortage of available water.

Art Connections

Figure **57.2.1**: Which of the following statements about biomes is false?

A. Chaparral is dominated by shrubs.
B. Savannas and temperate grasslands are dominated by grasses.
C. Boreal forests are dominated by deciduous trees.
D. Lichens are common in the arctic tundra.

Answer

C. Boreal forests are not dominated by deciduous trees.

Glossary

canopy
branches and foliage of trees that form a layer of overhead coverage in a forest

permafrost
perennially frozen portion of the Arctic tundra soil

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SECTION OVERVIEW

57.3: Freshwater Habitats

57.3.1: Aquatic Biomes

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57.3.1: Aquatic Biomes

Skills to Develop

- Describe the effects of abiotic factors on the composition of plant and animal communities in aquatic biomes
- Compare and contrast the characteristics of the ocean zones
- Summarize the characteristics of standing water and flowing water freshwater biomes

Abiotic Factors Influencing Aquatic Biomes

Like terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. The aquatic medium—water— has different physical and chemical properties than air, however. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (like fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems. In freshwater systems, stratification due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

The ocean is categorized by several areas or zones (Figure 57.3.1.1). All of the ocean's open water is referred to as the pelagic realm (or zone). The benthic realm (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the photic zone, which is the portion of the ocean that light can penetrate (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the aphotic zone. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep. These realms and zones are relevant to freshwater lakes as well.

Art Connection

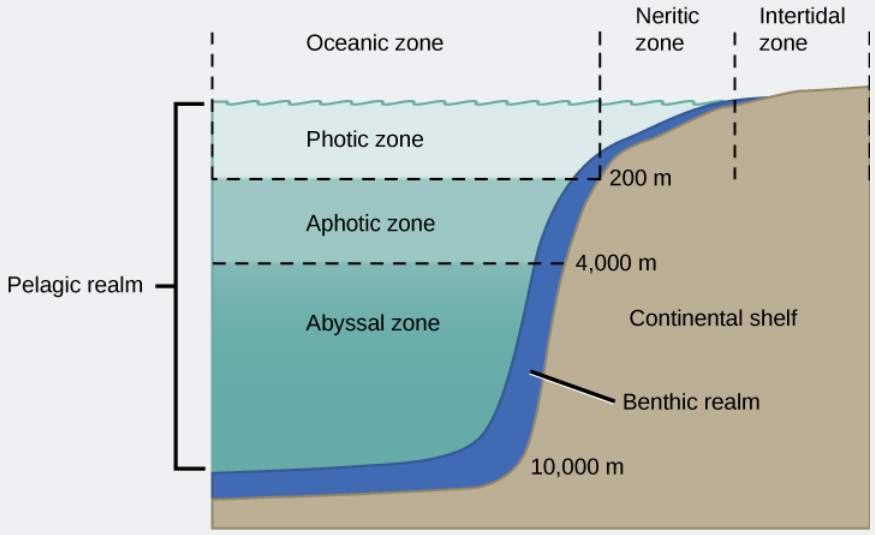


Figure 57.3.1.1: The ocean is divided into different zones based on water depth and distance from the shoreline.

In which of the following regions would you expect to find photosynthetic organisms?

A. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
B. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
C. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone

D. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

Marine Biomes

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome. Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

Ocean

The physical diversity of the ocean is a significant influence on plants, animals, and other organisms. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

The intertidal zone, which is the zone between high and low tide, is the oceanic region that is closest to land (Figure **57.3.1.1**). Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy beach, but it can also be rocky or muddy. The intertidal zone is an extremely variable environment because of tides. Organisms are exposed to air and sunlight at low tide and are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. The shore of the intertidal zone is also repeatedly struck by waves, and the organisms found there are adapted to withstand damage from the pounding action of the waves (Figure **57.3.1.2**). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from desiccation (drying out) and wave damage. Another consequence of the pounding waves is that few algae and plants establish themselves in the constantly moving rocks, sand, or mud.



Figure **57.3.1.2**: Sea urchins, mussel shells, and starfish are often found in the intertidal zone, shown here in Kachemak Bay, Alaska. (credit: NOAA)

The neritic zone (Figure **57.3.1.1**) extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the continental shelf. Since light can penetrate this depth, photosynthesis can occur in the neritic zone. The water here contains silt and is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating *Sargassum* (a type of free-floating marine seaweed) provide a habitat for some sea life found in the neritic zone. Zooplankton, protists, small fishes, and shrimp are found in the neritic zone and are the base of the food chain for most of the world's fisheries.

Beyond the neritic zone is the open ocean area known as the oceanic zone (Figure **57.3.1.1**). Within the oceanic zone there is thermal stratification where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals such as whales and dolphins. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean where they remain; unlike freshwater lakes, the open ocean lacks a process for bringing the organic nutrients back up to the surface. The majority of organisms in the aphotic zone include sea cucumbers (phylum Echinodermata) and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

Beneath the pelagic zone is the benthic realm, the deepwater region beyond the continental shelf (Figure 57.3.1.1). The bottom of the benthic realm is comprised of sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. This is a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exist.

The deepest part of the ocean is the abyssal zone, which is at depths of 4000 m or greater. The abyssal zone (Figure 57.3.1.1) is very cold and has very high pressure, high oxygen content, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants because of the lack of light. Hydrothermal vents are found primarily in the abyssal zone; chemosynthetic bacteria utilize the hydrogen sulfide and other minerals emitted from the vents. These chemosynthetic bacteria use the hydrogen sulfide as an energy source and serve as the base of the food chain found in the abyssal zone.

Coral Reefs

Coral reefs are ocean ridges formed by marine invertebrates living in warm shallow waters within the photic zone of the ocean. They are found within 30˚ north and south of the equator. The Great Barrier Reef is a well-known reef system located several miles off the northeastern coast of Australia. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms (members of phylum Cnidaria) are colonies of saltwater polyps that secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, forming the underwater reef (Figure 57.3.1.3). Corals found in shallower waters (at a depth of approximately 60 m or about 200 ft) have a mutualistic relationship with photosynthetic unicellular algae. The relationship provides corals with the majority of the nutrition and the energy they require. The waters in which these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow. Some corals living in deeper and colder water do not have a mutualistic relationship with algae; these corals attain energy and nutrients using stinging cells on their tentacles to capture prey.

It is estimated that more than 4,000 fish species inhabit coral reefs. These fishes can feed on coral, the cryptofauna (invertebrates found within the calcium carbonate substrate of the coral reefs), or the seaweed and algae that are associated with the coral. In addition, some fish species inhabit the boundaries of a coral reef; these species include predators, herbivores, or planktivores. Predators are animal species that hunt and are carnivores or “flesh eaters.” Herbivores eat plant material, and planktivores eat plankton.



Figure **57.3.1.3**: Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria. (credit: Terry Hughes)

Evolution Connection: Global Decline of Coral Reefs

It takes a long time to build a coral reef. The animals that create coral reefs have evolved over millions of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic algal partners evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. As global warming due to fossil fuel emissions raises ocean temperatures, coral reefs are suffering. The excessive warmth causes the reefs to expel their symbiotic, food-producing algae, resulting in a phenomenon known as bleaching. When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged.

Rising levels of atmospheric carbon dioxide further threaten the corals in other ways; as CO_2 dissolves in ocean waters, it lowers the pH and increases ocean acidity. As acidity increases, it interferes with the calcification that normally occurs as coral animals build their calcium carbonate homes.

When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.

Human population growth has damaged corals in other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased, too, causing some of the once-clear tropical waters to become cloudy. At the same time, overfishing of popular fish species has allowed the predator species that eat corals to go unchecked.

Although a rise in global temperatures of 1–2˚C (a conservative scientific projection) in the coming decades may not seem large, it is very significant to this biome. When change occurs rapidly, species can become extinct before evolution leads to

new adaptations. Many scientists believe that global warming, with its rapid (in terms of evolutionary time) and inexorable increases in temperature, is tipping the balance beyond the point at which many of the world's coral reefs can recover.

Estuaries: Where the Ocean Meets Fresh Water

Estuaries are biomes that occur where a source of fresh water, such as a river, meets the ocean. Therefore, both fresh water and salt water are found in the same vicinity; mixing results in a diluted (brackish) saltwater. Estuaries form protected areas where many of the young offspring of crustaceans, mollusks, and fish begin their lives. Salinity is a very important factor that influences the organisms and the adaptations of the organisms found in estuaries. The salinity of estuaries varies and is based on the rate of flow of its freshwater sources. Once or twice a day, high tides bring salt water into the estuary. Low tides occurring at the same frequency reverse the current of salt water.

The short-term and rapid variation in salinity due to the mixing of fresh water and salt water is a difficult physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are halophytes: plants that can tolerate salty conditions. Halophytic plants are adapted to deal with the salinity resulting from saltwater on their roots or from sea spray. In some halophytes, filters in the roots remove the salt from the water that the plant absorbs. Other plants are able to pump oxygen into their roots. Animals, such as mussels and clams (phylum Mollusca), have developed behavioral adaptations that expend a lot of energy to function in this rapidly changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills) to anaerobic respiration (a process that does not require oxygen). When high tide returns to the estuary, the salinity and oxygen content of the water increases, and these animals open their shells, begin feeding, and return to aerobic respiration.

Freshwater Biomes

Freshwater biomes include lakes and ponds (standing water) as well as rivers and streams (flowing water). They also include wetlands, which will be discussed later. Humans rely on freshwater biomes to provide aquatic resources for drinking water, crop irrigation, sanitation, and industry. These various roles and human benefits are referred to as ecosystem services. Lakes and ponds are found in terrestrial landscapes and are, therefore, connected with abiotic and biotic factors influencing these terrestrial biomes.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. In the summer, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun and does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton (algae and cyanobacteria) are found here and carry out photosynthesis, providing the base of the food web of lakes and ponds. Zooplankton, such as rotifers and small crustaceans, consume these phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and phosphorus are important limiting nutrients in lakes and ponds. Because of this, they are determining factors in the amount of phytoplankton growth in lakes and ponds. When there is a large input of nitrogen and phosphorus (from sewage and runoff from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation of algae called an algal bloom. Algal blooms (Figure **57.3.1.4**) can become so extensive that they reduce light penetration in water. As a result, the lake or pond becomes aphotic and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die, and resulting dead zones are found across the globe. Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and storm water runoff pose significant environmental challenges.



Figure **57.3.1.4**: The uncontrolled growth of algae in this lake has resulted in an algal bloom. (credit: Jeremy Nettleton)

Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or headwater, to a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mississippi River in North America.

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as source water. The source water is usually cold, low in nutrients, and clear. The channel (the width of the river or stream) is narrower than at any other place along the length of the river or stream. Because of this, the current is often faster here than at any other point of the river or stream.

The fast-moving water results in minimal silt accumulation at the bottom of the river or stream; therefore, the water is clear. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton. An additional input of energy can come from leaves or other organic material that falls into the river or stream from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, leeches (phylum Annelida) have elongated bodies and suckers on both ends. These suckers attach to the substrate, keeping the leech anchored in place. Freshwater trout species (phylum Chordata) are an important predator in these fast-moving rivers and streams.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer. Worms (phylum Annelida) and insects (phylum Arthropoda) can be found burrowing into the mud. The higher order predator vertebrates (phylum Chordata) include waterfowl, frogs, and fishes. These predators must find food in these slow moving, sometimes murky, waters and, unlike the trout in the waters at the source, these vertebrates may not be able to use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes because wetlands are shallow bodies of water whereas lakes vary in depth. Emergent vegetation consists of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes (Figure **57.3.1.5**). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.



Figure 57.3.1.5: Located in southern Florida, Everglades National Park is a vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. (credit: NPS)

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation. Percolation is the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen depleted because the oxygen that is used during the decomposition of organic matter is not replaced. As the oxygen in the water is depleted, decomposition slows. This leads to organic acids and other acids building up and lowering the pH of the water. At a lower pH, nitrogen becomes unavailable to plants. This creates a challenge for plants because nitrogen is an important limiting resource. Some types of bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects and extract the nitrogen from their bodies. Bogs have low net primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

Summary

Aquatic ecosystems include both saltwater and freshwater biomes. The abiotic factors important for the structuring of aquatic ecosystems can be different than those seen in terrestrial systems. Sunlight is a driving force behind the structure of forests and also is an important factor in bodies of water, especially those that are very deep, because of the role of photosynthesis in sustaining certain organisms. Density and temperature shape the structure of aquatic systems. Oceans may be thought of as consisting of different zones based on water depth and distance from the shoreline and light penetrance. Different kinds of organisms are adapted to the conditions found in each zone. Coral reefs are unique marine ecosystems that are home to a wide variety of species. Estuaries are found where rivers meet the ocean; their shallow waters provide nourishment and shelter for young crustaceans, mollusks, fishes, and many other species. Freshwater biomes include lakes, ponds, rivers, streams, and wetlands. Bogs are an interesting type of wetland characterized by standing water, lower pH, and a lack of nitrogen.

Art Connections

Figure 57.3.1.1: In which of the following regions would you expect to find photosynthetic organisms?

A. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
B. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
C. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone
D. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

Answer

C. Photosynthetic organisms would be found in the photic, abyssal, neritic, and oceanic zones.

Glossary

abyssal zone
deepest part of the ocean at depths of 4000 m or greater

algal bloom
rapid increase of algae in an aquatic system

aphotic zone
part of the ocean where no light penetrates

benthic realm
(also, benthic zone) part of the ocean that extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor

channel
width of a river or stream from one bank to the other bank

coral reef
ocean ridges formed by marine invertebrates living in warm, shallow waters within the photic zone

cryptofauna
invertebrates found within the calcium carbonate substrate of coral reefs

ecosystem services
human benefits and services provided by natural ecosystems

emergent vegetation
wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface

estuary
biomes where a source of fresh water, such as a river, meets the ocean

intertidal zone
part of the ocean that is closest to land; parts extend above the water at low tide

neritic zone
part of the ocean that extends from low tide to the edge of the continental shelf

oceanic zone
part of the ocean that begins offshore where the water measures 200 m deep or deeper

pelagic realm
(also, pelagic zone) open ocean waters that are not close to the bottom or near the shore

photic zone
portion of the ocean that light can penetrate

planktivore
animal species that eats plankton

predator

animal species that hunt and are carnivores or “flesh eaters”

Sargassum
type of free-floating marine seaweed

source water
point of origin of a river or stream

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57.4: Marine Habitats

Skills to Develop

- Describe the effects of abiotic factors on the composition of plant and animal communities in aquatic biomes
- Compare and contrast the characteristics of the ocean zones
- Summarize the characteristics of standing water and flowing water freshwater biomes

Abiotic Factors Influencing Aquatic Biomes

Like terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. The aquatic medium—water— has different physical and chemical properties than air, however. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (like fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems. In freshwater systems, stratification due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

The ocean is categorized by several areas or zones (Figure 57.4.1). All of the ocean's open water is referred to as the pelagic realm (or zone). The benthic realm (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the photic zone, which is the portion of the ocean that light can penetrate (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the aphotic zone. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep. These realms and zones are relevant to freshwater lakes as well.

Art Connection

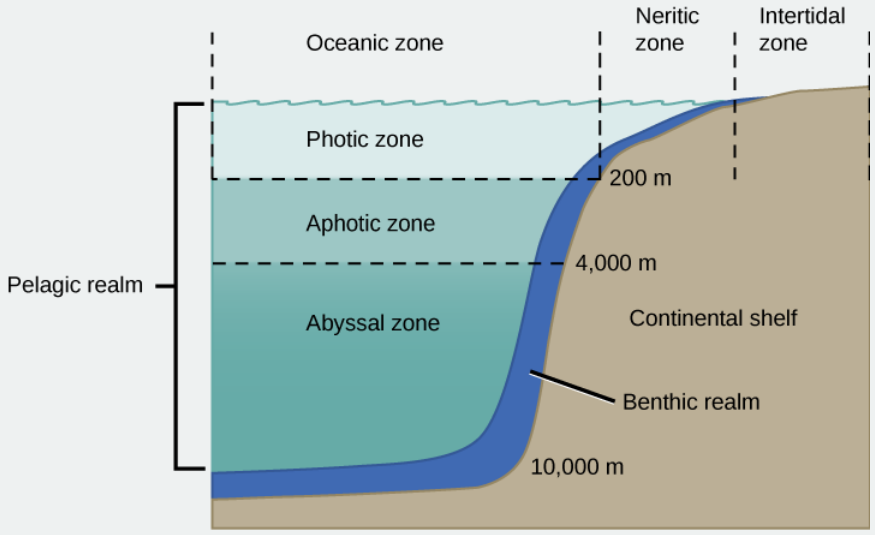


Figure 57.4.1: The ocean is divided into different zones based on water depth and distance from the shoreline.

In which of the following regions would you expect to find photosynthetic organisms?

A. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
B. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
C. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone

D. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

Marine Biomes

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome. Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

Ocean

The physical diversity of the ocean is a significant influence on plants, animals, and other organisms. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

The intertidal zone, which is the zone between high and low tide, is the oceanic region that is closest to land (Figure 57.4.1). Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy beach, but it can also be rocky or muddy. The intertidal zone is an extremely variable environment because of tides. Organisms are exposed to air and sunlight at low tide and are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. The shore of the intertidal zone is also repeatedly struck by waves, and the organisms found there are adapted to withstand damage from the pounding action of the waves (Figure 57.4.2). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from desiccation (drying out) and wave damage. Another consequence of the pounding waves is that few algae and plants establish themselves in the constantly moving rocks, sand, or mud.



Figure 57.4.2: Sea urchins, mussel shells, and starfish are often found in the intertidal zone, shown here in Kachemak Bay, Alaska. (credit: NOAA)

The neritic zone (Figure 57.4.1) extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the continental shelf. Since light can penetrate this depth, photosynthesis can occur in the neritic zone. The water here contains silt and is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating *Sargassum* (a type of free-floating marine seaweed) provide a habitat for some sea life found in the neritic zone. Zooplankton, protists, small fishes, and shrimp are found in the neritic zone and are the base of the food chain for most of the world's fisheries.

Beyond the neritic zone is the open ocean area known as the oceanic zone (Figure 57.4.1). Within the oceanic zone there is thermal stratification where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals such as whales and dolphins. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean where they remain; unlike freshwater lakes, the open ocean lacks a process for bringing the organic nutrients back up to the surface. The majority of organisms in the aphotic zone include sea cucumbers (phylum Echinodermata) and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

Beneath the pelagic zone is the benthic realm, the deepwater region beyond the continental shelf (Figure 57.4.1). The bottom of the benthic realm is comprised of sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. This is a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exist.

The deepest part of the ocean is the abyssal zone, which is at depths of 4000 m or greater. The abyssal zone (Figure 57.4.1) is very cold and has very high pressure, high oxygen content, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants because of the lack of light. Hydrothermal vents are found primarily in the abyssal zone; chemosynthetic bacteria utilize the hydrogen sulfide and other minerals emitted from the vents. These chemosynthetic bacteria use the hydrogen sulfide as an energy source and serve as the base of the food chain found in the abyssal zone.

Coral Reefs

Coral reefs are ocean ridges formed by marine invertebrates living in warm shallow waters within the photic zone of the ocean. They are found within 30˚ north and south of the equator. The Great Barrier Reef is a well-known reef system located several miles off the northeastern coast of Australia. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms (members of phylum Cnidaria) are colonies of saltwater polyps that secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, forming the underwater reef (Figure 57.4.3). Corals found in shallower waters (at a depth of approximately 60 m or about 200 ft) have a mutualistic relationship with photosynthetic unicellular algae. The relationship provides corals with the majority of the nutrition and the energy they require. The waters in which these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow. Some corals living in deeper and colder water do not have a mutualistic relationship with algae; these corals attain energy and nutrients using stinging cells on their tentacles to capture prey.

It is estimated that more than 4,000 fish species inhabit coral reefs. These fishes can feed on coral, the cryptofauna (invertebrates found within the calcium carbonate substrate of the coral reefs), or the seaweed and algae that are associated with the coral. In addition, some fish species inhabit the boundaries of a coral reef; these species include predators, herbivores, or planktivores. Predators are animal species that hunt and are carnivores or “flesh eaters.” Herbivores eat plant material, and planktivores eat plankton.



Figure **57.4.3**: Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria. (credit: Terry Hughes)

Evolution Connection: Global Decline of Coral Reefs

It takes a long time to build a coral reef. The animals that create coral reefs have evolved over millions of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic algal partners evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. As global warming due to fossil fuel emissions raises ocean temperatures, coral reefs are suffering. The excessive warmth causes the reefs to expel their symbiotic, food-producing algae, resulting in a phenomenon known as bleaching. When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged.

Rising levels of atmospheric carbon dioxide further threaten the corals in other ways; as CO_2 dissolves in ocean waters, it lowers the pH and increases ocean acidity. As acidity increases, it interferes with the calcification that normally occurs as coral animals build their calcium carbonate homes.

When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.

Human population growth has damaged corals in other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased, too, causing some of the once-clear tropical waters to become cloudy. At the same time, overfishing of popular fish species has allowed the predator species that eat corals to go unchecked.

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Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. In the summer, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun and does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton (algae and cyanobacteria) are found here and carry out photosynthesis, providing the base of the food web of lakes and ponds. Zooplankton, such as rotifers and small crustaceans, consume these phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and phosphorus are important limiting nutrients in lakes and ponds. Because of this, they are determining factors in the amount of phytoplankton growth in lakes and ponds. When there is a large input of nitrogen and phosphorus (from sewage and runoff from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation of algae called an algal bloom. Algal blooms (Figure **57.4.4**) can become so extensive that they reduce light penetration in water. As a result, the lake or pond becomes aphotic and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die, and resulting dead zones are found across the globe. Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and storm water runoff pose significant environmental challenges.



Figure **57.4.4**: The uncontrolled growth of algae in this lake has resulted in an algal bloom. (credit: Jeremy Nettleton)

Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or headwater, to a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mississippi River in North America.

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as source water. The source water is usually cold, low in nutrients, and clear. The channel (the width of the river or stream) is narrower than at any other place along the length of the river or stream. Because of this, the current is often faster here than at any other point of the river or stream.

The fast-moving water results in minimal silt accumulation at the bottom of the river or stream; therefore, the water is clear. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton. An additional input of energy can come from leaves or other organic material that falls into the river or stream from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, leeches (phylum Annelida) have elongated bodies and suckers on both ends. These suckers attach to the substrate, keeping the leech anchored in place. Freshwater trout species (phylum Chordata) are an important predator in these fast-moving rivers and streams.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer. Worms (phylum Annelida) and insects (phylum Arthropoda) can be found burrowing into the mud. The higher order predator vertebrates (phylum Chordata) include waterfowl, frogs, and fishes. These predators must find food in these slow moving, sometimes murky, waters and, unlike the trout in the waters at the source, these vertebrates may not be able to use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes because wetlands are shallow bodies of water whereas lakes vary in depth. Emergent vegetation consists of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes (Figure **57.4.5**). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.



Figure 57.4.5: Located in southern Florida, Everglades National Park is a vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. (credit: NPS)

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation. Percolation is the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen depleted because the oxygen that is used during the decomposition of organic matter is not replaced. As the oxygen in the water is depleted, decomposition slows. This leads to organic acids and other acids building up and lowering the pH of the water. At a lower pH, nitrogen becomes unavailable to plants. This creates a challenge for plants because nitrogen is an important limiting resource. Some types of bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects and extract the nitrogen from their bodies. Bogs have low net primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

Summary

Aquatic ecosystems include both saltwater and freshwater biomes. The abiotic factors important for the structuring of aquatic ecosystems can be different than those seen in terrestrial systems. Sunlight is a driving force behind the structure of forests and also is an important factor in bodies of water, especially those that are very deep, because of the role of photosynthesis in sustaining certain organisms. Density and temperature shape the structure of aquatic systems. Oceans may be thought of as consisting of different zones based on water depth and distance from the shoreline and light penetrance. Different kinds of organisms are adapted to the conditions found in each zone. Coral reefs are unique marine ecosystems that are home to a wide variety of species. Estuaries are found where rivers meet the ocean; their shallow waters provide nourishment and shelter for young crustaceans, mollusks, fishes, and many other species. Freshwater biomes include lakes, ponds, rivers, streams, and wetlands. Bogs are an interesting type of wetland characterized by standing water, lower pH, and a lack of nitrogen.

Art Connections

Figure 57.4.1: In which of the following regions would you expect to find photosynthetic organisms?

A. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
B. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
C. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone
D. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

Answer

C. Photosynthetic organisms would be found in the photic, abyssal, neritic, and oceanic zones.

Glossary

abyssal zone
deepest part of the ocean at depths of 4000 m or greater

algal bloom
rapid increase of algae in an aquatic system

aphotic zone
part of the ocean where no light penetrates

benthic realm
(also, benthic zone) part of the ocean that extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor

channel
width of a river or stream from one bank to the other bank

coral reef
ocean ridges formed by marine invertebrates living in warm, shallow waters within the photic zone

cryptofauna
invertebrates found within the calcium carbonate substrate of coral reefs

ecosystem services
human benefits and services provided by natural ecosystems

emergent vegetation
wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface

estuary
biomes where a source of fresh water, such as a river, meets the ocean

intertidal zone
part of the ocean that is closest to land; parts extend above the water at low tide

neritic zone
part of the ocean that extends from low tide to the edge of the continental shelf

oceanic zone
part of the ocean that begins offshore where the water measures 200 m deep or deeper

pelagic realm
(also, pelagic zone) open ocean waters that are not close to the bottom or near the shore

photic zone
portion of the ocean that light can penetrate

planktivore
animal species that eats plankton

predator

animal species that hunt and are carnivores or “flesh eaters”

Sargassum
type of free-floating marine seaweed

source water
point of origin of a river or stream

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57.5: Human Impacts of the Biosphere- Pollution and Resource Depletion

Skills to Develop

- Define global climate change
- Summarize the effects of the Industrial Revolution on global atmospheric carbon dioxide concentration
- Describe three natural factors affecting long-term global climate
- List two or more greenhouse gases and describe their role in the greenhouse effect

All biomes are universally affected by global conditions, such as climate, that ultimately shape each biome's environment. Scientists who study climate have noted a series of marked changes that have gradually become increasingly evident during the last sixty years. Global climate change is the term used to describe altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide.

Climate and Weather

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather.

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. In contrast, weather refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held on because it is difficult to accurately predict the weather on a specific day. Climate can be considered "average" weather.

Global Climate Change

Climate change can be understood by approaching three areas of study:

- current and past global climate change
- causes of past and present-day global climate change
- ancient and current results of climate change

It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. It is common for reports and discussions about global climate change to confuse the data showing that Earth's climate is changing with the factors that drive this climate change.

Evidence for Global Climate Change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on historical evidence of Earth's past climate.

Antarctic ice cores are a key example of such evidence. These ice cores are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure 57.5.1a). The 0 °C on this graph refers to the long-term average. Temperatures that are greater than 0 °C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0

°C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the graph in Figure **57.5.1**b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles; note the relationship between carbon dioxide concentration and temperature. Figure **57.5.1**b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

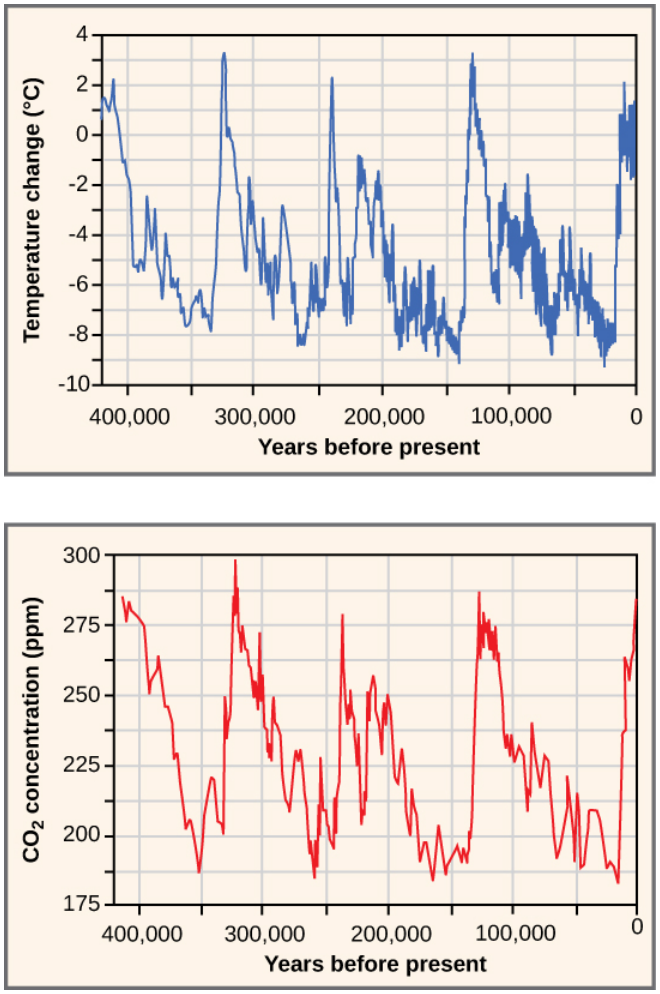


Figure **57.5.1:** Ice at the Russian Vostok station in East Antarctica was laid down over the course of 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern day were determined from the amount of deuterium (an isotope of hydrogen) present.

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The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is

a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The Industrial Revolution, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and the United States. New technologies were invented and provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a fossil fuel is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure **57.5.2**).

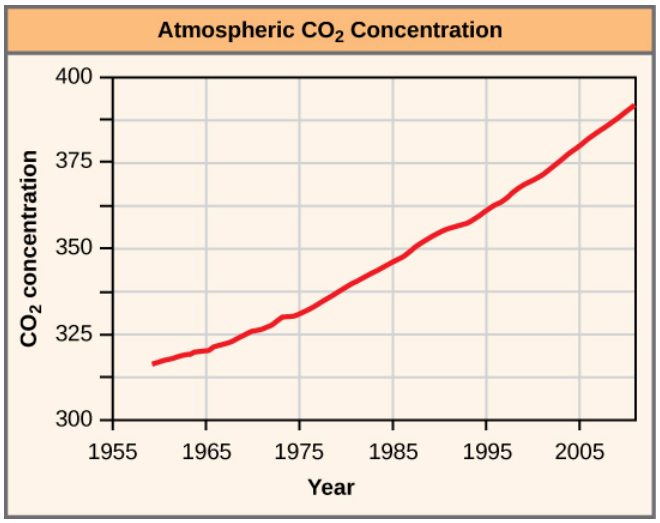


Figure **57.5.2**: The atmospheric concentration of CO_2 has risen steadily since the beginning of industrialization.

Current and Past Drivers of Global Climate Change

Since it is not possible to go back in time to directly observe and measure climate, scientists use indirect evidence to determine the drivers, or factors, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change: before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases. The first of these is the Milankovitch cycles. The Milankovitch cycles describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. Solar intensity is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanos in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to haze-effect cooling, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

Greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as greenhouse gases trap the heat in the atmosphere, as do the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of

the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's surface, and then a portion of that energy is re-radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface. Greenhouse gases absorb and emit radiation and are an important factor in the greenhouse effect: the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises, global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2011, the atmospheric carbon dioxide concentration was 392 ppm. However, the planet would not be inhabitable by current life forms if water vapor did not produce its drastic greenhouse warming effect.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm. Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas (Figure **57.5.3**). Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH_4) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Another source of methane is the melting of clathrates. Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.



Figure **57.5.3**: The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (credit: “Pöllö”/Wikimedia Commons)

Documented Results of Climate Change: Past and Present

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena such as retreating glaciers and melting polar ice cause a continual rise in sea level. Meanwhile, changes in climate can negatively affect organisms.

Geological Climate Change

Global warming has been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth’s geologic history. Scientists estimate that approximately 70 percent of the terrestrial plant and animal species and 84 percent of marine species became extinct, vanishing forever near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

Link to Learning



Watch this NASA video to discover the mixed effects of global warming on plant growth. While scientists found that warmer temperatures in the 1980s and 1990s caused an increase in plant productivity, this advantage has since been counteracted by more frequent droughts.

Present Climate Change

A number of global events have occurred that may be attributed to climate change during our lifetimes. Glacier National Park in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the Grinnell Glacier (Figure **57.5.4**) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km^3 of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.



Figure **57.5.4:** The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: modification of work by USGS)

This loss of ice is leading to increases in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, including the temperature of the water (the density of water is related to its temperature) and the amount of water found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the geographic distribution and phenology of

plants and animals. (Phenology is the study of the effects of climatic conditions on the timing of periodic lifecycle events, such as flowering in plants or migration in birds.) Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

Summary

The Earth has gone through periodic cycles of increases and decreases in temperature. During the past 2000 years, the Medieval Climate Anomaly was a warmer period, while the Little Ice Age was unusually cool. Both of these irregularities can be explained by natural causes of changes in climate, and, although the temperature changes were small, they had significant effects. Natural drivers of climate change include Milankovitch cycles, changes in solar activity, and volcanic eruptions. None of these factors, however, leads to rapid increases in global temperature or sustained increases in carbon dioxide. The burning of fossil fuels is an important source of greenhouse gases, which plays a major role in the greenhouse effect. Long ago, global warming resulted in the Permian extinction: a large-scale extinction event that is documented in the fossil record. Currently, modern-day climate change is associated with the increased melting of glaciers and polar ice sheets, resulting in a gradual increase in sea level. Plants and animals can also be affected by global climate change when the timing of seasonal events, such as flowering or pollination, is affected by global warming.

Glossary

clathrates
: frozen chunks of ice and methane found at the bottom of the ocean

climate
: long-term, predictable atmospheric conditions present in a specific area

global climate change
: altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide

greenhouse effect
: warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere

greenhouse gases
: atmospheric gases such as carbon dioxide and methane that absorb and emit radiation, thus trapping heat in Earth’s atmosphere

haze-effect cooling
: effect of the gases and solids from a volcanic eruption on global climate

Milankovitch cycles
: cyclic changes in the Earth's orbit that may affect climate

solar intensity
: amount of solar power energy the sun emits in a given amount of time

weather
: conditions of the atmosphere during a short period of time

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57.5.1: Climate and the Effects of Global Climate Change

Skills to Develop

- Define global climate change
- Summarize the effects of the Industrial Revolution on global atmospheric carbon dioxide concentration
- Describe three natural factors affecting long-term global climate
- List two or more greenhouse gases and describe their role in the greenhouse effect

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Global Climate Change

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Evidence for Global Climate Change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on historical evidence of Earth's past climate.

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°C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the graph in Figure **57.5.1.1**b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles; note the relationship between carbon dioxide concentration and temperature. Figure **57.5.1.1**b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

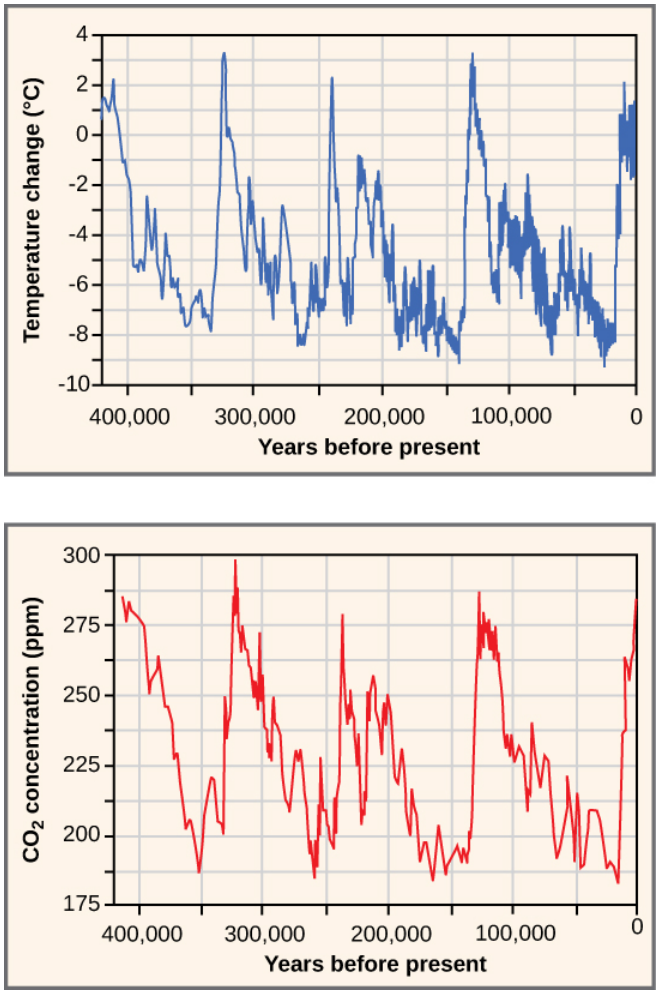


Figure **57.5.1.1:** Ice at the Russian Vostok station in East Antarctica was laid down over the course of 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern day were determined from the amount of deuterium (an isotope of hydrogen) present.

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The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is

a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The Industrial Revolution, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and the United States. New technologies were invented and provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a fossil fuel is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure **57.5.1.2**).

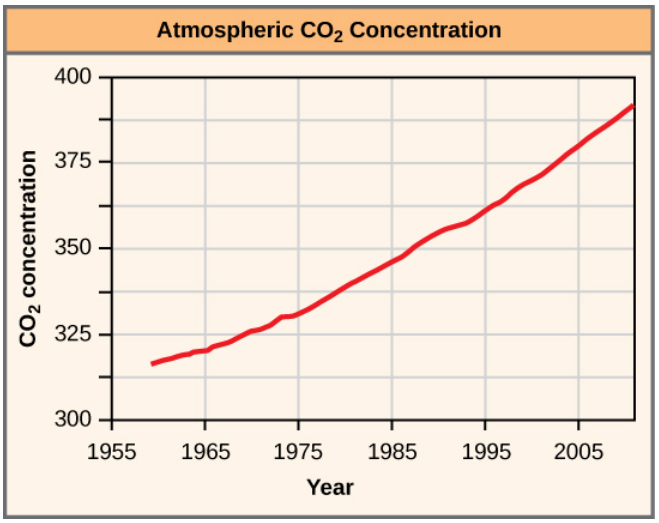


Figure **57.5.1.2**: The atmospheric concentration of CO_2 has risen steadily since the beginning of industrialization.

Current and Past Drivers of Global Climate Change

Since it is not possible to go back in time to directly observe and measure climate, scientists use indirect evidence to determine the drivers, or factors, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change: before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases. The first of these is the Milankovitch cycles. The Milankovitch cycles describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. Solar intensity is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanos in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to haze-effect cooling, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

Greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as greenhouse gases trap the heat in the atmosphere, as do the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of

the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's surface, and then a portion of that energy is re-radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface. Greenhouse gases absorb and emit radiation and are an important factor in the greenhouse effect: the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises, global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2011, the atmospheric carbon dioxide concentration was 392 ppm. However, the planet would not be inhabitable by current life forms if water vapor did not produce its drastic greenhouse warming effect.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm. Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas (Figure **57.5.1.3**). Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH_4) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Another source of methane is the melting of clathrates. Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.



Figure **57.5.1.3**: The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (credit: “Pöllö”/Wikimedia Commons)

Documented Results of Climate Change: Past and Present

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena such as retreating glaciers and melting polar ice cause a continual rise in sea level. Meanwhile, changes in climate can negatively affect organisms.

Geological Climate Change

Global warming has been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth’s geologic history. Scientists estimate that approximately 70 percent of the terrestrial plant and animal species and 84 percent of marine species became extinct, vanishing forever near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

Link to Learning



Watch this NASA video to discover the mixed effects of global warming on plant growth. While scientists found that warmer temperatures in the 1980s and 1990s caused an increase in plant productivity, this advantage has since been counteracted by more frequent droughts.

Present Climate Change

A number of global events have occurred that may be attributed to climate change during our lifetimes. Glacier National Park in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the Grinnell Glacier (Figure **57.5.1.4**) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km^3 of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.



Figure **57.5.1.4:** The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: modification of work by USGS)

This loss of ice is leading to increases in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, including the temperature of the water (the density of water is related to its temperature) and the amount of water found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the geographic distribution and phenology of

plants and animals. (Phenology is the study of the effects of climatic conditions on the timing of periodic lifecycle events, such as flowering in plants or migration in birds.) Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

Summary

The Earth has gone through periodic cycles of increases and decreases in temperature. During the past 2000 years, the Medieval Climate Anomaly was a warmer period, while the Little Ice Age was unusually cool. Both of these irregularities can be explained by natural causes of changes in climate, and, although the temperature changes were small, they had significant effects. Natural drivers of climate change include Milankovitch cycles, changes in solar activity, and volcanic eruptions. None of these factors, however, leads to rapid increases in global temperature or sustained increases in carbon dioxide. The burning of fossil fuels is an important source of greenhouse gases, which plays a major role in the greenhouse effect. Long ago, global warming resulted in the Permian extinction: a large-scale extinction event that is documented in the fossil record. Currently, modern-day climate change is associated with the increased melting of glaciers and polar ice sheets, resulting in a gradual increase in sea level. Plants and animals can also be affected by global climate change when the timing of seasonal events, such as flowering or pollination, is affected by global warming.

Glossary

clathrates
: frozen chunks of ice and methane found at the bottom of the ocean

climate
: long-term, predictable atmospheric conditions present in a specific area

global climate change
: altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide

greenhouse effect
: warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere

greenhouse gases
: atmospheric gases such as carbon dioxide and methane that absorb and emit radiation, thus trapping heat in Earth’s atmosphere

haze-effect cooling
: effect of the gases and solids from a volcanic eruption on global climate

Milankovitch cycles
: cyclic changes in the Earth's orbit that may affect climate

solar intensity
: amount of solar power energy the sun emits in a given amount of time

weather
: conditions of the atmosphere during a short period of time

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57.5.2: Biogeochemical Cycles

Skills to Develop

- Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur
- Explain how human activities have impacted these cycles and the potential consequences for Earth

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules—carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur—take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the Earth's surface. Geologic processes, such as weathering, erosion, water drainage, and the subduction of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a biogeochemical cycle.

Water contains hydrogen and oxygen, which is essential to all living processes. The hydrosphere is the area of the Earth where water movement and storage occurs: as liquid water on the surface and beneath the surface or frozen (rivers, lakes, oceans, groundwater, polar ice caps, and glaciers), and as water vapor in the atmosphere. Carbon is found in all organic macromolecules and is an important constituent of fossil fuels. Nitrogen is a major component of our nucleic acids and proteins and is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur, critical to the 3–D folding of proteins (as in disulfide binding), is released into the atmosphere by the burning of fossil fuels, such as coal.

The cycling of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

The Water (Hydrologic) Cycle

Water is the basis of all living processes. The human body is more than 1/2 water and human cells are more than 70 percent water. Thus, most land animals need a supply of fresh water to survive. However, when examining the stores of water on Earth, 97.5 percent of it is non-potable salt water (Figure **57.5.2.1**). Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1 percent of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on the small amount of fresh surface water supply, a lack of which can have massive effects on ecosystem dynamics. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean. Although this pursuit of drinkable water has been ongoing throughout human history, the supply of fresh water is still a major issue in modern times.

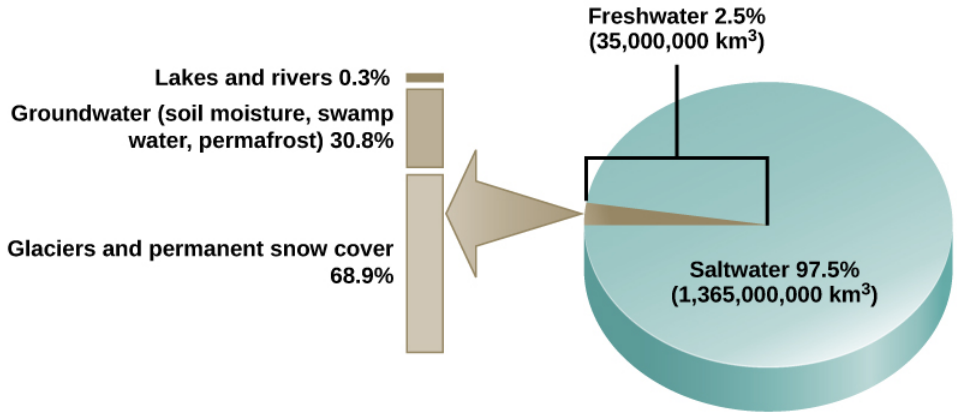


Figure **57.5.2.1**: Only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things.

Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems, some located on distant parts of the Earth. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. Figure **57.5.2.2** illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. Residence time is a measure of the average time an individual water molecule stays in a particular reservoir. A large amount of the Earth's water is locked in place in these reservoirs as ice, beneath the ground, and in the ocean, and, thus, is unavailable for short-term cycling (only surface water can evaporate).

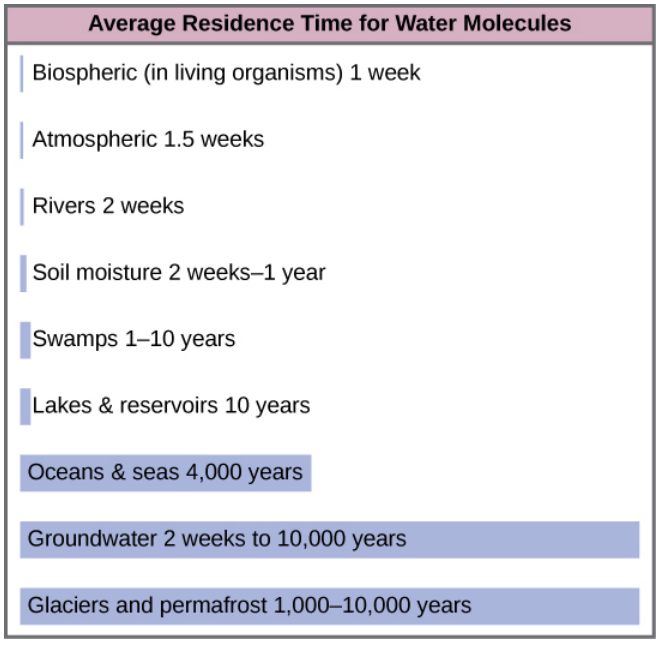


Figure **57.5.2.2**: This graph shows the average residence time for water molecules in the Earth's water reservoirs.

There are various processes that occur during the cycling of water, shown in Figure **57.5.2.3**. These processes include the following:

- evaporation/sublimation
- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

The water cycle is driven by the sun's energy as it warms the oceans and other surface waters. This leads to the evaporation (water to water vapor) of liquid surface water and the sublimation (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets and is eventually followed by precipitation (rain or snow), which returns water to the Earth's surface. Rain eventually permeates into the ground, where it may evaporate again if it is near the surface, flow beneath the surface, or be stored for long periods. More easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

Link to Learning

Head to this website to learn more about the world's fresh water supply.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. The environmental effects of runoff will be discussed later as these cycles are described.

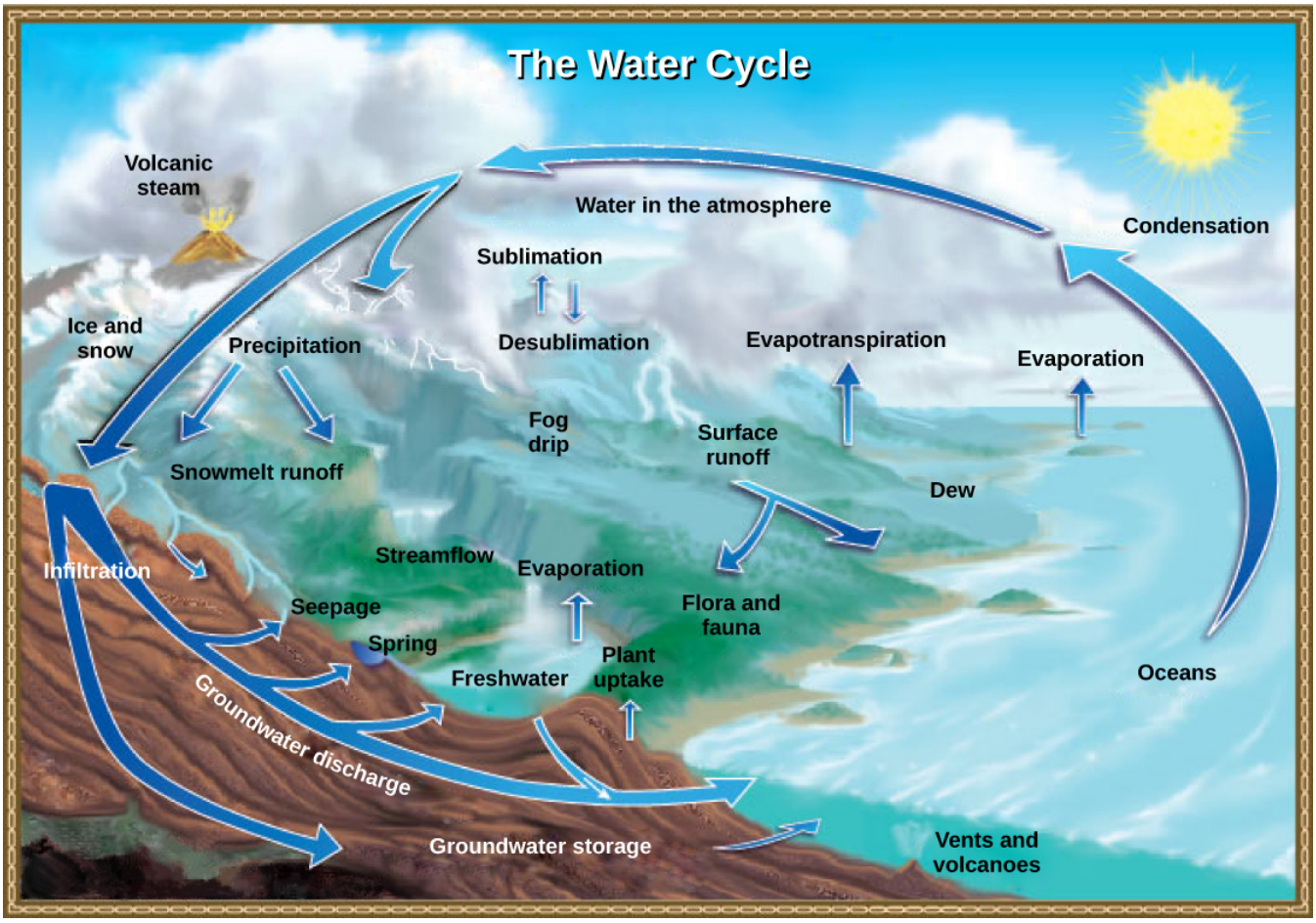


Figure 57.5.2.3: Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Carbon Cycle

Carbon is the second most abundant element in living organisms. Carbon is present in all organic molecules, and its role in the structure of macromolecules is of primary importance to living organisms. Carbon compounds contain especially high energy, particularly those derived from fossilized organisms, mainly plants, which humans use as fuel. Since the 1800s, the number of countries using massive amounts of fossil fuels has increased. Since the beginning of the Industrial Revolution, global demand for the Earth's limited fossil fuel supplies has risen; therefore, the amount of carbon dioxide in our atmosphere has increased. This increase in carbon dioxide has been associated with climate change and other disturbances of the Earth's ecosystems and is a major environmental concern worldwide. Thus, the "carbon footprint" is based on how much carbon dioxide is produced and how much fossil fuel countries consume.

The carbon cycle is most easily studied as two interconnected sub-cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes. The entire carbon cycle is shown in Figure 57.5.2.4.

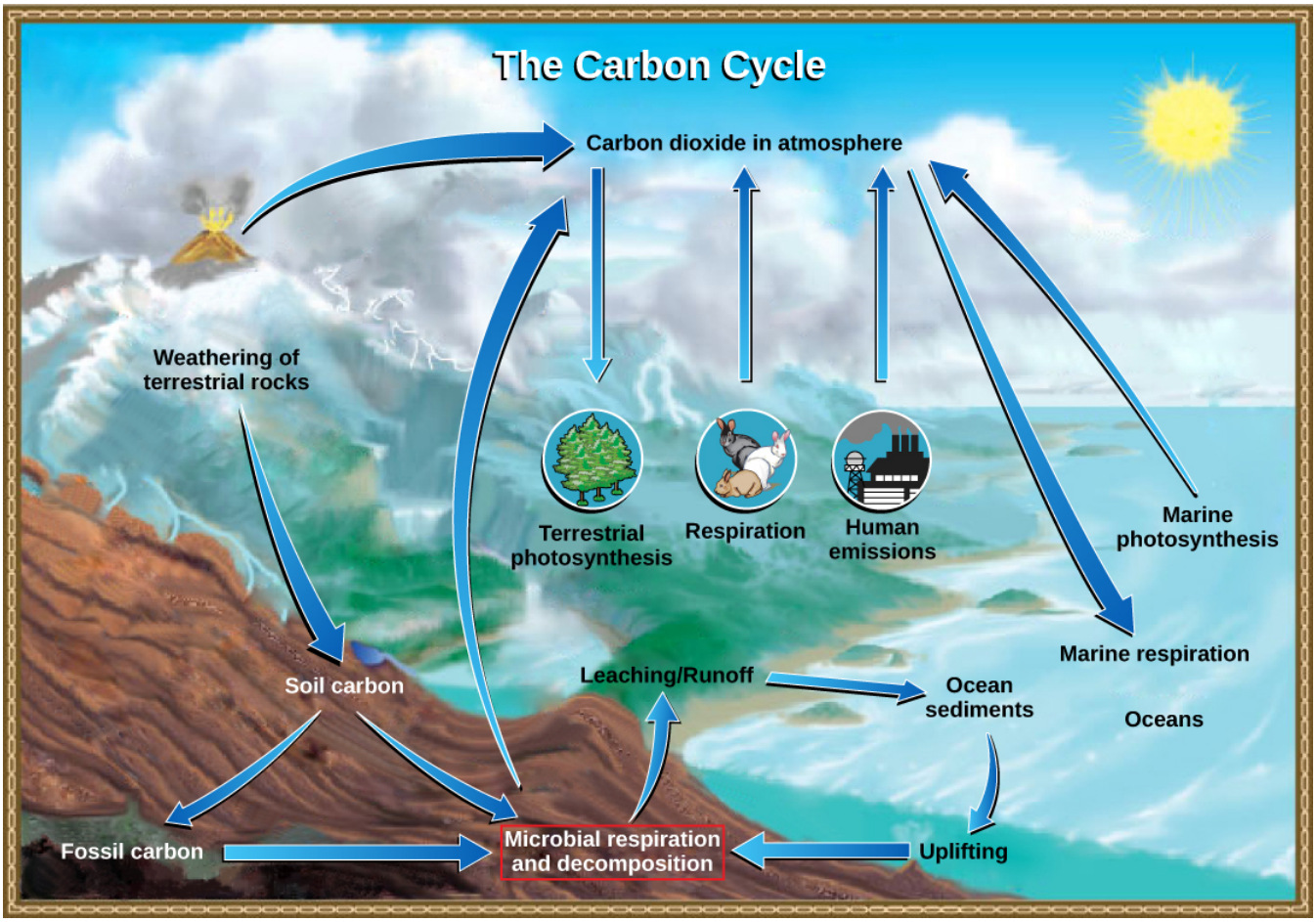


Figure **57.5.2.4**: Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions, bring this stored carbon back into the carbon cycle. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Link to Learning

Click this link to read information about the United States Carbon Cycle Science Program.

The Biological Carbon Cycle

Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs within and between ecosystems by way of atmospheric carbon dioxide. Carbon dioxide is the basic building block that most autotrophs use to build multi-carbon, high energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds thereby store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (carbonic acid, $H_2CO_3^-$). However

carbon dioxide is acquired, a by-product of the process is oxygen. The photosynthetic organisms are responsible for depositing approximately 21 percent oxygen content of the atmosphere that we observe today.

Heterotrophs and autotrophs are partners in biological carbon exchange (especially the primary consumers, largely herbivores). Heterotrophs acquire the high-energy carbon compounds from the autotrophs by consuming them, and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Gas exchange through the atmosphere and water is one way that the carbon cycle connects all living organisms on Earth.

The Biogeochemical Carbon Cycle

The movement of carbon through the land, water, and air is complex, and in many cases, it occurs much more slowly geologically than as seen between living organisms. Carbon is stored for long periods in what are known as carbon reservoirs, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, land sediments (including fossil fuels), and the Earth's interior.

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide and is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each location, and each one affects the other reciprocally. Carbon dioxide (CO_2) from the atmosphere dissolves in water and combines with water molecules to form carbonic acid, and then it ionizes to carbonate and bicarbonate ions (Figure **57.5.2.5**)

Step 1: CO_2 (atmospheric) $\rightleftharpoons$ CO_2 (dissolved)
Step 2: CO_2 (dissolved) + H_2O $\rightleftharpoons$ H_2CO_3 (carbonic acid)
Step 3: H_2CO_3 $\rightleftharpoons$ + H^+ + HCO_3^- (biocarbonate ion)
Step 4: HCO_3^- $\rightleftharpoons$ H^+ + CO_3^{2-} (carbonate ion)

Figure **57.5.2.5**: Carbon dioxide reacts with water to form bicarbonate and carbonate ions.

The equilibrium coefficients are such that more than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate ($CaCO_3$), a major component of marine organism shells. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

On land, carbon is stored in soil as a result of the decomposition of living organisms (by decomposers) or from weathering of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Deeper underground, on land and at sea, are fossil fuels: the anaerobically decomposed remains of plants that take millions of years to form. Fossil fuels are considered a non-renewable resource because their use far exceeds their rate of formation. A non-renewable resource, such as fossil fuel, is either regenerated very slowly or not at all. Another way for carbon to enter the atmosphere is from land (including land beneath the surface of the ocean) by the eruption of volcanoes and other geothermal systems. Carbon sediments from the ocean floor are taken deep within the Earth by the process of subduction: the movement of one tectonic plate beneath another. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.

Carbon dioxide is also added to the atmosphere by the animal husbandry practices of humans. The large numbers of land animals raised to feed the Earth's growing population results in increased carbon dioxide levels in the atmosphere due to farming practices and the respiration and methane production. This is another example of how human activity indirectly affects biogeochemical cycles in a significant way. Although much of the debate about the future effects of increasing atmospheric carbon on climate change focuses on fossils fuels, scientists take natural processes, such as volcanoes and respiration, into account as they model and predict the future impact of this increase.

The Nitrogen Cycle

Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly bonded, triple covalent N_2) even though this molecule comprises approximately 78 percent of

the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through nitrogen fixation (conversion of N_2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to "fix" nitrogen. *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. As shown in Figure **57.5.2.6**, the nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the ammonification process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by nitrifying bacteria, such as *Nitrosomonas*, through nitrification. Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of denitrification occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to re-enter the atmosphere.

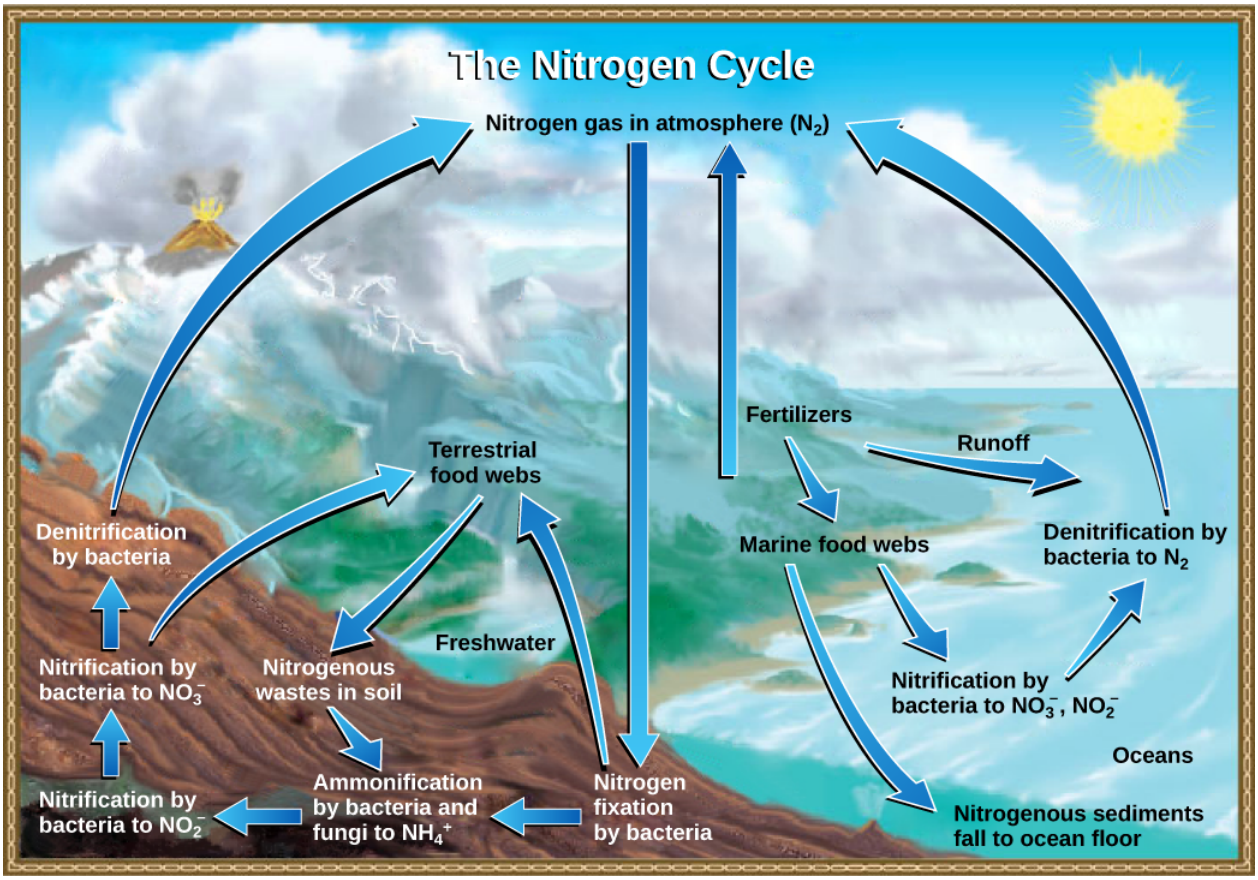


Figure **57.5.2.6**: Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Exercise

Which of the following statements about the nitrogen cycle is false?

A. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
B. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
C. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
D. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

Answer

C: Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers in agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on Earth's ecosystems including the production of acid rain (as nitric acid, HNO_3) and greenhouse gas (as nitrous oxide, N_2O) potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater eutrophication, a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the Earth's surface and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle.[1]

The Phosphorus Cycle

Phosphorus is an essential nutrient for living processes; it is a major component of nucleic acid and phospholipids, and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems (Figure **57.5.2.7**).

Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is moved to land over geologic time by the uplifting of areas of the Earth's surface.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.

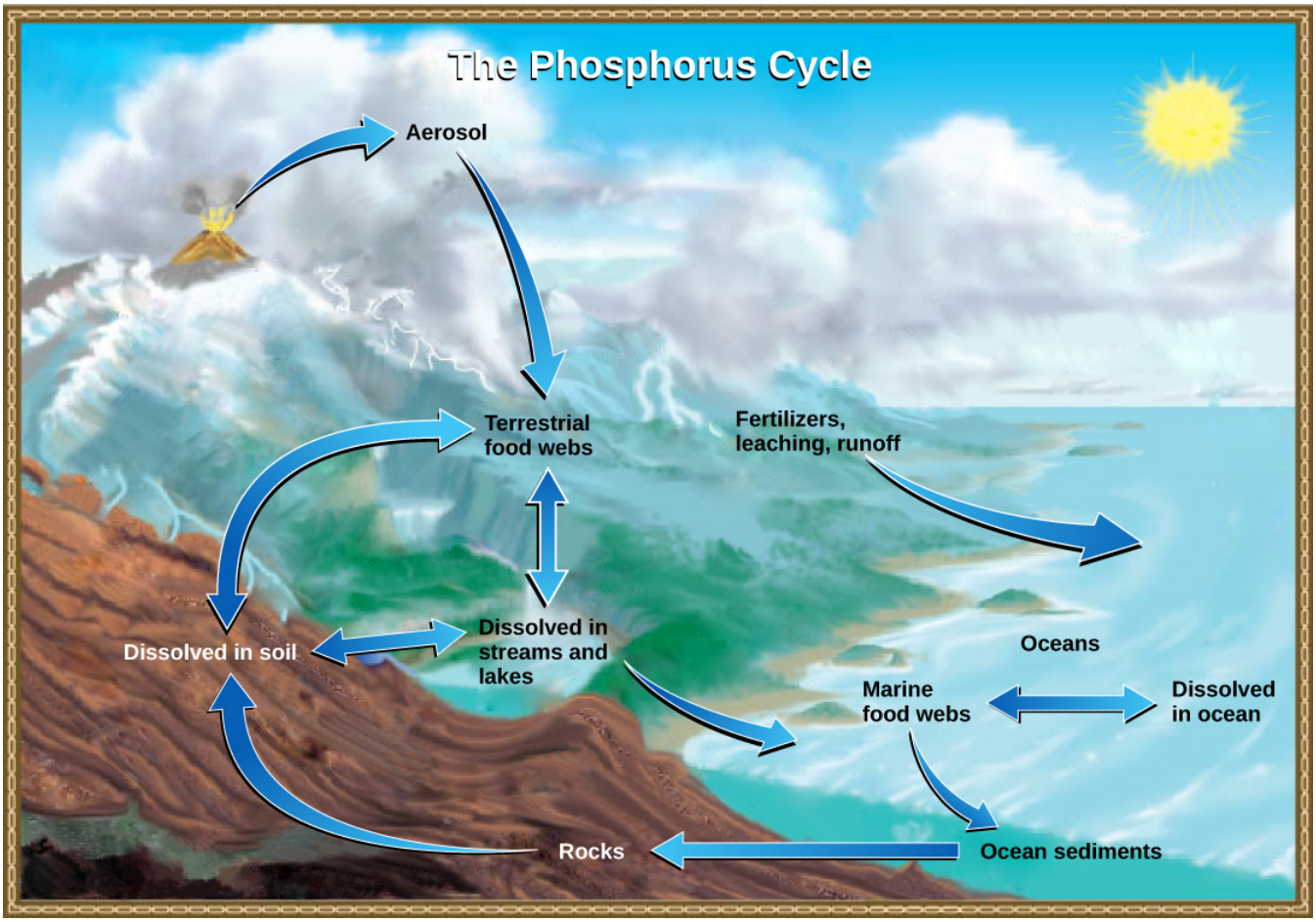


Figure **57.5.2.7**: In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers (Figure **57.5.2.8**).

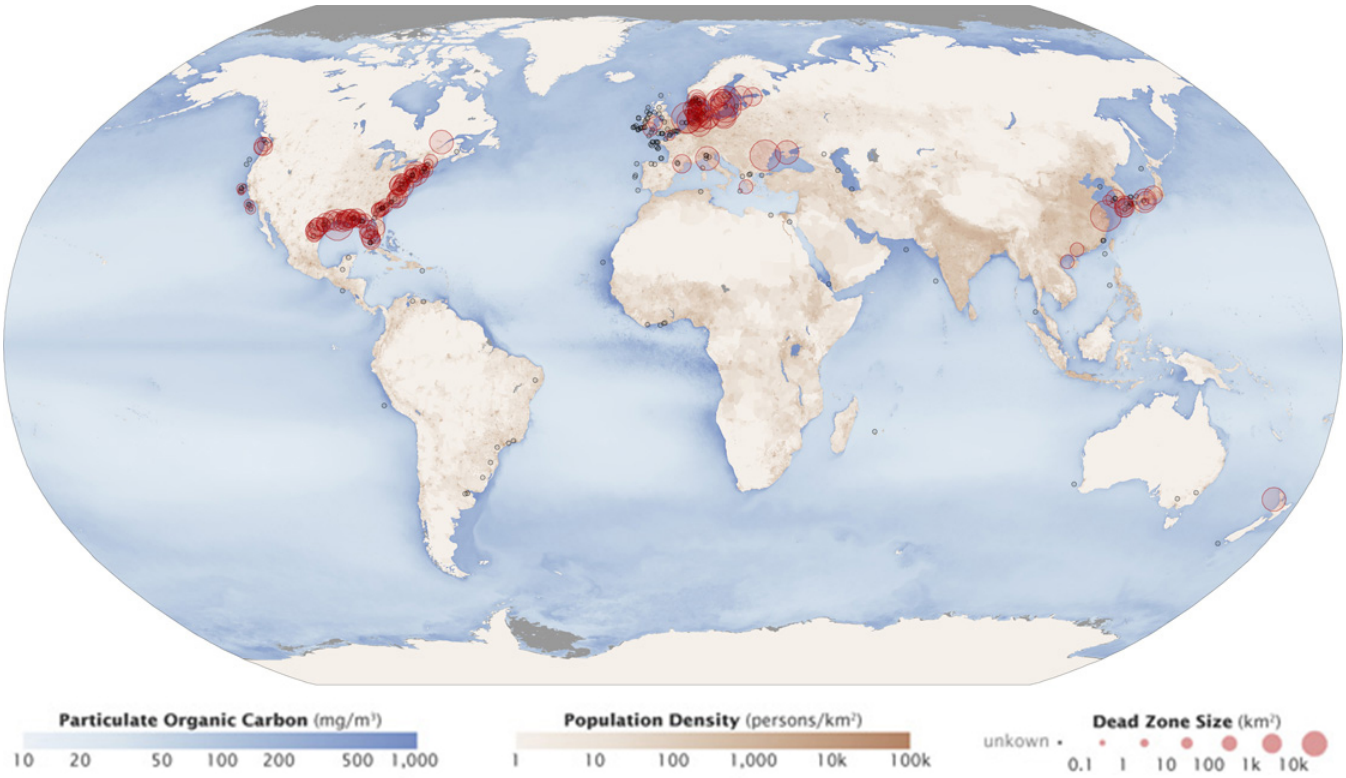


Figure **57.5.2.8**: Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

A dead zone is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years, and more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 8463 square miles. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States.

Everyday Connection: Chesapeake Bay

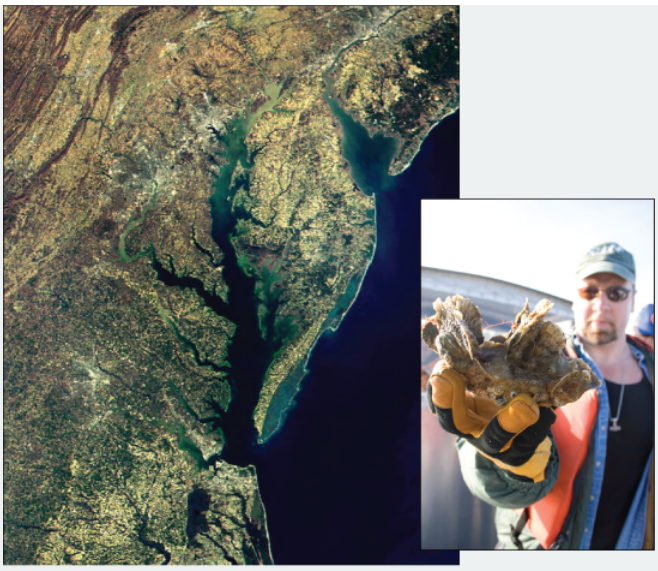


Figure **57.5.2.9**: This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay. (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army)

The Chesapeake Bay has long been valued as one of the most scenic areas on Earth; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms. Several species have declined in the Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overharvesting. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by non-profit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for inter-state cooperation to gain successful restoration.

The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

The Sulfur Cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns, and hence their functions. As shown in Figure **57.5.2.10**, sulfur cycles between the oceans, land, and atmosphere. Atmospheric sulfur is found in the form of sulfur dioxide (SO_2) and enters the atmosphere in three ways: from the decomposition of organic molecules, from volcanic activity and geothermal vents, and from the burning of fossil fuels by humans.

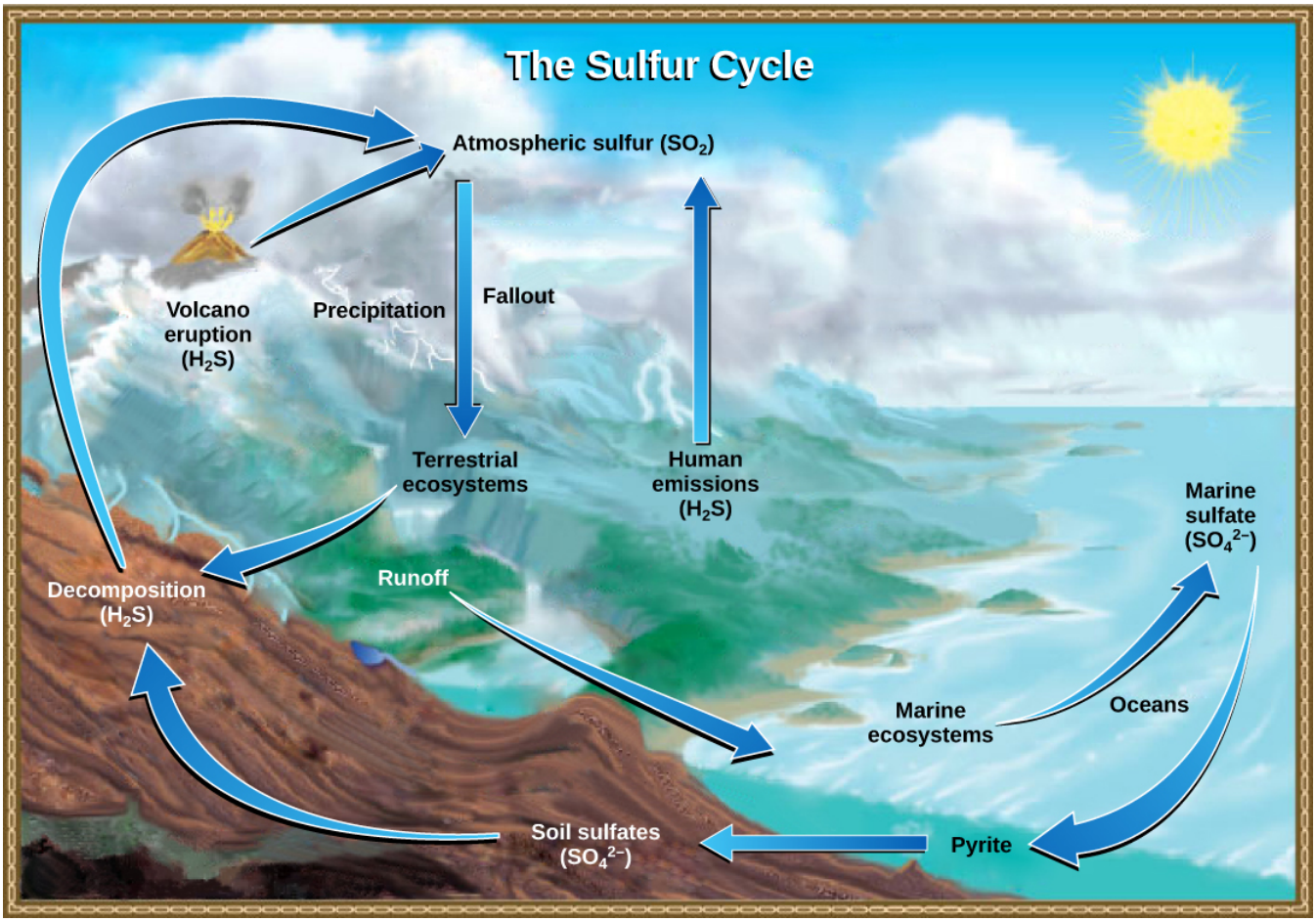


Figure **57.5.2.10**: Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the Earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil and atmosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and geothermal vents (Figure **57.5.2.11**). Atmospheric sulfur is found in the form of sulfur dioxide (SO_2), and as rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfuric acid (H_2SO_4). Sulfur can also fall directly from the atmosphere in a process called fallout. Also, the weathering of sulfur-containing rocks releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplifting of ocean sediments. Terrestrial ecosystems can then make use of these soil sulfates ($\mathbf{SO_4^{2-}}$), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide (H_2S) gas.



Figure **57.5.2.11**: At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially from coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. As rain falls through this gas, it creates the phenomenon known as acid rain. Acid rain is corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid, which causes damage to aquatic ecosystems. Acid rain damages the natural environment by lowering the pH of lakes, which kills many of the resident fauna; it also affects the man-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years. These examples show the wide-ranging effects of human activities on our environment and the challenges that remain for our future.

Link to Learning

Click this link to learn more about global climate change.

Summary

Mineral nutrients are cycled through ecosystems and their environment. Of particular importance are water, carbon, nitrogen, phosphorus, and sulfur. All of these cycles have major impacts on ecosystem structure and function. As human activities have caused major disturbances to these cycles, their study and modeling is especially important. A variety of human activities, such as pollution, oil spills, and other events have damaged ecosystems, potentially causing global climate change. The health of Earth depends on understanding these cycles and how to protect the environment from irreversible damage.

Footnotes

1. 1 Scott L. Morford, Benjamin Z. Houlton, and Randy A. Dahlgren, “Increased Forest Ecosystem Carbon and Nitrogen Storage from Nitrogen Rich Bedrock,” *Nature* 477, no. 7362 (2011): 78–81.

Glossary

acid rain
corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid; can damage structures and ecosystems

biogeochemical cycle
cycling of mineral nutrients through ecosystems and through the non-living world

dead zone
area within an ecosystem in lakes and near the mouths of rivers where large areas of ecosystems are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities

eutrophication
process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna

fallout
direct deposit of solid minerals on land or in the ocean from the atmosphere

hydrosphere
area of the Earth where water movement and storage occurs

non-renewable resource
resource, such as fossil fuel, that is either regenerated very slowly or not at all

residence time
measure of the average time an individual water molecule stays in a particular reservoir

subduction
movement of one tectonic plate beneath another

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57.5.3: Threats to Biodiversity

Skills to Develop

- Identify significant threats to biodiversity
- Explain the effects of habitat loss, exotic species, and hunting on biodiversity
- Identify the early and predicted effects of climate change on biodiversity

The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and resource exploitation. The human population requires resources to survive and grow, and those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are habitat loss, overharvesting, and introduction of exotic species. The first two of these are a direct result of human population growth and resource use. The third results from increased mobility and trade. A fourth major cause of extinction, anthropogenic climate change, has not yet had a large impact, but it is predicted to become significant during this century. Global climate change is also a consequence of human population needs for energy and the use of fossil fuels to meet those needs (Figure **57.5.3.1**). Environmental issues, such as toxic pollution, have specific targeted effects on species, but they are not generally seen as threats at the magnitude of the others.

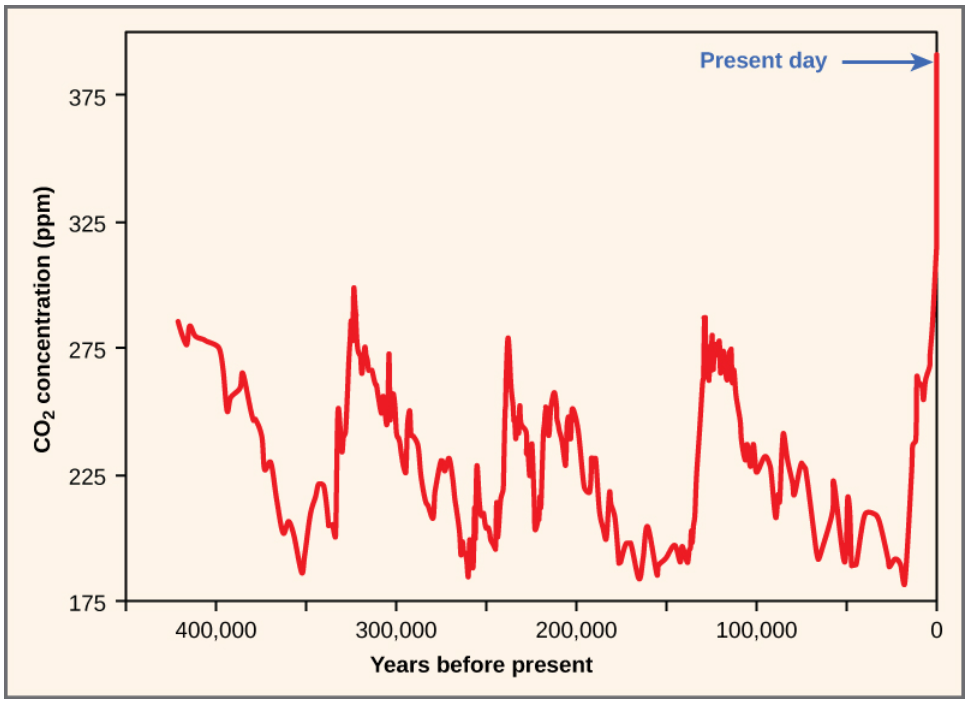


Figure **57.5.3.1**: Atmospheric carbon dioxide levels fluctuate in a cyclical manner. However, the burning of fossil fuels in recent history has caused a dramatic increase in the levels of carbon dioxide in the Earth's atmosphere, which have now reached levels never before seen in human history. Scientists predict that the addition of this "greenhouse gas" to the atmosphere is resulting in climate change that will significantly impact biodiversity in the coming century.

Habitat Loss

Humans rely on technology to modify their environment and replace certain functions that were once performed by the natural ecosystem. Other species cannot do this. Elimination of their ecosystem—whether it is a forest, a desert, a grassland, a freshwater estuarine, or a marine environment—will kill the individuals in the species. Remove the entire habitat within the range of a species and, unless they are one of the few species that do well in human-built environments, the species will become extinct. Human destruction of habitats accelerated in the latter half of the twentieth century. Consider the exceptional biodiversity of Sumatra: it is home to one species of orangutan, a species of critically endangered elephant, and the Sumatran tiger, but half of Sumatra's forest is now gone. The neighboring island of Borneo, home to the other species of orangutan, has lost a similar area of forest. Forest loss continues in protected areas of Borneo. The orangutan in Borneo is listed as endangered by the International Union for Conservation of Nature (IUCN), but it is simply the most visible of thousands of species that will not survive the disappearance of

the forests of Borneo. The forests are removed for timber and to plant palm oil plantations (Figure 57.5.3.2). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. A five-year estimate of global forest cover loss for the years 2000–2005 was 3.1 percent. In the humid tropics where forest loss is primarily from timber extraction, 272,000 km^2 was lost out of a global total of 11,564,000 km^2 (or 2.4 percent). In the tropics, these losses certainly also represent the extinction of species because of high levels of endemism.



(a)



(b)



(c)



(d)



(e)

Figure 57.5.3.2: (a) One species of orangutan, *Pongo pygmaeus*, is found only in the rainforests of Borneo, and the other species of orangutan (*Pongo abelii*) is found only in the rainforests of Sumatra. These animals are examples of the exceptional biodiversity of (c) the islands of Sumatra and Borneo. Other species include the (b) Sumatran tiger (*Panthera tigris sumatrae*) and the (d) Sumatran elephant (*Elephas maximus sumatranus*), both critically endangered species. Rainforest habitat is being removed to make way for (e) oil palm plantations such as this one in Borneo's Sabah Province. (credit a: modification of work by Thorsten Bachner; credit b: modification of work by Dick Mudde; credit c: modification of work by U.S. CIA World Factbook; credit d: modification of work by "Nonprofit Organizations"/Flickr; credit e: modification of work by Dr. Lian Pin Koh)

Everyday Connection: Preventing Habitat Destruction with Wise Wood Choices

Most consumers do not imagine that the home improvement products they buy might be contributing to habitat loss and species extinctions. Yet the market for illegally harvested tropical timber is huge, and the wood products often find themselves in building supply stores in the United States. One estimate is that 10 percent of the imported timber stream in the United States, which is the world's largest consumer of wood products, is potentially illegally logged. In 2006, this amounted to $3.6 billion in wood products. Most of the illegal products are imported from countries that act as intermediaries and are not the originators of the wood.

How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally? The Forest Stewardship Council (FSC) certifies sustainably harvested forest products, therefore, looking for their certification on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest. Certification applies to specific products, not to a producer; some producers' products may not have certification while other products are certified. While there are other industry-backed certifications other than the FSC, these are unreliable due to lack of independence from the industry. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal wood products, it is not that simple. Logging and forest management laws vary from country to country; what is illegal in one country may be legal in another. Where and how a product is harvested and whether the forest from which it comes is being maintained sustainably all factor into whether a wood product will be certified by the FSC. It is always a good idea to ask questions about where a wood product came from and how the supplier knows that it was harvested legally.

Habitat destruction can affect ecosystems other than forests. Rivers and streams are important ecosystems and are frequently modified through land development and from damming or water removal. Damming of rivers affects the water flow and access to all parts of a river. Differing flow regimes can reduce or eliminate populations that are adapted to these changes in flow patterns. For example, an estimated 91percent of river lengths in the United States have been developed: they have modifications like dams, to create energy or store water; levees, to prevent flooding; or dredging or rerouting, to create land that is more suitable for human development. Many fish species in the United States, especially rare species or species with restricted distributions, have seen declines caused by river damming and habitat loss. Research has confirmed that species of amphibians that must carry out parts of their life cycles in both aquatic and terrestrial habitats have a greater chance of suffering population declines and extinction because of the increased likelihood that one of their habitats or access between them will be lost.

Overharvesting

Overharvesting is a serious threat to many species, but particularly to aquatic species. There are many examples of regulated commercial fisheries monitored by fisheries scientists that have nevertheless collapsed. The western Atlantic cod fishery is the most spectacular recent collapse. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s and the pressure on the fishery led to it becoming unsustainable. The causes of fishery collapse are both economic and political in nature. Most fisheries are managed as a common (shared) resource even when the fishing territory lies within a country's territorial waters. Common resources are subject to an economic pressure known as the tragedy of the commons in which essentially no fisher has a motivation to exercise restraint in harvesting a fishery when it is not owned by that fisher. The natural outcome of harvests of resources held in common is their overexploitation. While large fisheries are regulated to attempt to avoid this pressure, it still exists in the background. This overexploitation is exacerbated when access to the fishery is open and unregulated and when technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases—whales are an example—economic forces will always drive toward fishing the population to extinction.

Link to Learning



Explore a U.S. Fish & Wildlife Service interactive map of critical habitat for endangered and threatened species in the United States. To begin, select “Visit the online mapper.”

For the most part, fishery extinction is not equivalent to biological extinction—the last fish of a species is rarely fished out of the ocean. At the same time, fishery extinction is still harmful to fish species and their ecosystems. There are some instances in which true extinction is a possibility. Whales have slow-growing populations and are at risk of complete extinction through hunting. There are some species of sharks with restricted distributions that are at risk of extinction. The groupers are another population of generally slow-growing fishes that, in the Caribbean, includes a number of species that are at risk of extinction from overfishing.

Coral reefs are extremely diverse marine ecosystems that face peril from several processes. Reefs are home to 1/3 of the world’s marine fish species—about 4,000 species—despite making up only 1 percent of marine habitat. Most home marine aquaria are stocked with wild-caught organisms, not cultured organisms. Although no species is known to have been driven extinct by the pet trade in marine species, there are studies showing that populations of some species have declined in response to harvesting, indicating that the harvest is not sustainable at those levels. There are concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutan.

Bush meat is the generic term used for wild animals killed for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten several species with extinction. Traditionally, bush meat in Africa was hunted to feed families directly; however, recent commercialization of the practice now has bush meat available in grocery stores, which has increased harvest rates to the level of unsustainability. Additionally, human population growth has increased the need for protein foods that are not being met from agriculture. Species threatened by the bush meat trade are mostly mammals including many primates living in the Congo basin.

Exotic Species

Exotic species are species that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Such introductions likely occur frequently as natural phenomena. For example, Kudzu (*Pueraria lobata*), which is native to Japan, was introduced in the United States in 1876. It was later planted for soil conservation. Problematically, it grows too well in the southeastern United States—up to a foot a day. It is now a pest species and covers over 7 million acres in the southeastern United States. If an introduced species is able to survive in its new habitat, that introduction is now reflected in the observed range of the species. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems, sometimes at distances that are well beyond the capacity of the species to ever travel itself and outside the range of the species’ natural predators.

Most exotic species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, possess preadaptations that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the species that exist there. For this reason, exotic species are also called invasive species. Exotic species can threaten other species through competition for resources, predation, or disease.

Link to Learning

Explore an interactive global database of exotic or invasive species.

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria, as mentioned earlier, the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of cichlids. The accidental introduction of the brown tree snake via aircraft (Figure **57.5.3.3**) from the Solomon Islands to Guam in 1950 has led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are still threatened. The brown tree snake is adept at exploiting human transportation as a means to migrate; one was even found on an aircraft arriving in Corpus Christi, Texas. Constant vigilance on the part of airport, military, and commercial aircraft personnel is required to prevent the snake from moving from Guam to other islands in the Pacific, especially Hawaii. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.

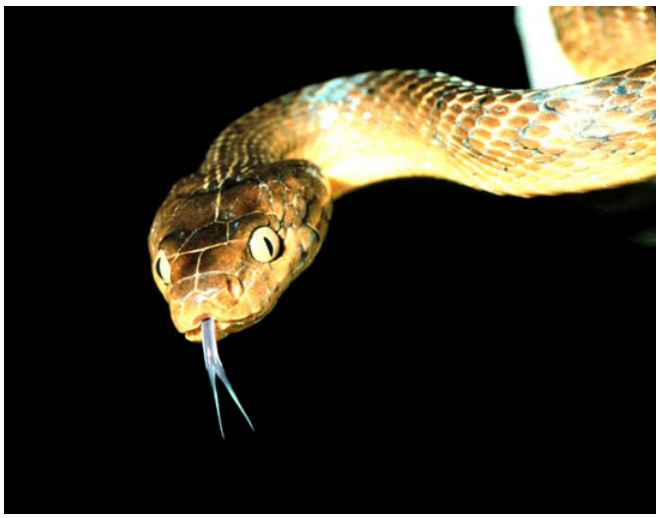


Figure **57.5.3.3**: The brown tree snake, *Boiga irregularis*, is an exotic species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950. (credit: NPS)

It now appears that the global decline in amphibian species recognized in the 1990s is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease chytridiomycosis (Figure **57.5.3.4**). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed toad (*Xenopus laevis*). It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *Batrachochytrium dendrobatidis* and can act as a reservoir for the disease.



Figure **57.5.3.4**: This Limosa Harlequin Frog (*Atelopus limosus*), an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease. (credit: Brian Gratwicke)

Early evidence suggests that another fungal pathogen, *Geomyces destructans*, introduced from Europe is responsible for white-nose syndrome, which infects cave-hibernating bats in eastern North America and has spread from a point of origin in western New York State (Figure **57.5.3.5**). The disease has decimated bat populations and threatens extinction of species already listed as endangered: the Indiana bat, *Myotis sodalis*, and potentially the Virginia big-eared bat, *Corynorhinus townsendii virginianus*. How the fungus was introduced is unclear, but one logical presumption would be that recreational cavers unintentionally brought the fungus on clothes or equipment from Europe.



Figure **57.5.3.5**: This little brown bat in Greeley Mine, Vermont, March 26, 2009, was found to have white-nose syndrome. (credit: Marvin Moriarty, USFWS)

Climate Change

Climate change, and specifically the anthropogenic (meaning, caused by humans) warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species committed to extinction by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way. The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears. Previously, these two species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring. Changing climates also throw off species' delicate timing adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.



Figure **57.5.3.6**: Since 2008, grizzly bears (*Ursus arctos horribilis*) have been spotted farther north than their historic range, a possible consequence of climate change. As a result, grizzly bear habitat now overlaps polar bear (*Ursus maritimus*) habitat. The two kinds of bears, which are capable of mating and producing viable offspring, are considered separate species as historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first wild hybrid ever found.

Range shifts are already being observed: for example, some European bird species ranges have moved 91 km northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are not moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The rate of warming appears to be accelerated in the arctic, which is recognized as a serious threat to polar bear populations that require sea ice to hunt seals during the winter months: seals are the only source of protein available to polar bears. A trend to decreasing sea ice coverage has occurred since observations began in the mid-twentieth century. The rate of decline observed in recent years is far greater than previously predicted by climate models.

Finally, global warming will raise ocean levels due to melt water from glaciers and the greater volume of warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher elevation mountains—a cycle that has provided freshwater to environments for centuries—will also be jeopardized. This could result in an overabundance of salt water and a shortage of fresh water.

Summary

The core threats to biodiversity are human population growth and unsustainable resource use. To date, the most significant causes of extinctions are habitat loss, introduction of exotic species, and overharvesting. Climate change is predicted to be a significant cause of extinctions in the coming century. Habitat loss occurs through deforestation, damming of rivers, and other activities.

Overharvesting is a threat particularly to aquatic species, while the taking of bush meat in the humid tropics threatens many species in Asia, Africa, and the Americas. Exotic species have been the cause of a number of extinctions and are especially damaging to islands and lakes. Exotic species' introductions are increasing because of the increased mobility of human populations and growing global trade and transportation. Climate change is forcing range changes that may lead to extinction. It is also affecting adaptations to the timing of resource availability that negatively affects species in seasonal environments. The impacts of climate change are greatest in the arctic. Global warming will also raise sea levels, eliminating some islands and reducing the area of all others.

Art Connections

Converting a prairie to a farm field is an example of _____.

A. overharvesting
B. habitat loss
C. exotic species
D. climate change

Answer

B

Glossary

bush meat
wild-caught animal used as food (typically mammals, birds, and reptiles); usually referring to hunting in the tropics of sub-Saharan Africa, Asia, and the Americas

chytridiomycosis
disease of amphibians caused by the fungus *Batrachochytrium dendrobatidis;* thought to be a major cause of the global amphibian decline

exotic species
(also, invasive species) species that has been introduced to an ecosystem in which it did not evolve

tragedy of the commons
economic principle that resources held in common will inevitably be overexploited

white-nose syndrome
disease of cave-hibernating bats in the eastern United States and Canada associated with the fungus *Geomyces destructans*

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57.6: Human Impacts on the Biosphere- Climate Change

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57.6.1: Climate and the Effects of Global Climate Change

Skills to Develop

- Define global climate change
- Summarize the effects of the Industrial Revolution on global atmospheric carbon dioxide concentration
- Describe three natural factors affecting long-term global climate
- List two or more greenhouse gases and describe their role in the greenhouse effect

All biomes are universally affected by global conditions, such as climate, that ultimately shape each biome's environment. Scientists who study climate have noted a series of marked changes that have gradually become increasingly evident during the last sixty years. Global climate change is the term used to describe altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide.

Climate and Weather

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather.

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. In contrast, weather refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held on because it is difficult to accurately predict the weather on a specific day. Climate can be considered "average" weather.

Global Climate Change

Climate change can be understood by approaching three areas of study:

- current and past global climate change
- causes of past and present-day global climate change
- ancient and current results of climate change

It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. It is common for reports and discussions about global climate change to confuse the data showing that Earth's climate is changing with the factors that drive this climate change.

Evidence for Global Climate Change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on historical evidence of Earth's past climate.

Antarctic ice cores are a key example of such evidence. These ice cores are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure **57.6.1.1**a). The 0 °C on this graph refers to the long-term average. Temperatures that are greater than 0 °C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0

°C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the graph in Figure **57.6.1.1**b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles; note the relationship between carbon dioxide concentration and temperature. Figure **57.6.1.1**b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

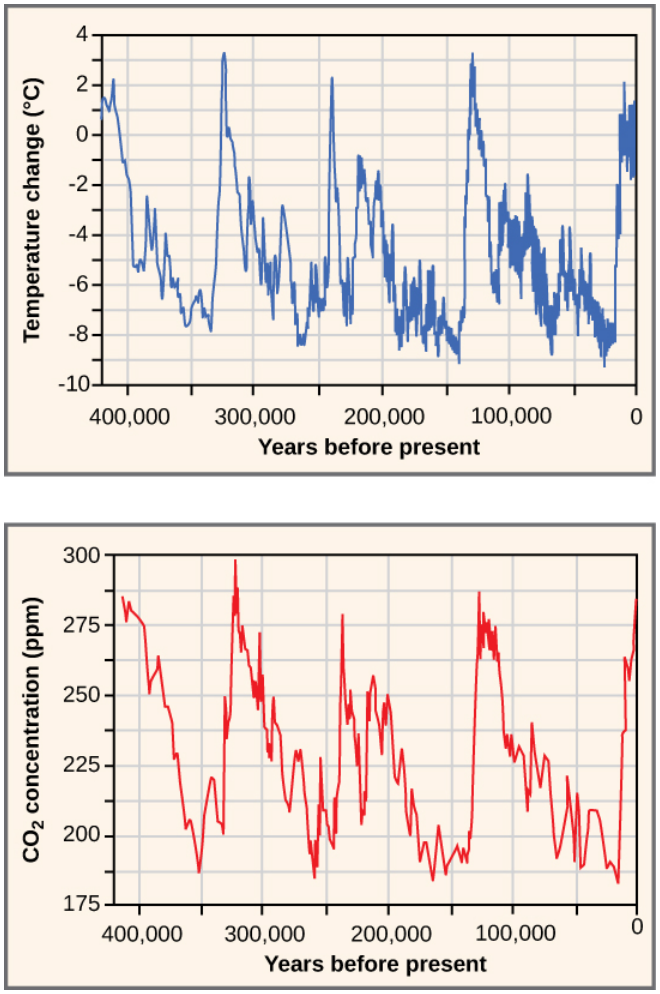


Figure **57.6.1.1:** Ice at the Russian Vostok station in East Antarctica was laid down over the course of 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern day were determined from the amount of deuterium (an isotope of hydrogen) present.

Figure **57.6.1.1**a does not show the last 2,000 years with enough detail to compare the changes of Earth's temperature during the last 400,000 years with the temperature change that has occurred in the more recent past. Two significant temperature anomalies, or irregularities, have occurred in the last 2000 years. These are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era. The Medieval Climate Anomaly occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Because of this warming, the Vikings were able to colonize Greenland.

The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is

a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The Industrial Revolution, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and the United States. New technologies were invented and provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a fossil fuel is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure **57.6.1.2**).

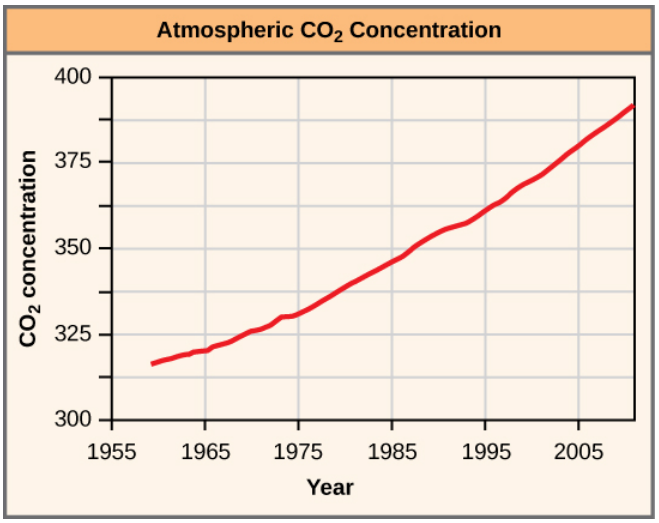


Figure **57.6.1.2**: The atmospheric concentration of CO_2 has risen steadily since the beginning of industrialization.

Current and Past Drivers of Global Climate Change

Since it is not possible to go back in time to directly observe and measure climate, scientists use indirect evidence to determine the drivers, or factors, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change: before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases. The first of these is the Milankovitch cycles. The Milankovitch cycles describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. Solar intensity is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanos in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to haze-effect cooling, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

Greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as greenhouse gases trap the heat in the atmosphere, as do the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of

the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's surface, and then a portion of that energy is re-radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface. Greenhouse gases absorb and emit radiation and are an important factor in the greenhouse effect: the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises, global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2011, the atmospheric carbon dioxide concentration was 392 ppm. However, the planet would not be inhabitable by current life forms if water vapor did not produce its drastic greenhouse warming effect.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm. Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas (Figure **57.6.1.3**). Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH_4) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Another source of methane is the melting of clathrates. Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.



Figure **57.6.1.3**: The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (credit: “Pöllö”/Wikimedia Commons)

Documented Results of Climate Change: Past and Present

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena such as retreating glaciers and melting polar ice cause a continual rise in sea level. Meanwhile, changes in climate can negatively affect organisms.

Geological Climate Change

Global warming has been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth’s geologic history. Scientists estimate that approximately 70 percent of the terrestrial plant and animal species and 84 percent of marine species became extinct, vanishing forever near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

Link to Learning



Watch this NASA video to discover the mixed effects of global warming on plant growth. While scientists found that warmer temperatures in the 1980s and 1990s caused an increase in plant productivity, this advantage has since been counteracted by more frequent droughts.

Present Climate Change

A number of global events have occurred that may be attributed to climate change during our lifetimes. Glacier National Park in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the Grinnell Glacier (Figure **57.6.1.4**) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km^3 of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.



Figure **57.6.1.4:** The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: modification of work by USGS)

This loss of ice is leading to increases in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, including the temperature of the water (the density of water is related to its temperature) and the amount of water found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the geographic distribution and phenology of

plants and animals. (Phenology is the study of the effects of climatic conditions on the timing of periodic lifecycle events, such as flowering in plants or migration in birds.) Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

Summary

The Earth has gone through periodic cycles of increases and decreases in temperature. During the past 2000 years, the Medieval Climate Anomaly was a warmer period, while the Little Ice Age was unusually cool. Both of these irregularities can be explained by natural causes of changes in climate, and, although the temperature changes were small, they had significant effects. Natural drivers of climate change include Milankovitch cycles, changes in solar activity, and volcanic eruptions. None of these factors, however, leads to rapid increases in global temperature or sustained increases in carbon dioxide. The burning of fossil fuels is an important source of greenhouse gases, which plays a major role in the greenhouse effect. Long ago, global warming resulted in the Permian extinction: a large-scale extinction event that is documented in the fossil record. Currently, modern-day climate change is associated with the increased melting of glaciers and polar ice sheets, resulting in a gradual increase in sea level. Plants and animals can also be affected by global climate change when the timing of seasonal events, such as flowering or pollination, is affected by global warming.

Glossary

clathrates
: frozen chunks of ice and methane found at the bottom of the ocean

climate
: long-term, predictable atmospheric conditions present in a specific area

global climate change
: altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide

greenhouse effect
: warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere

greenhouse gases
: atmospheric gases such as carbon dioxide and methane that absorb and emit radiation, thus trapping heat in Earth’s atmosphere

haze-effect cooling
: effect of the gases and solids from a volcanic eruption on global climate

Milankovitch cycles
: cyclic changes in the Earth's orbit that may affect climate

solar intensity
: amount of solar power energy the sun emits in a given amount of time

weather
: conditions of the atmosphere during a short period of time

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CHAPTER OVERVIEW

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58.3: Factors Responsible for Extinction

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58.1: Overview of The Biodiversity Crisis

Skills to Develop

- Define biodiversity
- Describe biodiversity as the equilibrium of naturally fluctuating rates of extinction and speciation
- Identify historical causes of high extinction rates in Earth's history

Traditionally, ecologists have measured biodiversity, a general term for the variety present in the biosphere, by taking into account both the number of species and their commonness. Biodiversity can be estimated at a number of levels of organization of living things. These estimation indexes, which came from information theory, are most useful as a first step in quantifying biodiversity between and within ecosystems; they are less useful when the main concern among conservation biologists is simply the loss of biodiversity. However, biologists recognize that measures of biodiversity, in terms of species diversity, may help focus efforts to preserve the biologically or technologically important elements of biodiversity.

The Lake Victoria cichlids provide an example through which we can begin to understand biodiversity. The biologists studying cichlids in the 1980s discovered hundreds of cichlid species representing a variety of specializations to particular habitat types and specific feeding strategies: eating plankton floating in the water, scraping and then eating algae from rocks, eating insect larvae from the bottom, and eating the eggs of other species of cichlid. The cichlids of Lake Victoria are the product of an adaptive radiation. An adaptive radiation is a rapid (less than three million years in the case of the Lake Victoria cichlids) branching through speciation of a phylogenetic tree into many closely related species; typically, the species "radiate" into different habitats and niches. The Galápagos finches are an example of a modest adaptive radiation with 15 species. The cichlids of Lake Victoria are an example of a spectacular adaptive radiation that includes about 500 species.

At the time biologists were making this discovery, some species began to quickly disappear. A culprit in these declines was a species of large fish that was introduced to Lake Victoria by fisheries to feed the people living around the lake. The Nile perch was introduced in 1963, but lay low until the 1980s when its populations began to surge. The Nile perch population grew by consuming cichlids, driving species after species to the point of extinction (the disappearance of a species). In fact, there were several factors that played a role in the extinction of perhaps 200 cichlid species in Lake Victoria: the Nile perch, declining lake water quality due to agriculture and land clearing on the shores of Lake Victoria, and increased fishing pressure. Scientists had not even catalogued all of the species present—so many were lost that were never named. The diversity is now a shadow of what it once was.

The cichlids of Lake Victoria are a thumbnail sketch of contemporary rapid species loss that occurs all over Earth and is caused by human activity. Extinction is a natural process of macroevolution that occurs at the rate of about one out of 1 million species becoming extinct per year. The fossil record reveals that there have been five periods of mass extinction in history with much higher rates of species loss, and the rate of species loss today is comparable to those periods of mass extinction. However, there is a major difference between the previous mass extinctions and the current extinction we are experiencing: human activity. Specifically, three human activities have a major impact: destruction of habitat, introduction of exotic species, and over-harvesting. Predictions of species loss within the next century, a tiny amount of time on geological timescales, range from 10 percent to 50 percent. Extinctions on this scale have only happened five other times in the history of the planet, and they have been caused by cataclysmic events that changed the course of the history of life in each instance. Earth is now in one of those times.

Types of Biodiversity

Scientists generally accept that the term biodiversity describes the number and kinds of species in a location or on the planet. Species can be difficult to define, but most biologists still feel comfortable with the concept and are able to identify and count eukaryotic species in most contexts. Biologists have also identified alternate measures of biodiversity, some of which are important for planning how to preserve biodiversity.

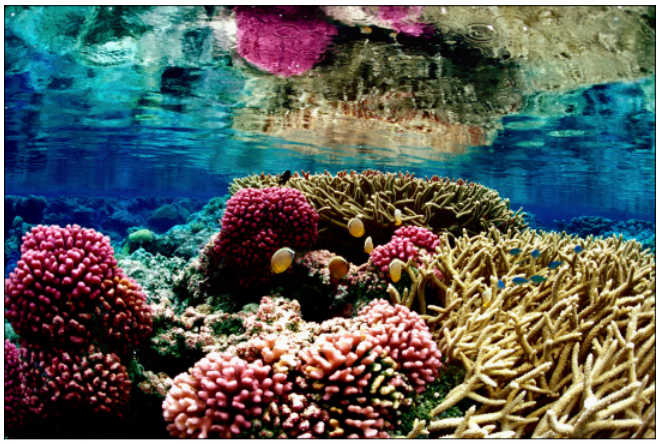
Genetic diversity is one of those alternate concepts. Genetic diversity or variation is the raw material for adaptation in a species. A species' future potential for adaptation depends on the genetic diversity held in the genomes of the individuals in populations that make up the species. The same is true for higher taxonomic categories. A genus with very different types of species will have more genetic diversity than a genus with species that look alike and have similar ecologies. If there were a choice between one of these

genera of species being preserved, the one with the greatest potential for subsequent evolution is the most genetically diverse one. It would be ideal not to have to make such choices, but increasingly this may be the norm.

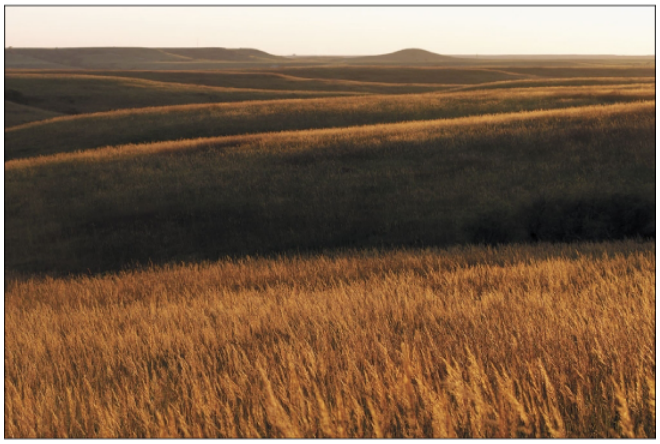
Many genes code for proteins, which in turn carry out the metabolic processes that keep organisms alive and reproducing. Genetic diversity can be measured as chemical diversity in that different species produce a variety of chemicals in their cells, both the proteins as well as the products and byproducts of metabolism. This chemical diversity has potential benefit for humans as a source of pharmaceuticals, so it provides one way to measure diversity that is important to human health and welfare.

Humans have generated diversity in domestic animals, plants, and fungi. This diversity is also suffering losses because of migration, market forces, and increasing globalism in agriculture, especially in heavily populated regions such as China, India, and Japan. The human population directly depends on this diversity as a stable food source, and its decline is troubling biologists and agricultural scientists.

It is also useful to define ecosystem diversity, meaning the number of different ecosystems on the planet or in a given geographic area (Figure **58.1.1**). Whole ecosystems can disappear even if some of the species might survive by adapting to other ecosystems. The loss of an ecosystem means the loss of interactions between species, the loss of unique features of coadaptation, and the loss of biological productivity that an ecosystem is able to create. An example of a largely extinct ecosystem in North America is the prairie ecosystem. Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. They are now all but gone, replaced by crop fields, pasture lands, and suburban sprawl. Many of the species survive, but the hugely productive ecosystem that was responsible for creating the most productive agricultural soils is now gone. As a consequence, soils are disappearing or must be maintained at greater expense.



(a)



(b)

Figure **58.1.1**: The variety of ecosystems on Earth—from (a) coral reef to (b) prairie—enables a great diversity of species to exist. (credit a: modification of work by Jim Maragos, USFWS; credit b: modification of work by Jim Minnerath, USFWS)

Current Species Diversity

Despite considerable effort, knowledge of the species that inhabit the planet is limited. A recent estimate suggests that the eukaryote species for which science has names, about 1.5 million species, account for less than 20 percent of the total number of eukaryote species present on the planet (8.7 million species, by one estimate). Estimates of numbers of prokaryotic species are largely guesses, but biologists agree that science has only begun to catalog their diversity. Even with what is known, there is no central repository of names or samples of the described species; therefore, there is no way to be sure that the 1.5 million descriptions is an accurate number. It is a best guess based on the opinions of experts in different taxonomic groups. Given that Earth is losing species at an accelerating pace, science is very much in the place it was with the Lake Victoria cichlids: knowing little about what is being lost. Table **58.1.1** presents recent estimates of biodiversity in different groups.

Table 58.1.1: Estimates of the described and predicted species by Taxonomic group

	Mora et al. 2011[1]		Chapman 2009[2]		Groombridge & Jenkins 2002[3]	
	Described	Predicted	Described	Predicted	Described	Predicted
Animalia	1,124,516	9,920,000	1,424,153	6,836,330	1,225,500	10,820,000
Chromista	17,892	34,900	25,044	200,500	—	—
Fungi	44,368	616,320	98,998	1,500,000	72,000	1,500,000
Plantae	224,244	314,600	310,129	390,800	270,000	320,000
Protozoa	16,236	72,800	28,871	1,000,000	80,000	600,000
Prokaryotes	—	—	10,307	1,000,000	10,175	—
Total	1,438,769	10,960,000	1,897,502	10,897,630	1,657,675	13,240,000

There are various initiatives to catalog described species in accessible ways, and the internet is facilitating that effort. Nevertheless, it has been pointed out that at the current rate of species description, which according to the State of Observed Species Report is 17,000 to 20,000 new species per year, it will take close to 500 years to finish describing life on this planet.[4] Over time, the task becomes both increasingly impossible and increasingly easier as extinction removes species from the planet.

Naming and counting species may seem an unimportant pursuit given the other needs of humanity, but it is not simply an accounting. Describing species is a complex process by which biologists determine an organism's unique characteristics and whether or not that organism belongs to any other described species. It allows biologists to find and recognize the species after the initial discovery, and allows them to follow up on questions about its biology. In addition, the unique characteristics of each species make it potentially valuable to humans or other species on which humans depend. Understanding these characteristics is the value of finding and naming species.

Patterns of Biodiversity

Biodiversity is not evenly distributed on Earth. Lake Victoria contained almost 500 species of cichlids alone, ignoring the other fish families present in the lake. All of these species were found only in Lake Victoria; therefore, the 500 species of cichlids were endemic. Endemic species are found in only one location. Endemics with highly restricted distributions are particularly vulnerable to extinction. Higher taxonomic levels, such as genera and families, can also be endemic. Lake Huron contains about 79 species of fish, all of which are found in many other lakes in North America. What accounts for the difference in fish diversity in these two lakes? Lake Victoria is a tropical lake, while Lake Huron is a temperate lake. Lake Huron in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old. Biogeographers have suggested these two factors, latitude and age, are two of several hypotheses to explain biodiversity patterns on the planet.

Career Connection: Biogeographer

Biogeography is the study of the distribution of the world's species—both in the past and in the present. The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how environmental changes impact the distribution of a species; it has also been critical to developing evolutionary theory. Biogeographers need to understand both biology and ecology. They also need to be well-versed in evolutionary studies, soil science, and climatology.

There are three main fields of study under the heading of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. Ecological biogeography studies the current factors affecting the distribution of plants and animals. Historical biogeography, as the name implies, studies the past distribution of species. Conservation biogeography, on the other hand, is focused on the protection and restoration of species based upon known historical and current ecological information. Each of these fields considers both zoogeography and phytogeography—the past and present distribution of animals and plants.

One of the oldest observed patterns in ecology is that species biodiversity in almost every taxonomic group increases as latitude declines. In other words, biodiversity increases closer to the equator (Figure **58.1.2**).

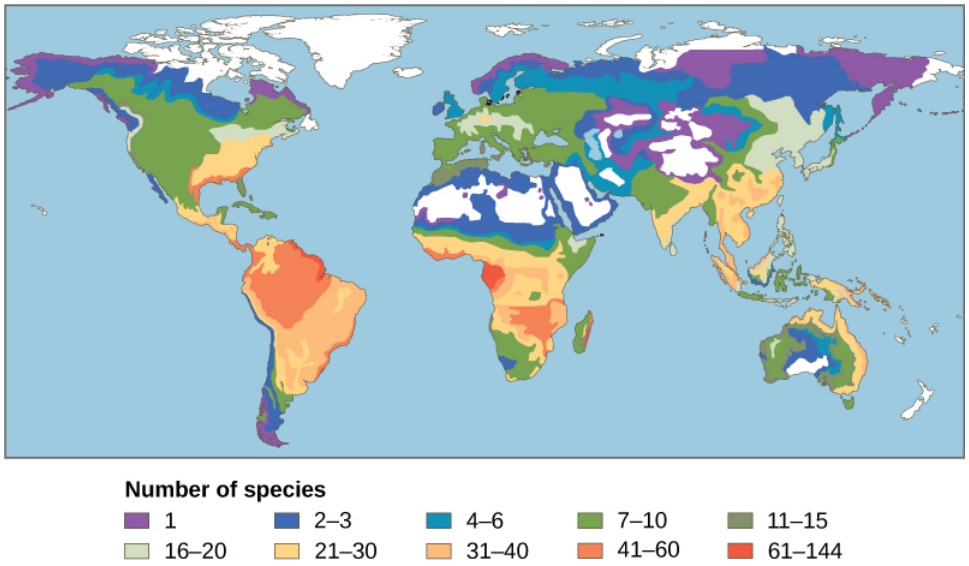


Figure **58.1.2**: This map illustrates the number of amphibian species across the globe and shows the trend toward higher biodiversity at lower latitudes. A similar pattern is observed for most taxonomic groups.

It is not yet clear why biodiversity increases closer to the equator, but hypotheses include the greater age of the ecosystems in the tropics versus temperate regions that were largely devoid of life or drastically impoverished during the last glaciation. The idea is that greater age provides more time for speciation. Another possible explanation is the increased energy the tropics receive from the sun versus the decreased energy that temperate and polar regions receive. It is not entirely clear how greater energy input could translate into more species. The complexity of tropical ecosystems may promote speciation by increasing the heterogeneity, or number of ecological niches, in the tropics relative to higher latitudes. The greater heterogeneity provides more opportunities for coevolution, specialization, and perhaps greater selection pressures leading to population differentiation. However, this hypothesis suffers from some circularity—ecosystems with more species encourage speciation, but how did they get more species to begin with? The tropics have been perceived as being more stable than temperate regions, which have a pronounced climate and day-length seasonality. The tropics have their own forms of seasonality, such as rainfall, but they are generally assumed to be more stable environments and this stability might promote speciation.

Regardless of the mechanisms, it is certainly true that all levels of biodiversity are greatest in the tropics. Additionally, the rate of endemism is highest, and there are more biodiversity hotspots. However, this richness of diversity also means that knowledge of species is lowest, and there is a high potential for biodiversity loss.

Conservation of Biodiversity

In 1988, British environmentalist Norman Myers developed a conservation concept to identify areas rich in species and at significant risk for species loss: biodiversity hotspots. Biodiversity hotspots are geographical areas that contain high numbers of endemic species. The purpose of the concept was to identify important locations on the planet for conservation efforts, a kind of conservation triage. By protecting hotspots, governments are able to protect a larger number of species. The original criteria for a hotspot included the presence of 1500 or more endemic plant species and 70 percent of the area disturbed by human activity. There are now 34 biodiversity hotspots (Figure **58.1.3**) containing large numbers of endemic species, which include half of Earth's endemic plants.

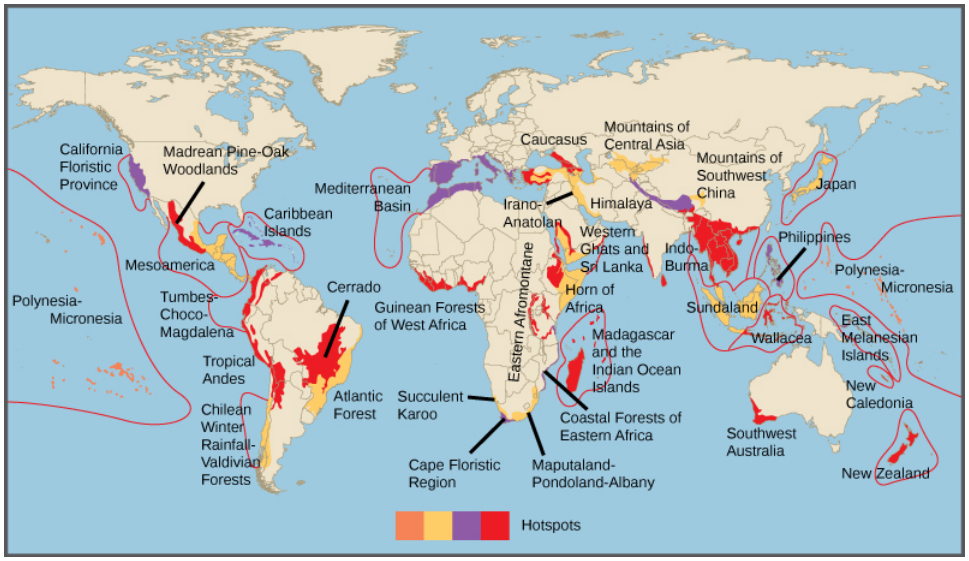


Figure **58.1.3**: Conservation International has identified 34 biodiversity hotspots, which cover only 2.3 percent of the Earth's surface but have endemic to them 42 percent of the terrestrial vertebrate species and 50 percent of the world's plants.

Biodiversity Change through Geological Time

The number of species on the planet, or in any geographical area, is the result of an equilibrium of two evolutionary processes that are ongoing: speciation and extinction. Both are natural "birth" and "death" processes of macroevolution. When speciation rates begin to outstrip extinction rates, the number of species will increase; likewise, the number of species will decrease when extinction rates begin to overtake speciation rates. Throughout Earth's history, these two processes have fluctuated—sometimes leading to dramatic changes in the number of species on Earth as reflected in the fossil record (Figure **58.1.4**).

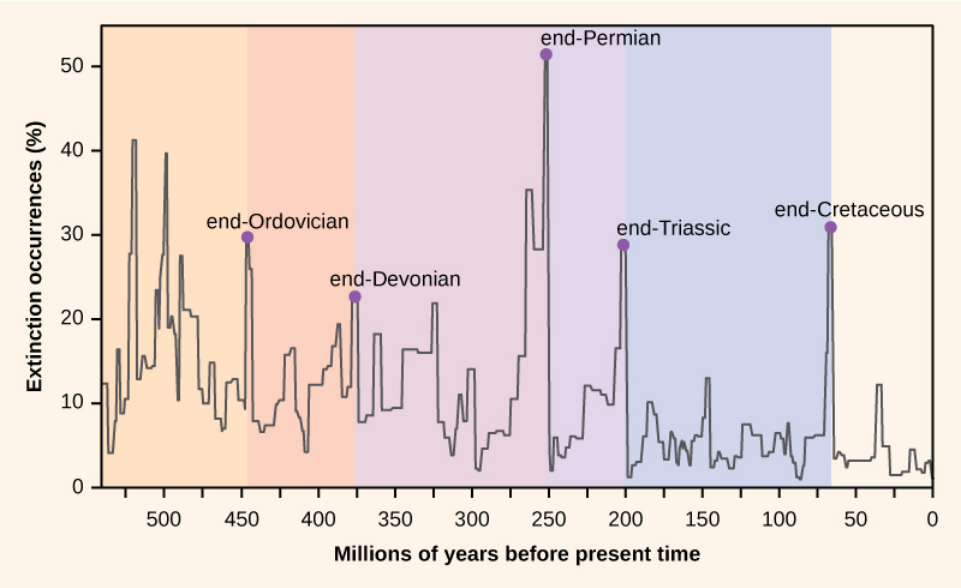


Figure 58.1.4: Percent extinction occurrences as reflected in the fossil record have fluctuated throughout Earth's history. Sudden and dramatic losses of biodiversity, called mass extinctions, have occurred five times.

Paleontologists have identified five strata in the fossil record that appear to show sudden and dramatic (greater than half of all extant species disappearing from the fossil record) losses in biodiversity. These are called mass extinctions. There are many lesser, yet still dramatic, extinction events, but the five mass extinctions have attracted the most research. An argument can be made that the five mass extinctions are only the five most extreme events in a continuous series of large extinction events throughout the Phanerozoic (since 542 million years ago). In most cases, the hypothesized causes are still controversial; however, the most recent event seems clear.

The Five Mass Extinctions

The fossil record of the mass extinctions was the basis for defining periods of geological history, so they typically occur at the transition point between geological periods. The transition in fossils from one period to another reflects the dramatic loss of species and the gradual origin of new species. These transitions can be seen in the rock strata. Table 58.1.2 provides data on the five mass extinctions.

This table shows the names and dates for the five mass extinctions in Earth's history.

Table 58.1.2: Mass extinctions

Geological Period	Mass Extinction Name	Time (millions of years ago)
Ordovician–Silurian	end-Ordovician O–S	450–440
Late Devonian	end-Devonian	375–360
Permian–Triassic	end-Permian	251
Triassic–Jurassic	end-Triassic	205
Cretaceous–Paleogene	end-Cretaceous K–Pg (K–T)	65.5

The Ordovician-Silurian extinction event is the first recorded mass extinction and the second largest. During this period, about 85 percent of marine species (few species lived outside the oceans) became extinct. The main hypothesis for its cause is a period of glaciation and then warming. The extinction event actually consists of two extinction events separated by about 1 million years. The first event was caused by cooling, and the second event was due to the subsequent warming. The climate changes affected temperatures and sea levels. Some researchers have suggested that a gamma-ray burst, caused by a nearby supernova, is a possible cause of the Ordovician-Silurian extinction. The gamma-ray burst would have stripped away the Earth's ozone layer causing intense ultraviolet radiation from the sun and may account for climate changes observed at the time. The hypothesis is speculative,

but extraterrestrial influences on Earth's history are an active line of research. Recovery of biodiversity after the mass extinction took from 5 to 20 million years, depending on the location.

The late Devonian extinction may have occurred over a relatively long period of time. It appears to have affected marine species and not the plants or animals inhabiting terrestrial habitats. The causes of this extinction are poorly understood.

The end-Permian extinction was the largest in the history of life. Indeed, an argument could be made that Earth nearly became devoid of life during this extinction event. The planet looked very different before and after this event. Estimates are that 96 percent of all marine species and 70 percent of all terrestrial species were lost. It was at this time, for example, that the trilobites, a group that survived the Ordovician–Silurian extinction, became extinct. The causes for this mass extinction are not clear, but the leading suspect is extended and widespread volcanic activity that led to a runaway global-warming event. The oceans became largely anoxic, suffocating marine life. Terrestrial tetrapod diversity took 30 million years to recover after the end-Permian extinction. The Permian extinction dramatically altered Earth's biodiversity makeup and the course of evolution.

The causes of the Triassic–Jurassic extinction event are not clear and hypotheses of climate change, asteroid impact, and volcanic eruptions have been argued. The extinction event occurred just before the breakup of the supercontinent Pangaea, although recent scholarship suggests that the extinctions may have occurred more gradually throughout the Triassic.

The causes of the end-Cretaceous extinction event are the ones that are best understood. It was during this extinction event about 65 million years ago that the dinosaurs, the dominant vertebrate group for millions of years, disappeared from the planet (with the exception of a theropod clade that gave rise to birds). Indeed, every land animal that weighed more then 25 kg became extinct. The cause of this extinction is now understood to be the result of a cataclysmic impact of a large meteorite, or asteroid, off the coast of what is now the Yucatán Peninsula. This hypothesis, proposed first in 1980, was a radical explanation based on a sharp spike in the levels of iridium (which rains down from space in meteors at a fairly constant rate but is otherwise absent on Earth's surface) at the rock stratum that marks the boundary between the Cretaceous and Paleogene periods (Figure 58.1.5). This boundary marked the disappearance of the dinosaurs in fossils as well as many other taxa. The researchers who discovered the iridium spike interpreted it as a rapid influx of iridium from space to the atmosphere (in the form of a large asteroid) rather than a slowing in the deposition of sediments during that period. It was a radical explanation, but the report of an appropriately aged and sized impact crater in 1991 made the hypothesis more believable. Now an abundance of geological evidence supports the theory. Recovery times for biodiversity after the end-Cretaceous extinction are shorter, in geological time, than for the end-Permian extinction, on the order of 10 million years.

Art Connection



Figure 58.1.5: In 1980, Luis and Walter Alvarez, Frank Asaro, and Helen Michels discovered, across the world, a spike in the concentration of iridium within the sedimentary layer at the K–Pg boundary. These researchers hypothesized that this iridium spike was caused by an asteroid impact that resulted in the K–Pg mass extinction. In the photo, the iridium layer is the light band. (credit: USGS)

Scientists measured the relative abundance of fern spores above and below the K–Pg boundary in this rock sample. Which of the following statements most likely represents their findings?

A. An abundance of fern spores from several species was found below the K–Pg boundary, but none was found above.
B. An abundance of fern spores from several species was found above the K–Pg boundary, but none was found below.

C. An abundance of fern spores was found both above and below the K–Pg boundary, but only one species was found below the boundary, and many species were found above the boundary.
D. Many species of fern spores were found both above and below the boundary, but the total number of spores was greater below the boundary.

Link to Learning

Explore this interactive website about mass extinctions.

The Pleistocene Extinction

The Pleistocene Extinction is one of the lesser extinctions, and a recent one. It is well known that the North American, and to some degree Eurasian, megafauna, or large animals, disappeared toward the end of the last glaciation period. The extinction appears to have happened in a relatively restricted time period of 10,000–12,000 years ago. In North America, the losses were quite dramatic and included the woolly mammoths (last dated about 4,000 years ago in an isolated population), mastodon, giant beavers, giant ground sloths, saber-toothed cats, and the North American camel, just to name a few. The possibility that the rapid extinction of these large animals was caused by over-hunting was first suggested in the 1900s. Research into this hypothesis continues today. It seems likely that over-hunting caused many pre-written history extinctions in many regions of the world.

In general, the timing of the Pleistocene extinctions correlated with the arrival of humans and not with climate-change events, which is the main competing hypothesis for these extinctions. The extinctions began in Australia about 40,000 to 50,000 years ago, just after the arrival of humans in the area: a marsupial lion, a giant one-ton wombat, and several giant kangaroo species disappeared. In North America, the extinctions of almost all of the large mammals occurred 10,000–12,000 years ago. All that are left are the smaller mammals such as bears, elk, moose, and cougars. Finally, on many remote oceanic islands, the extinctions of many species occurred coincident with human arrivals. Not all of the islands had large animals, but when there were large animals, they were lost. Madagascar was colonized about 2,000 years ago and the large mammals that lived there became extinct. Eurasia and Africa do not show this pattern, but they also did not experience a recent arrival of humans. Humans arrived in Eurasia hundreds of thousands of years ago after the origin of the species in Africa. This topic remains an area of active research and hypothesizing. It seems clear that even if climate played a role, in most cases human hunting precipitated the extinctions.

Present-Time Extinctions

The sixth, or Holocene, mass extinction appears to have begun earlier than previously believed and has mostly to do with the activities of *Homo sapiens*. Since the beginning of the Holocene period, there are numerous recent extinctions of individual species that are recorded in human writings. Most of these are coincident with the expansion of the European colonies since the 1500s.

One of the earlier and popularly known examples is the dodo bird. The dodo bird lived in the forests of Mauritius, an island in the Indian Ocean. The dodo bird became extinct around 1662. It was hunted for its meat by sailors and was easy prey because the dodo, which did not evolve with humans, would approach people without fear. Introduced pigs, rats, and dogs brought to the island by European ships also killed dodo young and eggs.

Steller's sea cow became extinct in 1768; it was related to the manatee and probably once lived along the northwest coast of North America. Steller's sea cow was first discovered by Europeans in 1741 and was hunted for meat and oil. The last sea cow was killed in 1768. That amounts to 27 years between the sea cow’s first contact with Europeans and extinction of the species.

In 1914, the last living passenger pigeon died in a zoo in Cincinnati, Ohio. This species had once darkened the skies of North America during its migrations, but it was hunted and suffered from habitat loss through the clearing of forests for farmland. In

1918, the last living Carolina parakeet died in captivity. This species was once common in the eastern United States, but it suffered from habitat loss. The species was also hunted because it ate orchard fruit when its native foods were destroyed to make way for farmland. The Japanese sea lion, which inhabited a broad area around Japan and the coast of Korea, became extinct in the 1950s due to fishermen. The Caribbean monk seal was distributed throughout the Caribbean Sea but was driven to extinction via hunting by 1952.

These are only a few of the recorded extinctions in the past 500 years. The International Union for Conservation of Nature (IUCN) keeps a list of extinct and endangered species called the Red List. The list is not complete, but it describes 380 extinct species of vertebrates after 1500 AD, 86 of which were driven extinct by overhunting or overfishing.

Estimates of Present-Time Extinction Rates

Estimates of extinction rates are hampered by the fact that most extinctions are probably happening without observation. The extinction of a bird or mammal is likely to be noticed by humans, especially if it has been hunted or used in some other way. But there are many organisms that are of less interest to humans (not necessarily of less value) and many that are undescribed.

The background extinction rate is estimated to be about one per million species per year (E/MSY). For example, assuming there are about ten million species in existence, the expectation is that ten species would become extinct each year (each year represents ten million species per year).

One contemporary extinction rate estimate uses the extinctions in the written record since the year 1500. For birds alone this method yields an estimate of 26 E/MSY. However, this value may be underestimated for three reasons. First, many species would not have been described until much later in the time period, so their loss would have gone unnoticed. Second, the number of recently extinct species is increasing because extinct species now are being described from skeletal remains. And third, some species are probably already extinct even though conservationists are reluctant to name them as such. Taking these factors into account raises the estimated extinction rate closer to 100 E/MSY. The predicted rate by the end of the century is 1500 E/MSY.

A second approach to estimating present-time extinction rates is to correlate species loss with habitat loss by measuring forest-area loss and understanding species-area relationships. The species-area relationship is the rate at which new species are seen when the area surveyed is increased. Studies have shown that the number of species present increases as the size of the island increases. This phenomenon has also been shown to hold true in other habitats as well. Turning this relationship around, if the habitat area is reduced, the number of species living there will also decline. Estimates of extinction rates based on habitat loss and species-area relationships have suggested that with about 90 percent habitat loss an expected 50 percent of species would become extinct. Species-area estimates have led to species extinction rate calculations of about 1000 E/MSY and higher. In general, actual observations do not show this amount of loss and suggestions have been made that there is a delay in extinction. Recent work has also called into question the applicability of the species-area relationship when estimating the loss of species. This work argues that the species-area relationship leads to an overestimate of extinction rates. A better relationship to use may be the endemics-area relationship. Using this method would bring estimates down to around 500 E/MSY in the coming century. Note that this value is still 500 times the background rate.

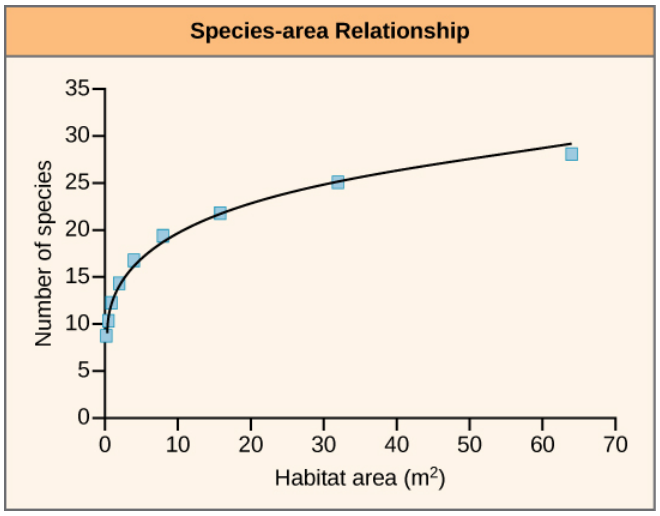


Figure 58.1.6: Studies have shown that the number of species present increases with the size of the habitat. (credit: modification of work by Adam B. Smith)

Link to Learning

Check out this interactive exploration of endangered and extinct species, their ecosystems, and the causes of the endangerment or extinction.

Summary

Biodiversity exists at multiple levels of organization and is measured in different ways depending on the goals of those taking the measurements. These measurements include numbers of species, genetic diversity, chemical diversity, and ecosystem diversity. The number of described species is estimated to be 1.5 million with about 17,000 new species being described each year. Estimates for the total number of species on Earth vary but are on the order of 10 million. Biodiversity is negatively correlated with latitude for most taxa, meaning that biodiversity is higher in the tropics. The mechanism for this pattern is not known with certainty, but several plausible hypotheses have been advanced.

Five mass extinctions with losses of more than 50 percent of extant species are observable in the fossil record. Biodiversity recovery times after mass extinctions vary, but have been up to 30 million years. Recent extinctions are recorded in written history and are the basis for one method of estimating contemporary extinction rates. The other method uses measures of habitat loss and species-area relationships. Estimates of contemporary extinction rates vary, but some rates are as high as 500 times the background rate, as determined from the fossil record, and are predicted to rise.

Art Connections

Figure 58.1.5: Scientists measured the relative abundance of fern spores above and below the K-Pg boundary in this rock sample. Which of the following statements most likely represents their findings?

A. An abundance of fern spores from several species was found below the K-Pg boundary, but none was found above.
B. An abundance of fern spores from several species was found above the K-Pg boundary, but none was found below.
C. An abundance of fern spores was found both above and below the K-Pg boundary, but only one species was found below the boundary , and many species were found above the boundary.

D. Many species of fern spores were found both above and below the boundary, but the total number of spores was greater below the boundary.

Answer

A. An abundance of fern spores from several species was found below the K-Pg boundary, but none was found above.

Footnotes

1. 1 Mora Camilo et al., "How Many Species Are There on Earth and in the Ocean?" *PLoS Biology* (2011), doi:10.1371/journal.pbio.1001127.
2. 2 Arthur D. Chapman, *Numbers of Living Species in Australia and the World*, 2nd ed. (Canberra, AU: Australian Biological Resources Study, 2009). www.environment.gov.au/biodiv...d-complete.pdf.
3. 3 Brian Groombridge and Martin D. Jenkins. *World Atlas of Biodiversity: Earth's Living Resources in the 21st Century*. Berkeley: University of California Press, 2002.
4. 4 International Institute for Species Exploration (IISE), *2011 State of Observed Species (SOS)*. Tempe, AZ: IISE, 2011. Accessed May, 20, 2012. species.asu.edu/SOS.

Glossary

adaptive radiation
rapid branching through speciation of a phylogenetic tree into many closely related species

biodiversity
variety of a biological system, typically conceived as the number of species, but also applying to genes, biochemistry, and ecosystems

biodiversity hotspot
concept originated by Norman Myers to describe a geographical region with a large number of endemic species and a large percentage of degraded habitat

chemical diversity
variety of metabolic compounds in an ecosystem

ecosystem diversity
variety of ecosystems

endemic species
species native to one place

extinction
disappearance of a species from Earth; local extinction is the disappearance of a species from a region

extinction rate
number of species becoming extinct over time, sometimes defined as extinctions per million species–years to make numbers manageable (E/MSY)

genetic diversity
variety of genes in a species or other taxonomic group or ecosystem, the term can refer to allelic diversity or genome-wide diversity

heterogeneity
number of ecological niches

megafauna

large animals

species-area relationship

relationship between area surveyed and number of species encountered; typically measured by incrementally increasing the area of a survey and determining the cumulative numbers of species

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58.2: The Value of Biodiversity

Skills to Develop

- Identify chemical diversity benefits to humans
- Identify biodiversity components that support human agriculture
- Describe ecosystem services

It may not be clear why biologists are concerned about biodiversity loss. When biodiversity loss is thought of as the extinction of the passenger pigeon, the dodo bird, and even the woolly mammoth, the loss may appear to be an emotional one. But is the loss practically important for the welfare of the human species? From the perspective of evolution and ecology, the loss of a particular individual species is unimportant (however, the loss of a keystone species can lead to ecological disaster). Extinction is a normal part of macroevolution. But the accelerated extinction rate means the loss of tens of thousands of species within our lifetimes, and it is likely to have dramatic effects on human welfare through the collapse of ecosystems and in added costs to maintain food production, clean air and water, and human health.

Agriculture began after early hunter-gatherer societies first settled in one place and heavily modified their immediate environment. This cultural transition has made it difficult for humans to recognize their dependence on undomesticated living things on the planet. Biologists recognize the human species is embedded in ecosystems and is dependent on them, just as every other species on the planet is dependent. Technology smoothes out the extremes of existence, but ultimately the human species cannot exist without its ecosystem.

Human Health

Contemporary societies that live close to the land often have a broad knowledge of the medicinal uses of plants growing in their area. Most plants produce secondary plant compounds, which are toxins used to protect the plant from insects and other animals that eat them, but some of which also work as medication. For centuries in Europe, older knowledge about the medical uses of plants was compiled in herbals—books that identified plants and their uses. Humans are not the only species to use plants for medicinal reasons: the great apes, orangutans, chimpanzees, bonobos, and gorillas have all been observed self-medicating with plants.

Modern pharmaceutical science also recognizes the importance of these plant compounds. Examples of significant medicines derived from plant compounds include aspirin, codeine, digoxin, atropine, and vincristine (Figure **58.2.1**). Many medicines were once derived from plant extracts but are now synthesized. It is estimated that, at one time, 25 percent of modern drugs contained at least one plant extract. That number has probably decreased to about 10 percent as natural plant ingredients are replaced by synthetic versions. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.



Figure **58.2.1**: *Catharanthus roseus*, the Madagascar periwinkle, has various medicinal properties. Among other uses, it is a source of vincristine, a drug used in the treatment of lymphomas. (credit: Forest and Kim Starr)

In recent years, animal venoms and poisons have excited intense research for their medicinal potential. By 2007, the FDA had approved five drugs based on animal toxins to treat diseases such as hypertension, chronic pain, and diabetes. Another five drugs are undergoing clinical trials, and at least six drugs are being used in other countries. Other toxins under investigation come from mammals, snakes, lizards, various amphibians, fish, snails, octopuses, and scorpions.

Aside from representing billions of dollars in profits, these medicines improve people's lives. Pharmaceutical companies are actively looking for new compounds synthesized by living organisms that can function as medicine. It is estimated that 1/3 of pharmaceutical research and development is spent on natural compounds and that about 35 percent of new drugs brought to market between 1981 and 2002 were from natural compounds. The opportunities for new medications will be reduced in direct proportion to the disappearance of species.

Agricultural Diversity

Since the beginning of human agriculture more than 10,000 years ago, human groups have been breeding and selecting crop varieties. This crop diversity matched the cultural diversity of highly subdivided populations of humans. For example, potatoes were domesticated beginning around 7,000 years ago in the central Andes of Peru and Bolivia. The potatoes grown in that region belong to seven species and the number of varieties likely is in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the diverse demands of the topography, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields.

Potatoes are only one example of human-generated diversity. Every plant, animal, and fungus that has been cultivated by humans has been bred from original wild ancestor species into diverse varieties arising from the demands for food value, adaptation to growing conditions, and resistance to pests. The potato demonstrates a well-known example of the risks of low crop diversity: the tragic Irish potato famine when the single variety grown in Ireland became susceptible to a potato blight, wiping out the crop. The loss of the crop led to famine, death, and mass emigration. Resistance to disease is a chief benefit to maintaining crop biodiversity, and lack of diversity in contemporary crop species carries similar risks. Seed companies, which are the source of most crop varieties in developed countries, must continually breed new varieties to keep up with evolving pest organisms. These same seed companies, however, have participated in the decline of the number of varieties available as they focus on selling fewer varieties in more areas of the world.

The ability to create new crop varieties relies on the diversity of varieties available and the accessibility of wild forms related to the crop plant. These wild forms are often the source of new gene variants that can be bred with existing varieties to create varieties with new attributes. Loss of wild species related to a crop will mean the loss of potential in crop improvement. Maintaining the genetic diversity of wild species related to domesticated species ensures our continued food supply.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. This system has flaws because, over time, seed banks are lost through accidents, and there is no way to replace them. In

2008, the Svalbard Global Seed Vault (Figure 58.2.2) began storing seeds from around the world as a backup system to the regional seed banks. If a regional seed bank stores varieties in Svalbard, losses can be replaced from Svalbard. The seed vault is located deep into the rock of an arctic island. Conditions within the vault are maintained at ideal temperature and humidity for seed survival, but the deep underground location of the vault in the arctic means that failure of the vault's systems will not compromise the climatic conditions inside the vault.

Art Connection



Figure 58.2.2: The Svalbard Global Seed Vault is a storage facility for seeds of Earth's diverse crops. (credit: Mari Tefre, Svalbard Global Seed Vault)

The Svalbard Global Seed Vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Crop success is largely dependent on the quality of the soil. Although some agricultural soils are rendered sterile using controversial cultivation and chemical treatments, most contain a huge diversity of organisms that maintain nutrient cycles—breaking down organic matter into nutrient compounds that crops need for growth. These organisms also maintain soil texture that affects water and oxygen dynamics in the soil that are necessary for plant growth. If farmers had to maintain arable soil using alternate means, the cost of food would be much higher than it is now. These kinds of processes are called ecosystem services. They occur within ecosystems, such as soil ecosystems, as a result of the diverse metabolic activities of the organisms living there, but they provide benefits to human food production, drinking water availability, and breathable air.

Other key ecosystem services related to food production are plant pollination and crop pest control. Over 150 crops in the United States require pollination to produce. One estimate of the benefit of honeybee pollination within the United States is $1.6 billion per year; other pollinators contribute up to $6.7 billion more.

Many honeybee populations are managed by apiarists who rent out their hives' services to farmers. Honeybee populations in North America have been suffering large losses caused by a syndrome known as colony collapse disorder, whose cause is unclear. Other pollinators include a diverse array of other bee species and various insects and birds. Loss of these species would make growing crops requiring pollination impossible, increasing dependence on other crops.

Finally, humans compete for their food with crop pests, most of which are insects. Pesticides control these competitors; however, pesticides are costly and lose their effectiveness over time as pest populations adapt. They also lead to collateral damage by killing non-pest species and risking the health of consumers and agricultural workers. Ecologists believe that the bulk of the work in removing pests is actually done by predators and parasites of those pests, but the impact has not been well studied. A review found that in 74 percent of studies that looked for an effect of landscape complexity on natural enemies of pests, the greater the complexity, the greater the effect of pest-suppressing organisms. An experimental study found that introducing multiple enemies of pea aphids (an important alfalfa pest) increased the yield of alfalfa significantly. This study shows the importance of landscape diversity via the question of whether a diversity of pests is more effective at control than one single pest; the results showed this to be the case. Loss of diversity in pest enemies will inevitably make it more difficult and costly to grow food.

Wild Food Sources

In addition to growing crops and raising animals for food, humans obtain food resources from wild populations, primarily fish populations. For approximately 1 billion people, aquatic resources provide the main source of animal protein. But since 1990, global fish production has declined. Despite considerable effort, few fisheries on the planet are managed for sustainability.

Fishery extinctions rarely lead to complete extinction of the harvested species, but rather to a radical restructuring of the marine ecosystem in which a dominant species is so over-harvested that it becomes a minor player, ecologically. In addition to humans losing the food source, these alterations affect many other species in ways that are difficult or impossible to predict. The collapse of fisheries has dramatic and long-lasting effects on local populations that work in the fishery. In addition, the loss of an inexpensive protein source to populations that cannot afford to replace it will increase the cost of living and limit societies in other ways. In general, the fish taken from fisheries have shifted to smaller species as larger species are fished to extinction. The ultimate outcome could clearly be the loss of aquatic systems as food sources.

Psychological and Moral Value

Finally, it has been argued that humans benefit psychologically from living in a biodiverse world. A chief proponent of this idea is entomologist E. O. Wilson. He argues that human evolutionary history has adapted us to live in a natural environment and that built environments generate stressors that affect human health and well-being. There is considerable research into the psychological regenerative benefits of natural landscapes that suggests the hypothesis may hold some truth. In addition, there is a moral argument that humans have a responsibility to inflict as little harm as possible on other species.

Summary

Humans use many compounds that were first discovered or derived from living organisms as medicines: secondary plant compounds, animal toxins, and antibiotics produced by bacteria and fungi. More medicines are expected to be discovered in nature. Loss of biodiversity will impact the number of pharmaceuticals available to humans.

Crop diversity is a requirement for food security, and it is being lost. The loss of wild relatives to crops also threatens breeders' abilities to create new varieties. Ecosystems provide ecosystem services that support human agriculture: pollination, nutrient cycling, pest control, and soil development and maintenance. Loss of biodiversity threatens these ecosystem services and risks making food production more expensive or impossible. Wild food sources are mainly aquatic, but few are being managed for sustainability. Fisheries' ability to provide protein to human populations is threatened when extinction occurs.

Biodiversity may provide important psychological benefits to humans. Additionally, there are moral arguments for the maintenance of biodiversity.

Art Connections

Figure 58.2.2: The Svalbard Global Seed Vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Answer

The ground is permanently frozen so the seeds will keep even if the electricity fails.

Glossary

secondary plant compound

compound produced as byproducts of plant metabolic processes that is usually toxic, but is sequestered by the plant to defend against herbivores

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58.3: Factors Responsible for Extinction

Skills to Develop

- Identify significant threats to biodiversity
- Explain the effects of habitat loss, exotic species, and hunting on biodiversity
- Identify the early and predicted effects of climate change on biodiversity

The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and resource exploitation. The human population requires resources to survive and grow, and those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are habitat loss, overharvesting, and introduction of exotic species. The first two of these are a direct result of human population growth and resource use. The third results from increased mobility and trade. A fourth major cause of extinction, anthropogenic climate change, has not yet had a large impact, but it is predicted to become significant during this century. Global climate change is also a consequence of human population needs for energy and the use of fossil fuels to meet those needs (Figure **58.3.1**). Environmental issues, such as toxic pollution, have specific targeted effects on species, but they are not generally seen as threats at the magnitude of the others.

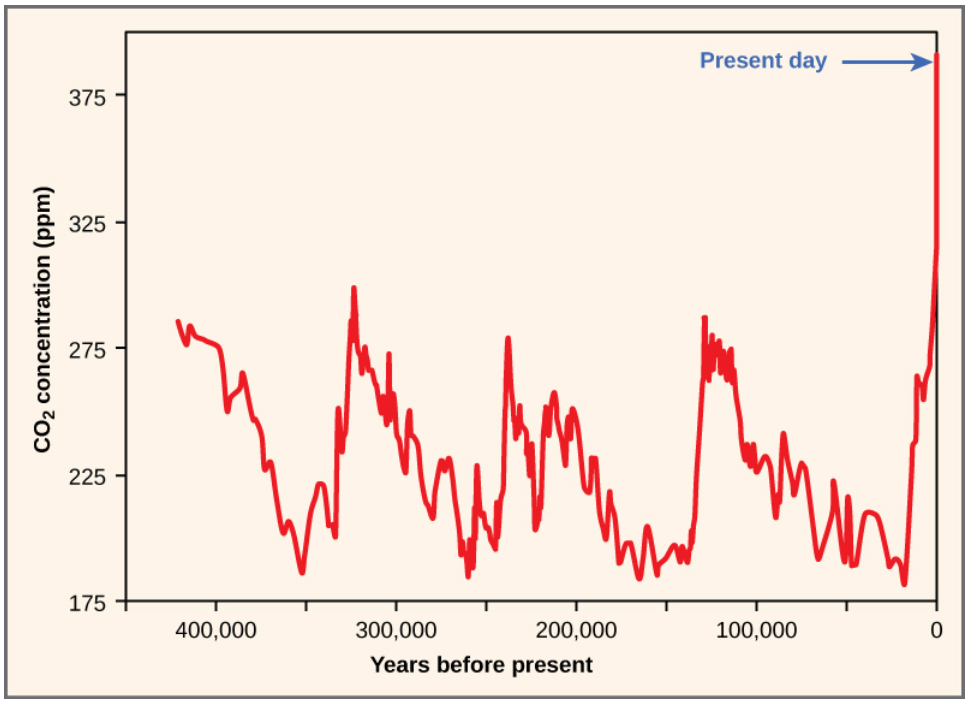


Figure **58.3.1**: Atmospheric carbon dioxide levels fluctuate in a cyclical manner. However, the burning of fossil fuels in recent history has caused a dramatic increase in the levels of carbon dioxide in the Earth's atmosphere, which have now reached levels never before seen in human history. Scientists predict that the addition of this "greenhouse gas" to the atmosphere is resulting in climate change that will significantly impact biodiversity in the coming century.

Habitat Loss

Humans rely on technology to modify their environment and replace certain functions that were once performed by the natural ecosystem. Other species cannot do this. Elimination of their ecosystem—whether it is a forest, a desert, a grassland, a freshwater estuarine, or a marine environment—will kill the individuals in the species. Remove the entire habitat within the range of a species and, unless they are one of the few species that do well in human-built environments, the species will become extinct. Human destruction of habitats accelerated in the latter half of the twentieth century. Consider the exceptional biodiversity of Sumatra: it is home to one species of orangutan, a species of critically endangered elephant, and the Sumatran tiger, but half of Sumatra's forest is now gone. The neighboring island of Borneo, home to the other species of orangutan, has lost a similar area of forest. Forest loss continues in protected areas of Borneo. The orangutan in Borneo is listed as endangered by the International Union for Conservation of Nature (IUCN), but it is simply the most visible of thousands of species that will not survive the disappearance of

the forests of Borneo. The forests are removed for timber and to plant palm oil plantations (Figure **58.3.2**). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. A five-year estimate of global forest cover loss for the years 2000–2005 was 3.1 percent. In the humid tropics where forest loss is primarily from timber extraction, 272,000 km^2 was lost out of a global total of 11,564,000 km^2 (or 2.4 percent). In the tropics, these losses certainly also represent the extinction of species because of high levels of endemism.

https://bio.libretexts.org/@go/page/74467



(a)



(b)



(c)



(d)



(e)

Figure 58.3.2: (a) One species of orangutan, *Pongo pygmaeus*, is found only in the rainforests of Borneo, and the other species of orangutan (*Pongo abelii*) is found only in the rainforests of Sumatra. These animals are examples of the exceptional biodiversity of (c) the islands of Sumatra and Borneo. Other species include the (b) Sumatran tiger (*Panthera tigris sumatrae*) and the (d) Sumatran elephant (*Elephas maximus sumatranus*), both critically endangered species. Rainforest habitat is being removed to make way for (e) oil palm plantations such as this one in Borneo's Sabah Province. (credit a: modification of work by Thorsten Bachner; credit b: modification of work by Dick Mudde; credit c: modification of work by U.S. CIA World Factbook; credit d: modification of work by "Nonprofit Organizations"/Flickr; credit e: modification of work by Dr. Lian Pin Koh)

Everyday Connection: Preventing Habitat Destruction with Wise Wood Choices

Most consumers do not imagine that the home improvement products they buy might be contributing to habitat loss and species extinctions. Yet the market for illegally harvested tropical timber is huge, and the wood products often find themselves in building supply stores in the United States. One estimate is that 10 percent of the imported timber stream in the United States, which is the world's largest consumer of wood products, is potentially illegally logged. In 2006, this amounted to $3.6 billion in wood products. Most of the illegal products are imported from countries that act as intermediaries and are not the originators of the wood.

How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally? The Forest Stewardship Council (FSC) certifies sustainably harvested forest products, therefore, looking for their certification on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest. Certification applies to specific products, not to a producer; some producers' products may not have certification while other products are certified. While there are other industry-backed certifications other than the FSC, these are unreliable due to lack of independence from the industry. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal wood products, it is not that simple. Logging and forest management laws vary from country to country; what is illegal in one country may be legal in another. Where and how a product is harvested and whether the forest from which it comes is being maintained sustainably all factor into whether a wood product will be certified by the FSC. It is always a good idea to ask questions about where a wood product came from and how the supplier knows that it was harvested legally.

Habitat destruction can affect ecosystems other than forests. Rivers and streams are important ecosystems and are frequently modified through land development and from damming or water removal. Damming of rivers affects the water flow and access to all parts of a river. Differing flow regimes can reduce or eliminate populations that are adapted to these changes in flow patterns. For example, an estimated 91percent of river lengths in the United States have been developed: they have modifications like dams, to create energy or store water; levees, to prevent flooding; or dredging or rerouting, to create land that is more suitable for human development. Many fish species in the United States, especially rare species or species with restricted distributions, have seen declines caused by river damming and habitat loss. Research has confirmed that species of amphibians that must carry out parts of their life cycles in both aquatic and terrestrial habitats have a greater chance of suffering population declines and extinction because of the increased likelihood that one of their habitats or access between them will be lost.

Overharvesting

Overharvesting is a serious threat to many species, but particularly to aquatic species. There are many examples of regulated commercial fisheries monitored by fisheries scientists that have nevertheless collapsed. The western Atlantic cod fishery is the most spectacular recent collapse. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s and the pressure on the fishery led to it becoming unsustainable. The causes of fishery collapse are both economic and political in nature. Most fisheries are managed as a common (shared) resource even when the fishing territory lies within a country's territorial waters. Common resources are subject to an economic pressure known as the tragedy of the commons in which essentially no fisher has a motivation to exercise restraint in harvesting a fishery when it is not owned by that fisher. The natural outcome of harvests of resources held in common is their overexploitation. While large fisheries are regulated to attempt to avoid this pressure, it still exists in the background. This overexploitation is exacerbated when access to the fishery is open and unregulated and when technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases—whales are an example—economic forces will always drive toward fishing the population to extinction.

Link to Learning



Explore a U.S. Fish & Wildlife Service interactive map of critical habitat for endangered and threatened species in the United States. To begin, select “Visit the online mapper.”

For the most part, fishery extinction is not equivalent to biological extinction—the last fish of a species is rarely fished out of the ocean. At the same time, fishery extinction is still harmful to fish species and their ecosystems. There are some instances in which true extinction is a possibility. Whales have slow-growing populations and are at risk of complete extinction through hunting. There are some species of sharks with restricted distributions that are at risk of extinction. The groupers are another population of generally slow-growing fishes that, in the Caribbean, includes a number of species that are at risk of extinction from overfishing.

Coral reefs are extremely diverse marine ecosystems that face peril from several processes. Reefs are home to 1/3 of the world’s marine fish species—about 4,000 species—despite making up only 1 percent of marine habitat. Most home marine aquaria are stocked with wild-caught organisms, not cultured organisms. Although no species is known to have been driven extinct by the pet trade in marine species, there are studies showing that populations of some species have declined in response to harvesting, indicating that the harvest is not sustainable at those levels. There are concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutan.

Bush meat is the generic term used for wild animals killed for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten several species with extinction. Traditionally, bush meat in Africa was hunted to feed families directly; however, recent commercialization of the practice now has bush meat available in grocery stores, which has increased harvest rates to the level of unsustainability. Additionally, human population growth has increased the need for protein foods that are not being met from agriculture. Species threatened by the bush meat trade are mostly mammals including many primates living in the Congo basin.

Exotic Species

Exotic species are species that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Such introductions likely occur frequently as natural phenomena. For example, Kudzu (*Pueraria lobata*), which is native to Japan, was introduced in the United States in 1876. It was later planted for soil conservation. Problematically, it grows too well in the southeastern United States—up to a foot a day. It is now a pest species and covers over 7 million acres in the southeastern United States. If an introduced species is able to survive in its new habitat, that introduction is now reflected in the observed range of the species. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems, sometimes at distances that are well beyond the capacity of the species to ever travel itself and outside the range of the species’ natural predators.

Most exotic species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, possess preadaptations that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the species that exist there. For this reason, exotic species are also called invasive species. Exotic species can threaten other species through competition for resources, predation, or disease.

Link to Learning

Explore an interactive global database of exotic or invasive species.

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria, as mentioned earlier, the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of cichlids. The accidental introduction of the brown tree snake via aircraft (Figure **58.3.3**) from the Solomon Islands to Guam in 1950 has led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are still threatened. The brown tree snake is adept at exploiting human transportation as a means to migrate; one was even found on an aircraft arriving in Corpus Christi, Texas. Constant vigilance on the part of airport, military, and commercial aircraft personnel is required to prevent the snake from moving from Guam to other islands in the Pacific, especially Hawaii. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.

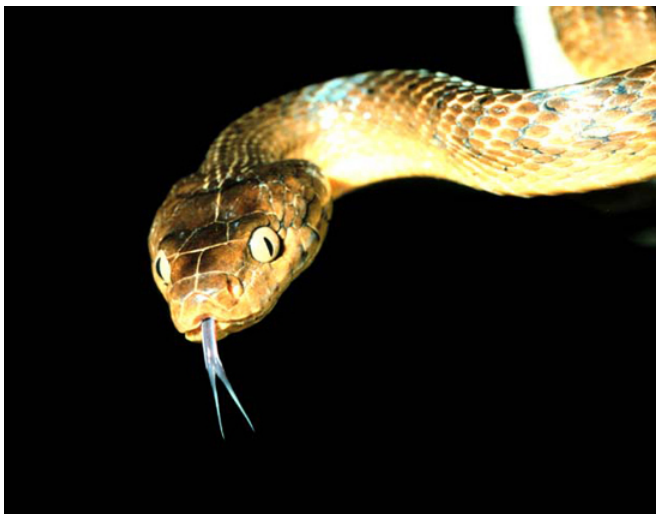


Figure **58.3.3**: The brown tree snake, *Boiga irregularis*, is an exotic species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950. (credit: NPS)

It now appears that the global decline in amphibian species recognized in the 1990s is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease chytridiomycosis (Figure **58.3.4**). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed toad (*Xenopus laevis*). It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *Batrachochytrium dendrobatidis* and can act as a reservoir for the disease.



Figure **58.3.4**: This Limosa Harlequin Frog (*Atelopus limosus*), an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease. (credit: Brian Gratwicke)

Early evidence suggests that another fungal pathogen, *Geomyces destructans*, introduced from Europe is responsible for white-nose syndrome, which infects cave-hibernating bats in eastern North America and has spread from a point of origin in western New York State (Figure **58.3.5**). The disease has decimated bat populations and threatens extinction of species already listed as endangered: the Indiana bat, *Myotis sodalis*, and potentially the Virginia big-eared bat, *Corynorhinus townsendii virginianus*. How the fungus was introduced is unclear, but one logical presumption would be that recreational cavers unintentionally brought the fungus on clothes or equipment from Europe.



Figure **58.3.5**: This little brown bat in Greeley Mine, Vermont, March 26, 2009, was found to have white-nose syndrome. (credit: Marvin Moriarty, USFWS)

Climate Change

Climate change, and specifically the anthropogenic (meaning, caused by humans) warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species committed to extinction by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way. The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears. Previously, these two species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring. Changing climates also throw off species' delicate timing adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.



Figure **58.3.6**: Since 2008, grizzly bears (*Ursus arctos horribilis*) have been spotted farther north than their historic range, a possible consequence of climate change. As a result, grizzly bear habitat now overlaps polar bear (*Ursus maritimus*) habitat. The two kinds of bears, which are capable of mating and producing viable offspring, are considered separate species as historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first wild hybrid ever found.

Range shifts are already being observed: for example, some European bird species ranges have moved 91 km northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are not moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The rate of warming appears to be accelerated in the arctic, which is recognized as a serious threat to polar bear populations that require sea ice to hunt seals during the winter months: seals are the only source of protein available to polar bears. A trend to decreasing sea ice coverage has occurred since observations began in the mid-twentieth century. The rate of decline observed in recent years is far greater than previously predicted by climate models.

Finally, global warming will raise ocean levels due to melt water from glaciers and the greater volume of warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher elevation mountains—a cycle that has provided freshwater to environments for centuries—will also be jeopardized. This could result in an overabundance of salt water and a shortage of fresh water.

Summary

The core threats to biodiversity are human population growth and unsustainable resource use. To date, the most significant causes of extinctions are habitat loss, introduction of exotic species, and overharvesting. Climate change is predicted to be a significant cause of extinctions in the coming century. Habitat loss occurs through deforestation, damming of rivers, and other activities.

Overharvesting is a threat particularly to aquatic species, while the taking of bush meat in the humid tropics threatens many species in Asia, Africa, and the Americas. Exotic species have been the cause of a number of extinctions and are especially damaging to islands and lakes. Exotic species' introductions are increasing because of the increased mobility of human populations and growing global trade and transportation. Climate change is forcing range changes that may lead to extinction. It is also affecting adaptations to the timing of resource availability that negatively affects species in seasonal environments. The impacts of climate change are greatest in the arctic. Global warming will also raise sea levels, eliminating some islands and reducing the area of all others.

Art Connections

Converting a prairie to a farm field is an example of _____.

A. overharvesting
B. habitat loss
C. exotic species
D. climate change

Answer

B

Glossary

bush meat
wild-caught animal used as food (typically mammals, birds, and reptiles); usually referring to hunting in the tropics of sub-Saharan Africa, Asia, and the Americas

chytridiomycosis
disease of amphibians caused by the fungus *Batrachochytrium dendrobatidis;* thought to be a major cause of the global amphibian decline

exotic species
(also, invasive species) species that has been introduced to an ecosystem in which it did not evolve

tragedy of the commons
economic principle that resources held in common will inevitably be overexploited

white-nose syndrome
disease of cave-hibernating bats in the eastern United States and Canada associated with the fungus *Geomyces destructans*

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58.3.1: Preserving Biodiversity

Skills to Develop

- Identify new technologies for describing biodiversity
- Explain the legislative framework for conservation
- Describe principles and challenges of conservation preserve design
- Identify examples of the effects of habitat restoration
- Discuss the role of zoos in biodiversity conservation

Preserving biodiversity is an extraordinary challenge that must be met by greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies.

Measuring Biodiversity

The technology of molecular genetics and data processing and storage are maturing to the point where cataloguing the planet's species in an accessible way is close to feasible. DNA barcoding is one molecular genetic method, which takes advantage of rapid evolution in a mitochondrial gene present in eukaryotes, excepting the plants, to identify species using the sequence of portions of the gene. Plants may be barcoded using a combination of chloroplast genes. Rapid mass sequencing machines make the molecular genetics portion of the work relatively inexpensive and quick. Computer resources store and make available the large volumes of data. Projects are currently underway to use DNA barcoding to catalog museum specimens, which have already been named and studied, as well as testing the method on less studied groups. As of mid 2012, close to 150,000 named species had been barcoded. Early studies suggest there are significant numbers of undescribed species that looked too much like sibling species to previously be recognized as different. These now can be identified with DNA barcoding.

Numerous computer databases now provide information about named species and a framework for adding new species. However, as already noted, at the present rate of description of new species, it will take close to 500 years before the complete catalog of life is known. Many, perhaps most, species on the planet do not have that much time.

There is also the problem of understanding which species known to science are threatened and to what degree they are threatened. This task is carried out by the non-profit IUCN which, as previously mentioned, maintains the Red List—an online listing of endangered species categorized by taxonomy, type of threat, and other criteria (Figure **58.3.1.1**). The Red List is supported by scientific research. In 2011, the list contained 61,000 species, all with supporting documentation.

Art Connection

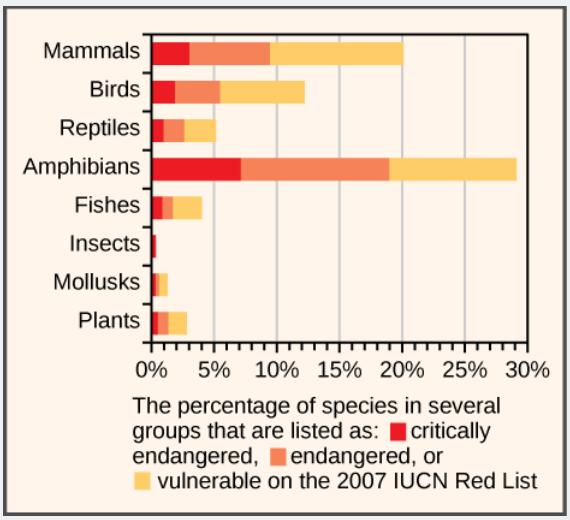


Figure **58.3.1.1**: This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007.

Which of the following statements is not supported by this graph?

A. There are more vulnerable fishes than critically endangered and endangered fishes combined.

B. There are more critically endangered amphibians than vulnerable, endangered and critically endangered reptiles combined.
C. Within each group, there are more critically endangered species than vulnerable species.
D. A greater percentage of bird species are critically endangered than mollusk species.

Changing Human Behavior

Legislation throughout the world has been enacted to protect species. The legislation includes international treaties as well as national and state laws. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) treaty came into force in 1975. The treaty, and the national legislation that supports it, provides a legal framework for preventing approximately 33,000 listed species from being transported across nations' borders, thus protecting them from being caught or killed when international trade is involved. The treaty is limited in its reach because it only deals with international movement of organisms or their parts. It is also limited by various countries' ability or willingness to enforce the treaty and supporting legislation. The illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars. Illegal wildlife trade is monitored by another non-profit: Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC).

Within many countries there are laws that protect endangered species and regulate hunting and fishing. In the United States, the Endangered Species Act (ESA) was enacted in 1973. Species at risk are listed by the Act; the U.S. Fish & Wildlife Service is required by law to develop management plans that protect the listed species and bring them back to sustainable numbers. The Act, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed, or to get an effective management plan in place once it is listed. Additionally, species may be controversially taken off the list without necessarily having had a change in their situation. More fundamentally, the approach to protecting individual species rather than entire ecosystems is both inefficient and focuses efforts on a few highly visible and often charismatic species, perhaps at the expense of other species that go unprotected. At the same time, the Act has a critical habitat provision outlined in the recovery mechanism that may benefit species other than the one targeted for management.

The Migratory Bird Treaty Act (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers).

The international response to global warming has been mixed. The Kyoto Protocol, an international agreement that came out of the United Nations Framework Convention on Climate Change that committed countries to reducing greenhouse gas emissions by 2012, was ratified by some countries, but spurned by others. Two important countries in terms of their potential impact that did not ratify the Kyoto Protocol were the United States and China. The United States rejected it as a result of a powerful fossil fuel industry and China because of a concern it would stifle the nation's growth. Some goals for reduction in greenhouse gasses were met and exceeded by individual countries, but worldwide, the effort to limit greenhouse gas production is not succeeding. The intended replacement for the Kyoto Protocol has not materialized because governments cannot agree on timelines and benchmarks. Meanwhile, climate scientists predict the resulting costs to human societies and biodiversity will be high.

As already mentioned, the private non-profit sector plays a large role in the conservation effort both in North America and around the world. The approaches range from species-specific organizations to the broadly focused IUCN and TRAFFIC. The Nature Conservancy takes a novel approach. It purchases land and protects it in an attempt to set up preserves for ecosystems. Ultimately, human behavior will change when human values change. At present, the growing urbanization of the human population is a force that poses challenges to the valuing of biodiversity.

Conservation in Preserves

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts. A preserve is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Preserves can be effective in the short term for protecting both species and ecosystems, but they face challenges that scientists are still exploring to strengthen their viability as long-term solutions.

How Much Area to Preserve?

Due to the way protected lands are allocated (they tend to contain less economically valuable resources rather than being set aside specifically for the species or ecosystems at risk) and the way biodiversity is distributed, determining a target percentage of land or marine habitat that should be protected to maintain biodiversity levels is challenging. The IUCN World Parks Congress estimated that 11.5 percent of Earth's land surface was covered by preserves of various kinds in 2003. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes. Research has shown that 12 percent of all species live only outside preserves; these percentages are much higher when only threatened species and high quality preserves are considered. For example, high quality preserves include only about 50 percent of threatened amphibian species. The conclusion must be that either the percentage of area protected must increase, or the percentage of high quality preserves must increase, or preserves must be targeted with greater attention to biodiversity protection. Researchers argue that more attention to the latter solution is required.

Preserve Design

There has been extensive research into optimal preserve designs for maintaining biodiversity. The fundamental principle behind much of the research has been the seminal theoretical work of Robert H. MacArthur and Edward O. Wilson published in 1967 on island biogeography.[1] This work sought to understand the factors affecting biodiversity on islands. The fundamental conclusion was that biodiversity on an island was a function of the origin of species through migration, speciation, and extinction on that island. Islands farther from a mainland are harder to get to, so migration is lower and the equilibrium number of species is lower. Within island populations, evidence suggests that the number of species gradually increases to a level similar to the numbers on the mainland from which the species is suspected to have migrated. In addition, smaller islands are harder to find, so their immigration rates for new species are lower. Smaller islands are also less geographically diverse so there are fewer niches to promote speciation. And finally, smaller islands support smaller populations, so the probability of extinction is higher.

As islands get larger, the number of species accelerates, although the effect of island area on species numbers is not a direct correlation. Conservation preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. For a species to persist in a preserve, the preserve must be large enough. The critical size depends, in part, on the home range that is characteristic of the species. A preserve for wolves, which range hundreds of kilometers, must be much larger than a preserve for butterflies, which might range within ten kilometers during its lifetime. But larger preserves have more core area of optimal habitat for individual species, they have more niches to support more species, and they attract more species because they can be found and reached more easily.

Preserves perform better when there are buffer zones around them of suboptimal habitat. The buffer allows organisms to exit the boundaries of the preserve without immediate negative consequences from predation or lack of resources. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by edges. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing wildlife corridors between them so that individuals and their genes can move between the preserves, for example along rivers and streams, will make the smaller preserves behave more like a large one. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

In addition to the physical, biological, and ecological specifications of a preserve, there are a variety of policy, legislative, and enforcement specifications related to uses of the preserve for functions other than protection of species. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive human recreation. Many of these policy decisions are made based on political pressures rather than conservation considerations. In some cases, wildlife protection policies have been so strict that subsistence-living indigenous populations have been forced from ancestral lands that fell within a preserve. In other cases, even if a preserve is designed to protect wildlife, if the protections are not or cannot be enforced, the preserve status will have little meaning in the face of illegal poaching and timber extraction. This is a widespread problem with preserves in areas of the tropics.

Limitations on Preserves

Some of the limitations on preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, never larger, so setting aside areas that are large enough is difficult. If the area set aside is sufficiently large, there may not be sufficient area to create a buffer around the preserve. In this case, an area on the outer edges of the preserve inevitably becomes a riskier suboptimal habitat for the species in the preserve. Enforcement of

protections is also a significant issue in countries without the resources or political will to prevent poaching and illegal resource extraction.

Climate change will create inevitable problems with the location of preserves. The species within them will migrate to higher latitudes as the habitat of the preserve becomes less favorable. Scientists are planning for the effects of global warming on future preserves and striving to predict the need for new preserves to accommodate anticipated changes to habitats; however, the end effectiveness is tenuous since these efforts are prediction based.

Finally, an argument can be made that conservation preserves reinforce the cultural perception that humans are separate from nature, can exist outside of it, and can only operate in ways that do damage to biodiversity. Creating preserves reduces the pressure on human activities outside the preserves to be sustainable and non-damaging to biodiversity. Ultimately, the political, economic, and human demographic pressures will degrade and reduce the size of conservation preserves if the activities outside them are not altered to be less damaging to biodiversity.

Link to Learning



An interactive global data system of protected areas can be found at website. Review data about individual protected areas by location or study statistics on protected areas by country or region.

Habitat Restoration

Habitat restoration holds considerable promise as a mechanism for restoring and maintaining biodiversity. Of course once a species has become extinct, its restoration is impossible. However, restoration can improve the biodiversity of degraded ecosystems. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity. The wolves (Figure **58.3.1.2**) function to suppress elk and coyote populations and provide more abundant resources to the guild of carrion eaters. Reducing elk populations has allowed revegetation of riparian areas, which has increased the diversity of species in that habitat. Decreasing the coyote population has increased the populations of species that were previously suppressed by this predator. The number of species of carrion eaters has increased because of the predatory activities of the wolves. In this habitat, the wolf is a keystone species, meaning a species that is instrumental in maintaining diversity in an ecosystem. Removing a keystone species from an ecological community may cause a collapse in diversity. The results from the Yellowstone experiment suggest that restoring a keystone species can have the effect of restoring biodiversity in the community. Ecologists have argued for the identification of keystone species where possible and for focusing protection efforts on those species; likewise, it also makes sense to attempt to return them to their ecosystem if they have been removed.

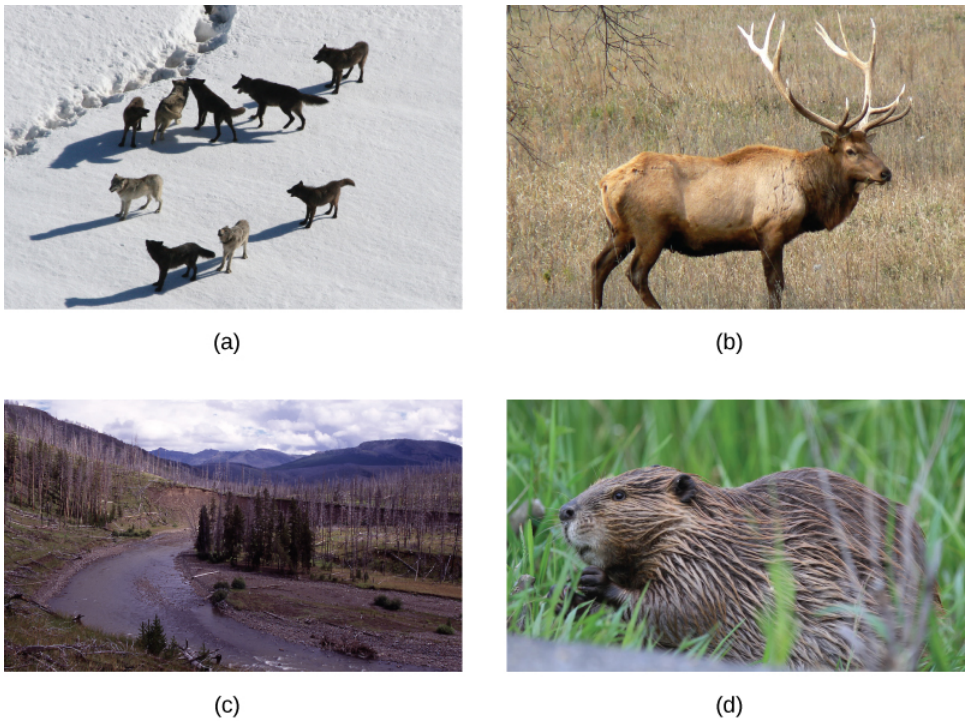


Figure **58.3.1.2**: (a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change. (credit a: modification of work by Doug Smith, NPS; credit c: modification of work by Jim Peaco, NPS; credit d: modification of work by "Shiny Things"/Flickr)

Other large-scale restoration experiments underway involve dam removal. In the United States, since the mid-1980s, many aging dams are being considered for removal rather than replacement because of shifting beliefs about the ecological value of free-flowing rivers and because many dams no longer provide the benefit and functions that they did when they were first built. The measured benefits of dam removal include restoration of naturally fluctuating water levels (the purpose of dams is frequently to reduce variation in river flows), which leads to increased fish diversity and improved water quality. In the Pacific Northwest, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports key nutrients to inland ecosystems during its annual spawning migrations. In other regions such as the Atlantic coast, dam removal has allowed the return of spawning anadromous fish species (species that are born in fresh water, live most of their lives in salt water, and return to fresh water to spawn). Some of the largest dam removal projects have yet to occur or have happened too recently for the consequences to be measured. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

The Role of Captive Breeding

Zoos have sought to play a role in conservation efforts both through captive breeding programs and education. The transformation of the missions of zoos from collection and exhibition facilities to organizations that are dedicated to conservation is ongoing. In general, it has been recognized that, except in some specific targeted cases, captive breeding programs for endangered species are inefficient and often prone to failure when the species are reintroduced to the wild. Zoo facilities are far too limited to contemplate captive breeding programs for the numbers of species that are now at risk. Education is another potential positive impact of zoos on conservation efforts, particularly given the global trend to urbanization and the consequent reduction in contacts between people and wildlife. A number of studies have been performed to look at the effectiveness of zoos on people's attitudes and actions regarding conservation; at present, the results tend to be mixed.

Summary

New technological methods such as DNA barcoding and information processing and accessibility are facilitating the cataloging of the planet's biodiversity. There is also a legislative framework for biodiversity protection. International treaties such as CITES regulate the transportation of endangered species across international borders. Legislation within individual countries protecting species and agreements on global warming have had limited success; there is at present no international agreement on targets for greenhouse gas emissions. In the United States, the Endangered Species Act protects listed species but is hampered by procedural difficulties and a focus on individual species. The Migratory Bird Act is an agreement between Canada and the United States to protect migratory birds. The non-profit sector is also very active in conservation efforts in a variety of ways.

Conservation preserves are a major tool in biodiversity protection. Presently, 11 percent of Earth's land surface is protected in some way. The science of island biogeography has informed the optimal design of preserves; however, preserves have limitations imposed by political and economic forces. In addition, climate change will limit the effectiveness of preserves in the future. A downside of preserves is that they may lessen the pressure on human societies to function more sustainably outside the preserves.

Habitat restoration has the potential to restore ecosystems to previous biodiversity levels before species become extinct. Examples of restoration include reintroduction of keystone species and removal of dams on rivers. Zoos have attempted to take a more active role in conservation and can have a limited role in captive breeding programs. Zoos also may have a useful role in education.

Art Connections

Figure **58.3.1.1**: Which of the following statements is not supported by this graph?

A. There are more vulnerable fishes than critically endangered and endangered fishes combined.
B. There are more critically endangered amphibians than vulnerable, endangered and critically endangered reptiles combined.
C. Within each group, there are more critically endangered species than vulnerable species.
D. A greater percentage of bird species are critically endangered than mollusk species.

Answer

C

Footnotes

1. 1 Robert H. MacArthur and Edward O. Wilson, E. O., *The Theory of Island Biogeography* (Princeton, N.J.: Princeton University Press, 1967).

Glossary

DNA barcoding

molecular genetic method for identifying a unique genetic sequence to associate with a species

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58.4: An Evolutionary Perspective on the Biodiversity Crisis

> *This discussion is excerpted from Santamaría, L., & Mendez, P. F. (2012). Evolution in biodiversity policy–current gaps and future needs. Evolutionary applications, 5(2), 202-218. Blackwell Publishing Ltd under CC-BY-NC license. Accessed from*
>
> *https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3353340/ on 14 November 2023*

To date, biodiversity policy largely rested in the assumption that evolutionary processes take place at a temporal scale that largely exceeds that of most human operations. However, evidence indicating that detectable evolutionary changes commonly occur over ecological time scales has mounted over the last decade (e.g. Thompson 1998). Rapid evolutionary changes often arise in response to new forms of selection caused (directly or indirectly) by human action – termed 'anthropogenic selection', as opposed to natural selection (Palumbi 2001; Stockwell et al. 2003). Anthropogenic evolution is widespread in nature, and numerous recent examples show that anthropogenic trait change in the wild is a global phenomenon, documented in marine, freshwater and terrestrial ecosystems worldwide (Palkovacs 2011). Moreover, and because eco-evolutionary dynamics are inherently bi-directional, contemporary evolution can have important effects on the dynamics of populations, communities and ecosystems; these effects may occur over large spatial scales and impact system-wide processes, such as trophic cascades (Carroll et al. 2007; Palkovacs 2011).

Anthropogenic trait changes take place, in the wild, in two primary contexts: anthropogenic disturbance (especially harvest, but also habitat loss and fragmentation, pollution/acidification, and climate change) and biotic exchange (Hendry et al. 2008). Harvest is, probably, the most potent agent of anthropogenic trait change. Trait changes associated with the harvest of wild populations are, on average, three times faster than those caused by non-anthropogenic selection (Darimont et al. 2009). Fisheries, for example, drive the evolution of earlier age and smaller size at maturation in target populations, which affects their population persistence and sustainable yield (Hutchings and Fraser 2008) and results in considerable impacts on food-web interactions, trophic cascades and nutrient cycling in aquatic ecosystems (Palkovacs 2011). For example, fisheries of northwest Atlantic cod resulted, between the mid 1950s and the early 1990s, in estimated declines in age at 50% maturity from 6.5–7.0 to 5.0–5.5 years, resulting in an estimated reduction of population growth by 25–30% (Hutchings and Fraser 2008). These evolutionary consequences are often difficult to reverse; in some cases, the reduction or even cessation of fishing does not lead to rapid population recovery, particularly if directional selection continues over protracted periods as fisheries continue to harvest the largest available individuals (Conover 2000; Stockwell et al. 2003). Indeed, one prediction common to all studies of fisheries-induced evolution is that genetic change effected by exploitation will be slow to reverse (Hutchings and Fraser 2008) – as confirmed by the persistence of small size-at-age in some populations of Atlantic cod, for at least 15 years after the cessation of heavy fishing and despite favourable environmental conditions for growth (Swain et al. 2007).

Sport hunting, the main cause of death for prime-aged adults in many populations of ungulates, may result in selective effects that affect their morphological and life-history traits, favoring an earlier reproduction and increased reproductive investment in young adults – particularly when combined with regulations prohibiting the killing of lactating females, which enhance the survival of early-reproducing ones (Festa-Bianchet 2003; Fenberg and Roy 2007). Trophy hunting selects for smaller horn/antler size, delayed horn/antler development and earlier reproduction – influencing male reproductive success and the economic profitability of harvested populations (Festa-Bianchet 2003). Comparable trends may be expected in game-bird species, especially those subjected to trophy hunting (such as capercaillie and black grouse). Even poaching may result in evolutionary pressures that compromise the long-term viability of poached populations – for example, poaching of African elephants for the illegal ivory trade may select for tusklessness (Jachmann et al. 1995).

Habitat loss and fragmentation, the main global driver of biodiversity loss, often result in reduced population size and increased isolation of the affected biota, which in turns erodes its genetic variation and reduces its evolutionary potential. Small, isolated populations are subject to genetic drift and inbreeding; these processes tend to cause decreased fitness, decreased tolerance to environmental stress, and impeded adaptive responses to changing environmental conditions (K. Bijlsma in Grant et al. 2010). Habitat fragmentation can also impact traits related to migration, movement and habitat selection, with dramatic ecological consequences – such as the reduction of marine-derived subsidies to continental waters, or changed food-web interactions that in turn trigger new evolutionary responses in prey species (see examples in the study by Palkovacs 2011). While the destructive

aspects of fragmentation may be accompanied by evolutionary opportunities (e.g. genetic drift may promote evolutionary processes, isolation may promote local adaptation and the rise of evolutionary novelties; F. Boero and F. Bonhomme in Grant et al. 2010), genetic erosion in permanently small, fragmented populations will generally result in decreased adaptive potential, impaired evolutionary processes and local extinctions (K. Bijlsma in Grant et al. 2010). Some species are, however, able to broaden their functional niche and make use of the anthropogenic matrix – a process that may involve evolutionary changes in traits related to both perception and dispersal (Van Dijk 2011).

Climate change is expected to result in shifts in the geographical distribution and phenology of natural populations, as well as in the (local or global) extinction of species unable to counter its speed and magnitude. Rapid evolutionary adaptation can help species counter stressful conditions or realize ecological opportunities arising from climate change, influencing the resulting patterns of colonization, extinction and distribution shifts (Hoffmann and Sgrò 2011). The 'evolving metacommunity' framework (Urban 2011) emphasizes that interactions between ecological and evolutionary mechanisms, taking place at both local and regional scales, will drive community dynamics during climate change. In particular, ecological and evolutionary dynamics are likely to interact to produce outcomes different from those predicted based on either mechanism alone. While some of these dynamics have received recent attention (e.g. species interactions may prevent adaptation of other species to new niches, and resident species may adapt to changing climates and thereby prevent colonization by other species; Urban 2011), the realization that we know much more about how climates will change across the globe than about the likely responses of species to these changes and their effects on global biological diversity is profoundly worrisome.

Biotic exchange, by which species are moved beyond the limits of their normal geographical ranges by human actions – often to produce biological invasions (Blackburn et al. 2011), can also affect the rates and the trajectories of evolutionary change (Shine 2011). Evolutionary responses are important to both predict the likelihood of biological invasions and manage the spread and impact of already-established invaders. These responses are double-sided: invasive species can induce rapid evolutionary responses on native taxa, which may reduce their ecological impact or exploit the opportunities provided by them, but the invasion process itself can cause substantial evolutionary shifts in invader's traits (Cox 2004; Carroll 2007; Shine 2011). Many of these changes are adaptive, but others may result from nonadaptive evolutionary processes (e.g. spatial sorting; Shine 2011). From an applied point of view, evolutionary changes influencing the invader's dispersal rate and establishment ability are particularly important.

> *Readers are also referred to Myers, N., & Knoll, A. H. (2001). The biotic crisis and the future of evolution. Proceedings of the National Academy of Sciences, 98(10), 5389-5392. Accessed from https://www.pnas.org/doi/abs/10.1073/pnas.091092498 on 14 November 2024*

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58.5: Approaches for Preserving Endangered Species and Ecosystems

Skills to Develop

- Identify new technologies for describing biodiversity
- Explain the legislative framework for conservation
- Describe principles and challenges of conservation preserve design
- Identify examples of the effects of habitat restoration
- Discuss the role of zoos in biodiversity conservation

Preserving biodiversity is an extraordinary challenge that must be met by greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies.

Measuring Biodiversity

The technology of molecular genetics and data processing and storage are maturing to the point where cataloguing the planet's species in an accessible way is close to feasible. DNA barcoding is one molecular genetic method, which takes advantage of rapid evolution in a mitochondrial gene present in eukaryotes, excepting the plants, to identify species using the sequence of portions of the gene. Plants may be barcoded using a combination of chloroplast genes. Rapid mass sequencing machines make the molecular genetics portion of the work relatively inexpensive and quick. Computer resources store and make available the large volumes of data. Projects are currently underway to use DNA barcoding to catalog museum specimens, which have already been named and studied, as well as testing the method on less studied groups. As of mid 2012, close to 150,000 named species had been barcoded. Early studies suggest there are significant numbers of undescribed species that looked too much like sibling species to previously be recognized as different. These now can be identified with DNA barcoding.

Numerous computer databases now provide information about named species and a framework for adding new species. However, as already noted, at the present rate of description of new species, it will take close to 500 years before the complete catalog of life is known. Many, perhaps most, species on the planet do not have that much time.

There is also the problem of understanding which species known to science are threatened and to what degree they are threatened. This task is carried out by the non-profit IUCN which, as previously mentioned, maintains the Red List—an online listing of endangered species categorized by taxonomy, type of threat, and other criteria (Figure **58.5.1**). The Red List is supported by scientific research. In 2011, the list contained 61,000 species, all with supporting documentation.

Art Connection

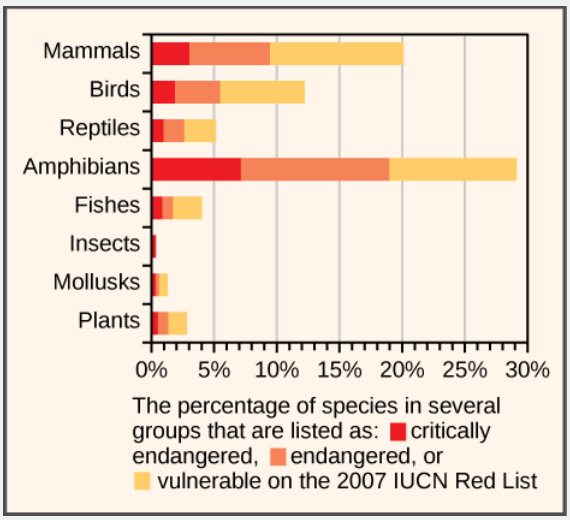


Figure **58.5.1**: This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007.

Which of the following statements is not supported by this graph?

A. There are more vulnerable fishes than critically endangered and endangered fishes combined.

B. There are more critically endangered amphibians than vulnerable, endangered and critically endangered reptiles combined.
C. Within each group, there are more critically endangered species than vulnerable species.
D. A greater percentage of bird species are critically endangered than mollusk species.

Changing Human Behavior

Legislation throughout the world has been enacted to protect species. The legislation includes international treaties as well as national and state laws. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) treaty came into force in 1975. The treaty, and the national legislation that supports it, provides a legal framework for preventing approximately 33,000 listed species from being transported across nations' borders, thus protecting them from being caught or killed when international trade is involved. The treaty is limited in its reach because it only deals with international movement of organisms or their parts. It is also limited by various countries' ability or willingness to enforce the treaty and supporting legislation. The illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars. Illegal wildlife trade is monitored by another non-profit: Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC).

Within many countries there are laws that protect endangered species and regulate hunting and fishing. In the United States, the Endangered Species Act (ESA) was enacted in 1973. Species at risk are listed by the Act; the U.S. Fish & Wildlife Service is required by law to develop management plans that protect the listed species and bring them back to sustainable numbers. The Act, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed, or to get an effective management plan in place once it is listed. Additionally, species may be controversially taken off the list without necessarily having had a change in their situation. More fundamentally, the approach to protecting individual species rather than entire ecosystems is both inefficient and focuses efforts on a few highly visible and often charismatic species, perhaps at the expense of other species that go unprotected. At the same time, the Act has a critical habitat provision outlined in the recovery mechanism that may benefit species other than the one targeted for management.

The Migratory Bird Treaty Act (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers).

The international response to global warming has been mixed. The Kyoto Protocol, an international agreement that came out of the United Nations Framework Convention on Climate Change that committed countries to reducing greenhouse gas emissions by 2012, was ratified by some countries, but spurned by others. Two important countries in terms of their potential impact that did not ratify the Kyoto Protocol were the United States and China. The United States rejected it as a result of a powerful fossil fuel industry and China because of a concern it would stifle the nation's growth. Some goals for reduction in greenhouse gasses were met and exceeded by individual countries, but worldwide, the effort to limit greenhouse gas production is not succeeding. The intended replacement for the Kyoto Protocol has not materialized because governments cannot agree on timelines and benchmarks. Meanwhile, climate scientists predict the resulting costs to human societies and biodiversity will be high.

As already mentioned, the private non-profit sector plays a large role in the conservation effort both in North America and around the world. The approaches range from species-specific organizations to the broadly focused IUCN and TRAFFIC. The Nature Conservancy takes a novel approach. It purchases land and protects it in an attempt to set up preserves for ecosystems. Ultimately, human behavior will change when human values change. At present, the growing urbanization of the human population is a force that poses challenges to the valuing of biodiversity.

Conservation in Preserves

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts. A preserve is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Preserves can be effective in the short term for protecting both species and ecosystems, but they face challenges that scientists are still exploring to strengthen their viability as long-term solutions.

How Much Area to Preserve?

Due to the way protected lands are allocated (they tend to contain less economically valuable resources rather than being set aside specifically for the species or ecosystems at risk) and the way biodiversity is distributed, determining a target percentage of land or marine habitat that should be protected to maintain biodiversity levels is challenging. The IUCN World Parks Congress estimated that 11.5 percent of Earth's land surface was covered by preserves of various kinds in 2003. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes. Research has shown that 12 percent of all species live only outside preserves; these percentages are much higher when only threatened species and high quality preserves are considered. For example, high quality preserves include only about 50 percent of threatened amphibian species. The conclusion must be that either the percentage of area protected must increase, or the percentage of high quality preserves must increase, or preserves must be targeted with greater attention to biodiversity protection. Researchers argue that more attention to the latter solution is required.

Preserve Design

There has been extensive research into optimal preserve designs for maintaining biodiversity. The fundamental principle behind much of the research has been the seminal theoretical work of Robert H. MacArthur and Edward O. Wilson published in 1967 on island biogeography.[1] This work sought to understand the factors affecting biodiversity on islands. The fundamental conclusion was that biodiversity on an island was a function of the origin of species through migration, speciation, and extinction on that island. Islands farther from a mainland are harder to get to, so migration is lower and the equilibrium number of species is lower. Within island populations, evidence suggests that the number of species gradually increases to a level similar to the numbers on the mainland from which the species is suspected to have migrated. In addition, smaller islands are harder to find, so their immigration rates for new species are lower. Smaller islands are also less geographically diverse so there are fewer niches to promote speciation. And finally, smaller islands support smaller populations, so the probability of extinction is higher.

As islands get larger, the number of species accelerates, although the effect of island area on species numbers is not a direct correlation. Conservation preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. For a species to persist in a preserve, the preserve must be large enough. The critical size depends, in part, on the home range that is characteristic of the species. A preserve for wolves, which range hundreds of kilometers, must be much larger than a preserve for butterflies, which might range within ten kilometers during its lifetime. But larger preserves have more core area of optimal habitat for individual species, they have more niches to support more species, and they attract more species because they can be found and reached more easily.

Preserves perform better when there are buffer zones around them of suboptimal habitat. The buffer allows organisms to exit the boundaries of the preserve without immediate negative consequences from predation or lack of resources. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by edges. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing wildlife corridors between them so that individuals and their genes can move between the preserves, for example along rivers and streams, will make the smaller preserves behave more like a large one. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

In addition to the physical, biological, and ecological specifications of a preserve, there are a variety of policy, legislative, and enforcement specifications related to uses of the preserve for functions other than protection of species. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive human recreation. Many of these policy decisions are made based on political pressures rather than conservation considerations. In some cases, wildlife protection policies have been so strict that subsistence-living indigenous populations have been forced from ancestral lands that fell within a preserve. In other cases, even if a preserve is designed to protect wildlife, if the protections are not or cannot be enforced, the preserve status will have little meaning in the face of illegal poaching and timber extraction. This is a widespread problem with preserves in areas of the tropics.

Limitations on Preserves

Some of the limitations on preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, never larger, so setting aside areas that are large enough is difficult. If the area set aside is sufficiently large, there may not be sufficient area to create a buffer around the preserve. In this case, an area on the outer edges of the preserve inevitably becomes a riskier suboptimal habitat for the species in the preserve. Enforcement of

protections is also a significant issue in countries without the resources or political will to prevent poaching and illegal resource extraction.

Climate change will create inevitable problems with the location of preserves. The species within them will migrate to higher latitudes as the habitat of the preserve becomes less favorable. Scientists are planning for the effects of global warming on future preserves and striving to predict the need for new preserves to accommodate anticipated changes to habitats; however, the end effectiveness is tenuous since these efforts are prediction based.

Finally, an argument can be made that conservation preserves reinforce the cultural perception that humans are separate from nature, can exist outside of it, and can only operate in ways that do damage to biodiversity. Creating preserves reduces the pressure on human activities outside the preserves to be sustainable and non-damaging to biodiversity. Ultimately, the political, economic, and human demographic pressures will degrade and reduce the size of conservation preserves if the activities outside them are not altered to be less damaging to biodiversity.

Link to Learning



An interactive global data system of protected areas can be found at website. Review data about individual protected areas by location or study statistics on protected areas by country or region.

Habitat Restoration

Habitat restoration holds considerable promise as a mechanism for restoring and maintaining biodiversity. Of course once a species has become extinct, its restoration is impossible. However, restoration can improve the biodiversity of degraded ecosystems. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity. The wolves (Figure **58.5.2**) function to suppress elk and coyote populations and provide more abundant resources to the guild of carrion eaters. Reducing elk populations has allowed revegetation of riparian areas, which has increased the diversity of species in that habitat. Decreasing the coyote population has increased the populations of species that were previously suppressed by this predator. The number of species of carrion eaters has increased because of the predatory activities of the wolves. In this habitat, the wolf is a keystone species, meaning a species that is instrumental in maintaining diversity in an ecosystem. Removing a keystone species from an ecological community may cause a collapse in diversity. The results from the Yellowstone experiment suggest that restoring a keystone species can have the effect of restoring biodiversity in the community. Ecologists have argued for the identification of keystone species where possible and for focusing protection efforts on those species; likewise, it also makes sense to attempt to return them to their ecosystem if they have been removed.

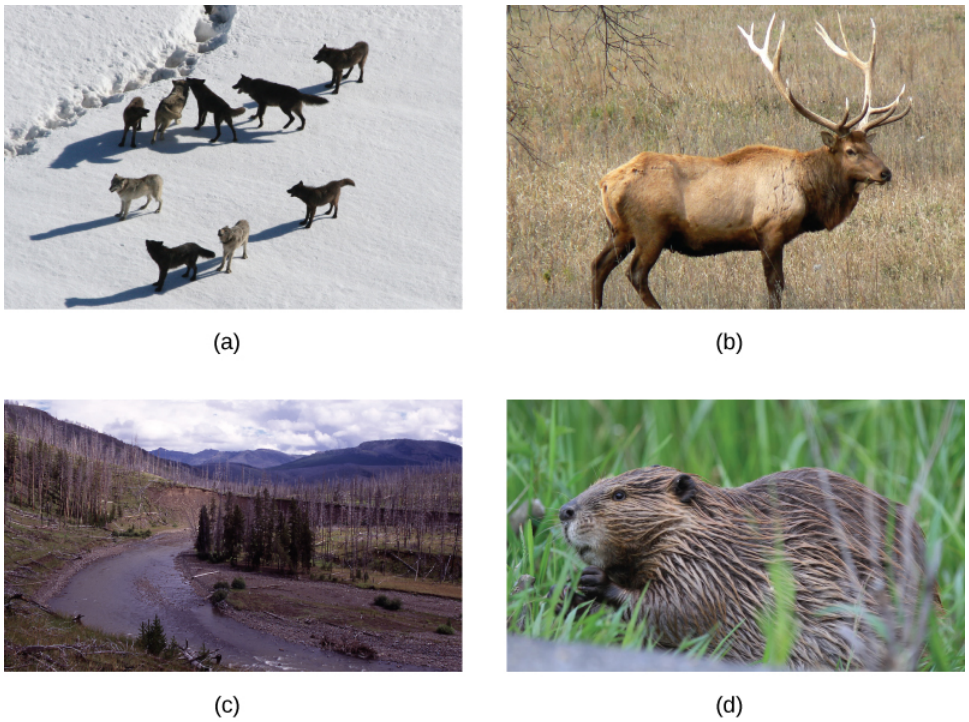


Figure 58.5.2: (a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change. (credit a: modification of work by Doug Smith, NPS; credit c: modification of work by Jim Peaco, NPS; credit d: modification of work by "Shiny Things"/Flickr)

Other large-scale restoration experiments underway involve dam removal. In the United States, since the mid-1980s, many aging dams are being considered for removal rather than replacement because of shifting beliefs about the ecological value of free-flowing rivers and because many dams no longer provide the benefit and functions that they did when they were first built. The measured benefits of dam removal include restoration of naturally fluctuating water levels (the purpose of dams is frequently to reduce variation in river flows), which leads to increased fish diversity and improved water quality. In the Pacific Northwest, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports key nutrients to inland ecosystems during its annual spawning migrations. In other regions such as the Atlantic coast, dam removal has allowed the return of spawning anadromous fish species (species that are born in fresh water, live most of their lives in salt water, and return to fresh water to spawn). Some of the largest dam removal projects have yet to occur or have happened too recently for the consequences to be measured. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

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Summary

New technological methods such as DNA barcoding and information processing and accessibility are facilitating the cataloging of the planet's biodiversity. There is also a legislative framework for biodiversity protection. International treaties such as CITES regulate the transportation of endangered species across international borders. Legislation within individual countries protecting species and agreements on global warming have had limited success; there is at present no international agreement on targets for greenhouse gas emissions. In the United States, the Endangered Species Act protects listed species but is hampered by procedural difficulties and a focus on individual species. The Migratory Bird Act is an agreement between Canada and the United States to protect migratory birds. The non-profit sector is also very active in conservation efforts in a variety of ways.

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Answer

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Glossary

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